Domestication and Diversity in Manioc (*Manihot esculenta* Crantz ssp. *esculenta*, Euphorbiaceae)

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Recent work reviewed here offers new insights into the evolution of manioc (*Manihot esculenta*) under domestication and contributes to current scientific efforts aimed at documenting forms of environmental management, local knowledge systems, and cultural practices that enhance genetic diversity. This work shows that human and natural selection jointly shape manioc diversity through (1) the overall cultivation system, which is highly adapted to environmental pressures; (2) the knowledge, categorization, and valorization of phenotypically expressed varietal differences; and (3) the incorporation, in this clonally propagated crop, of sexually reproduced plants, which encourages intravarietal diversity and occasionally leads to the creation of new varieties, that is, new categories that are phenotypically distinct and receive a new name before being multiplied. We conclude that genetic research, when placed in an interdisciplinary context, generates new questions for anthropologists working with manioc cultivators and with tropical forest horticulturalists whose subsistence depends on other clonally propagated crops.

This report focuses on an interdisciplinary research program on manioc carried out over the past 10 years[1] that looked at agrobiodiversity and its relationship with genetic diversity from the perspective of a single plant, manioc (also known as cassava, yuca, and mandioca).[2] A domesticated species belonging to the genus *Manihot* in the family Euphorbiaceae, with hundreds of different landraces, manioc (*Manihot esculenta* Crantz) has been described by botanists (Rogers 1965; Rogers and Appan 1973) and agronomists (Cock 1985). Its cultivation, processing, and use have long fascinated archaeologists and anthropologists and, before them, the Spanish, Portuguese, French, and Dutch travelers to the Americas.[3] Initially domesticated in South America 8000–10,000 years ago (Olsen and Schaal 1999; Allem 2002), manioc was introduced into West Africa more than 400 years ago, where it often supplanted yam (*Dioscorea* spp.) cultivation (Jones

1959; Hillocks, Tresh, and Bellotti 2002). Whereas native Amazonians domesticated manioc and have actively shaped the ecological, material, and physical forces that condition its diversity, the crop is now widely grown throughout the tropics, where it feeds at least 500 million people (FAO, IFAD 2000). This importance has stimulated genetic research on manioc. Molecular markers have been used to solve long-standing questions concerning manioc's evolutionary and geographical origins (Olsen and Schaal 2006; Schaal, Olsen, and Carvalho 2006). Biotechnology research has both facilitated the exploration of manioc germplasm resources and generated new ideas for the crop's genetic improvement.[4] It is now considered the highest-priority remaining candidate species for complete sequencing of the genome (Raven et al. 2006).

We review here the team's findings in light of existing literature on manioc domestication, and we outline new research directions. Although many questions still remain, some of the wider implications of the research findings for an ethnobiological analysis are now clear, and a preliminary synthesis aimed at an anthropological audience is timely. By examining the biological and cultural history of manioc through this work, we hope to show how successful collaboration between traditional cultivators and scientists from different disciplinary backgrounds allows for a dynamic and holistic understanding of the relationship between cultivated plants and human societies, which in turn may renew critical engagement with various schools of thought within Amazonianist anthropology.

The Interdisciplinary Research Program

Building on Rindos's (1984) theory of domestication, an integrative research methodology bringing together ecological, ethnological, ethnobotanical, and genetic data was designed

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2. See Gade (2002) for a defense of "manioc" as the best term to refer to this cultigen in English.

3. For works on the material culture associated with manioc processing, storage, and food recipes, see Hugh-Jones and Hugh-Jones (1993), Dufour (1995), Carneiro (2000), and Westby (2002).

4. See for instance the special issue of *Plant Molecular Biology* (vol. 56, no. 4, 2004), which presents the work of scientists associated with the Global Cassava Partnership for Genetic Improvement. Jennings (1995, 131) argues that manioc's "basic polyploid genetic structure ensures that there is still plenty of stored variation" and that the use of biotechnology methods will widen manioc's germplasm.

with the objective of interpreting population genetics and evolutionary patterns in light of ecological information and ethnographic documentation. A combination of field and laboratory studies was used to document the ways in which people affect the genetics of a crop propagated through cloning. The main guiding research questions were as follows: how can the paradox of high varietal diversity and clonal reproduction best be explained, what farming practices are involved in creating and maintaining so many manioc landraces, and what in the biology of the plant makes it so plastic and amenable to diversity? In short, how is genetic and varietal diversity created and maintained in a plant reproduced vegetatively, and how does it evolve?

To answer these questions, field studies were carried out in various Makushi villages around the Iwokrama Park (North Rupununi, southern Guyana) and in the Palikur villages of Saint Georges de l'Oyapock and Kamuyene (near Macouria) in northeastern French Guiana.[5] Standard ethnographic methods involving observations, participation in farming practices and food processing, open discussions, structured and semistructured interviews, and questionnaires were used, as well as structured participatory research involving close collaboration between Laura Rival and two remunerated Makushi women researchers. Field studies shed light on how indigenous and traditional cultivators create, classify, and understand manioc phenotypic diversity and transmit their knowledge. Codominant and highly polymorphic microsatellite markers developed for manioc by Chavarriaga-Aguirre et al. (1998) were used in lab analyses of field-collected plants. Both Elias (2000) and Pujol (2004) used these microsatellite markers[6] to measure the genetic diversity that underpins the phenotypic diversity recognized by cultivators.

Studies of the population biology and ecology of domesticated plants in traditional agroecosystems constitute a privileged field in which to test the explanatory power of methodologies that integrate bioevolutionary and anthropological approaches within a single framework. The research program started with a study of manioc varietal diversity in relation to the ecology of slash-and-burn agrosystems and the properties of indigenous taxonomic systems (Elias, Rival, and McKey 2000). A complementary focus of our work has been to compare the biology of manioc with that of its wild ancestors, to understand what traits of the plant have evolved under domestication, and to frame questions about how cultivators' practices interacted with biological traits of the wild parent to shape evolution under domestication.

Recent molecular studies provide evidence that the wild

progenitor of cassava is *Manihot esculenta* ssp. *flabellifolia* (Pohl) Ciferri (Olsen and Schaal 1999, 2001). As delimited by Allem (1994), this taxon is distributed on an arc partly encircling the Amazon basin, from eastern Bolivia and Peru eastward to northeastern Brazil, northward to the Guianas, and then westward to Venezuela. Studies point to a single domestication event in southern Brazil-Rondônia and Acre (Olsen and Schaal 1999, 2001). We studied the ecology of this species primarily in the Guianas. Comparative data on populations in Rondônia have confirmed the pertinence of this work for understanding the evolution of manioc under domestication (Pujol et al. 2005*b*).

Ethnobiology and the Evolution of Manioc

Prelude: The Biology of Manioc's Wild Ancestors

To understand the new findings about how manioc biology interacts with Amerindian farming practices, it is first necessary to present a brief synopsis of the biology of the plant's wild ancestors. The wild ancestors of manioc are plants adapted to forest and savanna ecotones. In the shifting mosaics of forest and savanna environments, ecological succession to forest is frequently interrupted by disturbances such as fire. The wild ancestors of manioc depend on disturbances. They grow and reproduce in open, sunny conditions, eventually disappearing as vegetation cover becomes denser. Several traits adapt them to these dynamic environments. Their tuberous roots store underground reserves, enabling rapid regrowth after fire or other disturbances. They show great plasticity in growth form; much-branched shrubs in open environments, they become viny as vegetation becomes denser, enabling them to persist, if not to reproduce, long after a disturbance. Finally, they possess a suite of adaptations allowing rapid regeneration from a soil bank of dormant seeds once a new disturbance occurs.

As in many other Euphorbiaceae (Webster 1994), seed dispersal is a two-stage process. In the first stage, the plant's three-seeded capsules dry in the sun, finally "exploding," projecting seeds up to several meters. Each seed bears an appendage (caruncle) that functions as an elaiosome, attracting ground-foraging ants. Like other elaiosomes, *Manihot* caruncles are rich in lipids but also contain many other nutrients (amino acids, proteins, sugars). This "dead-insect analogue" (Carroll and Janzen 1973) attracts predatory or scavenger ant species that carry diaspores to nests, discarding the seed after eating the elaiosome (which is usually fed to brood). Seeds are buried at varying depths in refuse piles near nests (D. Renard and D. McKey, unpublished data). As in many other ant-dispersed plants, burial of seeds probably protects them from predation, fire, and other hazards of being on the soil surface. Seeds are characterized by temperature-sensitive physiological dormancy: they remain dormant at temperatures typical of vegetation-shaded soil in tropical latitudes and require elevated soil temperatures (above 35°C) to germinate. Heating of the soil is in effect used as a signal of the absence

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5. There are many similarities between the manioc cultivation practices of the Carib-speaking Makushi and those of the Arawak-speaking Palikur, but there are also some notable differences. We also collected some data on beliefs and practices of Wapishana and Patamona individuals married to Makushi and of Creole and Saramaka married to Palikur men and women.

6. These molecular markers have also been used with success by Roa et al. (1997, 2000).

of vegetation cover and thus of favorable light conditions (which cannot be directly perceived by buried seeds). This seed and seedling biology has been largely inherited intact by domesticated manioc (Pujol et al. 2002) and, as will be shown, greatly conditions the plant's interactions with Amerindian farming practices.

Domestication of Manioc: The Importance of Sexual Reproduction in a Clonally Propagated Crop

Manioc was selected by its first cultivators for large tubers and for traits that increased the ease with which it could be asexually propagated from stem cuttings (Jennings 1995, 129; Schaal, Olsen, and Carvalho 2006, 271). In contrast to the wild ancestors of many clonally propagated domesticated plants, which possess adaptations for vegetative reproduction that facilitate their clonal propagation by cultivators (e.g., corms of bananas, bud-bearing tubers of potatoes and yams), vegetative reproduction plays no role in the biology of manioc's wild ancestors. Their underground storage organs are roots, not tubers, and have no buds that could sprout. Manioc's wild ancestors do not readily sprout from stem cuttings; this ability evolved during domestication. Clonal propagation by stem cuttings must have been accompanied by substantial mortality initially, suggesting that this practice must have conferred a very strong agronomic advantage.

Why did Amerindian cultivators choose to propagate manioc clonally? The answer to this question is certainly complex, but part of it lies with the plant's breeding system. Like most other plants that cultivators have chosen to propagate clonally (Zohary 1984), manioc and its wild ancestors are primarily outbreeders. Whereas some are obligate outcrossers (e.g., yams [*Dioscorea* spp.], in which plants are either male or female, and sweet potato, which is self-incompatible), manioc and its wild ancestors are self-compatible but preferentially outcrossing, individuals performing best when they issue from seeds resulting from cross-pollination with other individuals. Most pulse crops and cereals (maize is a conspicuous exception) are inbreeders: most seeds result from self-pollination or matings with close relatives. This makes it easy to "capture" desirable new traits in purebred family lines. In contrast, outbreeders do not "breed true to type": the traits of plants grown from seed only partly resemble those of their mother because half of their genetic constitution is usually from a different, unrelated individual. To the cultivator who notices a plant with desirable traits (e.g., larger roots) and wishes to have more like it, this means that sowing seeds from that plant is a very inefficient way to do so. In outbreeders, clonal propagation of plants with desirable traits is a much more efficient means of selection. This advantage of clonal propagation is reflected in the genetic composition of manioc landraces. Most established clones of manioc landraces are highly heterozygous for neutral genetic markers such as microsatellites (Elias et al. 2004). Their high heterozygosity across the genome indicates that they originated from matings between unrelated plants. In habitually outcrossing plants, inbred individuals suffer from inbreeding depression, often expressed in lower vigor. The highly heterozygous clones of landraces were presumably selectively multiplied by cultivators precisely because they were vigorous, giving high yields. Sexual recombination would often break down their favorable genetic combinations, while clonal multiplication preserves them.

However, clonal propagation by cultivators is only part of the story of manioc's initial domestication. Manioc differs from its closest wild ancestors in a large number of diverse traits, including size and production of tuberous roots, and traits facilitating clonal propagation (Jennings 1995; Schaal, Olsen, and Carvalho 2006), as well as leaf tannin content (Mondolot et al. 2008), traits of leaf structure and composition that affect photosynthetic rates (Pujol et al. 2008), and seedling functional morphology (Pujol et al. 2005*b*). The great divergence between wild ancestor and domesticated manioc, appearing in only 10,000 years, is difficult to square with well-known limitations to evolution in strictly clonal populations. In such populations, somatic mutations are the only source of new genetic variation. Mutations with undesirable effects slowly accumulate in clonal lineages, reducing their fitness ("Muller's ratchet"; Felsenstein 1974). Mutations producing desirable traits are much rarer, and the probability that numerous favorable mutations all appear in the same clonal lineage before it succumbs to Muller's ratchet is infinitesimal. Sex solves both problems. By producing genotypes that eliminate unfavorable mutations (escaping Muller's ratchet) and that unite several favorable mutations, so that these no longer compete within populations but cooperate ("Fisher-Muller mechanism"; Fisher 1930; Muller 1932), recombination allows much more rapid evolution. The diversity of traits that evolved during the domestication of manioc thus suggests the action of repeated cycles of recombination (necessary to generate variation) and selection (to fix certain traits and maintain agronomic performance).

The Continued Importance of Mixed Clonal/Sexual Systems in Manioc Populations Today

Sex continues to be important in the reproductive ecology of manioc. Although the sexual fecundity of manioc has been reduced during domestication—largely as a consequence of reduced branching and a peculiar architecture that links branching to inflorescence production (Jennings 1995; Elias, Lenoir, and McKey 2007)—most plants can still produce seeds in abundance. In fact, seed production is favored by a peculiar agronomic advantage of manioc, which Amerindian cultivators fully exploit, that is, the plant's capacity for "live storage." Mature plants, which can be left in fields for long periods (their roots being harvested as needed), often have time to produce flowers and fruits before being uprooted.

The way Amerindian cultivators manage manioc leaves ample scope for the plant's sexual reproduction, and much evidence indicates that the opportunities thus presented for in-

corporating genetic diversity—and thereby conserving the evolutionary potential that confers tolerance to risks in traditional cultivation systems (Brush 1995)—are indeed exploited. The apparent paradox between clonal reproduction and the great varietal diversity long known to characterize manioc populations managed by Amerindians (Boster 1984*a*; Chernela 1986; Dufour and Wilson 1996; Emperaire and Pinton 1999) could have several explanations. For example, the apparent diversity may have a narrow genetic base. In a strictly clonal population, genotypes are ineluctably lost over time due to chance (for rare genotypes) or to natural or human selection, which is probably accelerated by Muller's ratchet. Varieties may owe their existence solely to the cultivators' ability to observe, capture, and multiply by clonal propagation rare somatic mutations, as seems to be the case for taro in Hawaii (Meilleur 1998). However, recent studies have shown that named diversity in manioc populations cultivated by Amerindians is the result of great genetic diversity generated by sexual reproduction.

Sex gets into the reproductive cycle of manioc by means of the interaction between the biology of manioc and the actions of cultivators. As for a number of other crop plants clonally propagated by cultivators,[7] the Amazonianist anthropological literature mentions that Amerindians pay attention to volunteer manioc seedlings appearing spontaneously in their fields, sometimes letting them grow and incorporating them as new clones. These observations were reviewed by McKey and Beckerman (1993). More recently, Salick, Cellinese, and Knapp (1997) and Sambatti, Martins, and Ando (2001) have also emphasized such practices as a source of diversity.[8] However, the frequency of this practice and its role in the evolutionary dynamics of manioc were unknown. Our recent work in the Guianas has demonstrated that at least in this part of Amazonia, conscious incorporation of volunteer seedlings is very frequent indeed. This work has also shown that the mixed clonal/sexual system that results when cultivators clonally propagate manioc plants from seed (each of which is a unique genetic combination) is central to any understanding of the crop's initial domestication, its management in Amerindian farming systems, and its ongoing evolution.

The doctoral dissertations of Marianne Elias (2000), Benoît Pujol (2004), and Anne Duputié (2008) form the nucleus of this work. Elias, who quantitatively documented for the first time how Amerindian cultivators identify, manage, classify, and name volunteer seedlings, showed the consequences of this management for the varietal and genetic structure of manioc populations. Following this work, Pujol quantified

the demography and genetics of entire cohorts of volunteer seed-grown plants from their germination when a new field is opened in an old fallow throughout the entire life span of the field and up until harvest. His work showed in some detail the evolutionary consequences of the mixed clonal/sexual reproductive system of manioc under Amerindian management. Duputié's work begins to address the possible consequences of the substantial diversity of practices among different groups of Amazonian manioc cultivators.

This work has shown that the reproductive traits of manioc, inherited largely intact from its wild ancestors of forest and savanna ecotones, in fact nicely "preadapt" the plant to the field-and-fallow cycles of swidden agriculture. Its flowers are pollinated by insects (stingless bees appear to be the most frequent pollinators), and its seeds are dispersed and buried by ants (Elias and McKey 2000), often the same ones that disperse seeds of wild relatives in savannas. While seeds remain dormant in the shaded, cool soils throughout the fallow period, volunteer seedlings emerge in large numbers in response to slash-and-burn disturbance, appearing in newly cleared fields at the time when cultivators plant stem cuttings.

From our detailed studies among Makushi, Palikur, and Wayãpi manioc cultivators,[9] the following picture of manioc reproductive biology and evolutionary dynamics under Amerindian cultivation emerges. Volunteer seedlings are closely observed by cultivators, who allow them to grow. Like the clonally propagated landraces, those that survive to maturity are harvested and their roots processed. If the cultivator is satisfied with the yield and the characteristics of the root, the stem is divided into cuttings that are soon replanted and multiplied. If the roots are found unsatisfactory, the stem is generally discarded, although some cultivators multiply even these plants. Although volunteers presenting novel combinations of morphological characters are sometimes multiplied as new landraces, most are assimilated into already named landraces they resemble phenotypically (Elias, Rival, and McKey 2000). A landrace is thus constituted of a multitude of clones, some common, some rare, which all share phenotypic traits (Elias et al. 2001*a*) but may be genetically quite diverse (Elias et al. 2001*b*).

Pujol's work highlighted the consequences of the peculiar spatial structure of manioc populations resulting from such management. Volunteer seedlings always represent a small proportion of all flowering plants in a field, most plants being clones, either established for many generations or only recently. Because the aim of clonal propagation is to multiply selected genotypes to high frequencies, many plants in a field will be clone mates: in genetic terms, they are the same individual. The abundance of clone mates and the fact that

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7. See Scarcelli et al. (2006) for yam, Caillon et al. (2006) for taro, Shigeta (1996) for ensete, Quiros et al. (1992) for potato, and Yen (1974) for sweet potato.

8. Sadly, the highly original work done by Paulo Sodero Martins's research group was cut short by his untimely death. See also Silva, Bandel, and Martins (2003) and the remarkable unpublished master's thesis by Cury (1993), which we discovered long after our research began.

9. For the Makushi, see Elias (2000); Elias and McKey (2000); Elias, Panaud, and Robert (2000); Elias, Rival, and McKey (2000); Elias et al. (2001*a*, 2001*b*, 2004); Elias, Lenoir, and McKey (2007); and McKey et al. (2001). For the Palikur, see Pujol (2004); Pujol and McKey (2006); Pujol et al. (2002, 2005*b*, 2007, 2008); and Pujol, David, and McKey (2005*a*). For the Wayãpi, see Duputié et al. (2007).

cultivators tend to plant cuttings in monovarietal patches (so that clone mates are often planted in proximity to one another) together have important consequences for the population's mating system. Because pollinators transport pollen mostly between neighboring plants, a considerable proportion of plants issued from seed are highly inbred. As Amerindian cultivators also usually plant several highly differentiated varieties in each field, pollen transfer between them produces highly outcrossed individuals. The combination of clonal propagation, spatial clumping of related plants, and juxtaposition of clumps of unrelated plants results in a highly unusual mating structure with great variance in the extent of inbreeding.

This inbreeding variance has important consequences for evolutionary dynamics. Detailed work in Palikur farms showed that from field opening to harvest, volunteer plants issued from seeds are subjected to high mortality. This mortality is selective at both phenotypic and genotypic levels, and cultivators are the source of some of this selection. A few months after clearing, cultivators weed their fields. During weeding, some volunteer manioc seedlings are removed along with other adventitious plants. Because cultivators are more likely to weed smaller plants and because smaller plants are more inbred, survivors of this human-induced mortality are more outbred (more heterozygous) than those weeded (Pujol, David, and McKey 2005a). Natural selection also plays a role. Natural mortality of volunteer plants is mainly due to intraspecific competition, in which initially larger plants have an advantage. Because larger plants are more outcrossed, the plants that survive competition are more heterozygous than those that die. By depositing manioc seeds in clusters, thereby increasing the intensity of competition between seedlings, seed-dispersing ants help create the conditions that make it advantageous to be outcrossed. Finally, among the volunteer seedlings that survive to harvest time, cultivators again select large, vigorous (and outcrossed) plants for propagation. Thus, both human and natural forces of selection by at least three very different mechanisms favor outcrossed plants throughout the cultivation cycle (Pujol and McKey 2006). Whereas a strong heterozygote deficit in volunteer plants at the beginning of the cycle testifies to a globally inbred mating system, those volunteers that survive to harvest and thus become candidates for incorporation into the stock of clones are highly heterozygous, like the clones that constitute established landraces (Elias et al. 2004). Sexual reproduction is thus integrated into a mixed reproductive regime that confers the benefits of both sexual reproduction (diversity, adaptive potential) and clonal propagation (maintenance of highly vigorous outcrossed clones) while minimizing their respective disadvantages.

For the first time, a window has been opened on the processes that have produced the genetic structure we see in Amerindian manioc populations today: numerous genetically differentiated, phenotypically distinct landraces consisting of multiple clones of independent sexual origin that are highly heterozygous, having been winnowed by repeated recombination/selection cycles and then selectively multiplied. An outstanding research priority is to examine whether the same processes are at work in manioc populations managed by Amerindians in other parts of Amazonia.

Implications for Anthropology

Makushi, Palikur, and Wayãpi cultivators may be somewhat exceptional in their readiness to experiment with volunteer manioc plants, but we doubt it. A new research program would be needed to find out the extent to which the basic findings we report here apply to other parts of Amazonia. In any case, the management of manioc agrobiodiversity we have described and analyzed has real implications for scientific understanding of plant selection and the overall process of domestication not only in manioc but also in other root crops reproduced vegetatively.

If significant advances in our knowledge and understanding of the domestication process and the spread of agriculture can be made through combining the complementary perspectives of evolutionary biology, genetics, archaeology, linguistics, and anthropology (Ellen and Fukui 1996; Bellwood 2005), the use of the findings from genetic and molecular biology reviewed here can help Amazonianist anthropologists and archaeologists look at issues that have concerned them for some time in a new way. Given space constraints, we touch on only four issues: the relationship between ecological variability and genetic diversity, the strong cultural preference—beyond productive criteria—for high varietal diversity, the historical spread of manioc cultivars, and the role of indigenous conceptualizations of life and being.

Although we now better understand many aspects of manioc diversity in relation to the dynamic ecology of traditional agroecosystems, a number of ecological questions are yet to be settled, such as the impact of seasonal variation (parts of the Amazon basin are characterized by high seasonal aridity while others receive high, continual rainfall) on seed and seedling biology, the effect of the length of the fallow period on soil seed banks and thereby seedling populations, and the ecological role of hydrocyanic acid content.[10]

More comparative research on regional and cultural patterning of manioc "varieties" would further our understanding of the interrelations between recognition, naming, and diversity. Indigenous landrace recognition (an instantaneous and integrative process guided by an unconscious ranking of salient characters) and variety naming (according to a predetermined taxonomic classification system consistently applied but not excluding synonymy or homonymy) to some extent reflect the fact that diversity is culturally valorized for

10. Nye (1991), McKey and Beckerman (1993), Wilson and Dufour (2002), and Wilson (2003) discuss the spatial distribution of sweet and bitter manioc varieties first noted by Nordenskiöld (1924).

its own sake.[11] This fact calls for a closer examination of the relationship between aesthetic and functional reasoning (Sherman and Billing 1999). An experimental approach would be required to elucidate why Amerindians are so curious about new morphotypes and what would happen, for instance, if they did not incorporate seed-grown plants.

Diamond and Bellwood (2003) have recently called for the development of a vast comparative and interdisciplinary research program on agricultural expansions during Holocene human history, which would shed new light on the parallel dispersal of crops, livestock, farming techniques, lifestyles, languages, and human genes. For this, we need better knowledge of the earliest crops and their wild relatives as well as their dates and places of domestication in regions of the world less understood than the Fertile Crescent. As noted by these authors, the spread patterns of farming and language families in the New World, and most particularly in lowland South America, are very difficult to reconstruct. The research reviewed here helps clarify some of the complexities likely to underlie Amazonian agricultural expansions and the plant's diffusion across Amazonia (see in particular Pujol et al. 2007 on the role of seed banks in enabling the indirect "exchange" of manioc germplasm between cultural groups). However, more research is needed to answer the many questions arising from Bellwood's (2005) model and Lathrap's (1977) related evolutionist thesis that the preference for bitter manioc varieties marked the historical passage from subsistence horticulture to intensified farming for trade. Many questions also continue to arise from studies of the role played by political choices and cultural values in shaping the diffusion of manioc cultivation and processing practices (van der Hammen 1992; Hugh-Jones and Hugh-Jones 1993; Carneiro 2000; Rival 2007).

Finally, further research is needed on the ways in which local understandings of manioc natural history have come to play a role in the coevolutionary processes at work in plant domestication. By researching local understandings of the manioc plant further and more systematically, we may be able to determine whether its domestication has mobilized symbolic representations of life and personhood structured by ontological animism (Descola 2005). Is the manioc plant treated as an "Other"? This is an important question, given that research on Amazonian animism is for the most part based on the study of human-animal interactions and the ways in which these are conceptualized in myth and shamanic practice. If intersubjectivity as a form of ascribed intentionality is constitutive of the interlocking of human and animal lives, with humans taming animals and animals emulating humans—and this either directly or through the mediation

of master spirits—the situation seems much more uncertain and ambiguous when it comes to the world of plants, particularly domesticated ones. There is, for instance, an intriguing contrast between the fluidity of manioc diversity management and the rigidity of indigenous taxonomic and dual classifications (Rival 2001). We therefore need to know more about the ways in which indigenous epistemologies, which extend the world of social relations to include nonhuman persons in various contrastive ways, have guided indigenous domestication practices. For instance, it would be interesting to know how widespread the representation of manioc as a plant person animated by a "spirit owner" is (Rival 2001). It is found among the Makushi as well as in many Northwestern and Upper Amazon cultures (Hugh-Jones 1979*a*, 1979*b*; Roe 1982; van der Hammen 1992; Descola 1994). Whether it is present in other parts of Amazonia is an issue worth investigating.[12]

Manioc and Agrobiodiversity: Concluding Remarks

Building on the thesis that domestication involves coevolutionary processes resulting from the combined action of human selection for valued traits and natural selection for survival and resistance (Salick 1995), we have focused on manioc to illustrate the importance of bringing together biological studies of particular crops and historical studies of crop cultivation, especially in Amazonia, where there is "a strong relationship between landscape and plant domestication" (Clement 1999, 191). The work we have reviewed here has established that human and natural selection jointly shape manioc diversity through (1) the overall cultivation system, which is highly adapted to environmental pressures; (2) the knowledge, categorization, and valorization of phenotypically expressed varietal differences; and (3) the incorporation of sexually reproduced plants, which encourages intravarietal diversity and occasionally leads to the creation of new varieties, that is, new categories that are phenotypically distinct and receive a new name before being multiplied. By demonstrating through detailed empirical research and transdisciplinary analysis that manioc diversity, far from being static, represents a dynamic response to a range of environmental and human selective factors, this research has confirmed a number of facts previously assumed but not yet documented about the role of traditional shifting agriculture in maintaining high levels of manioc genetic and varietal diversity.

Amerindians have created and maintained a high diversity of manioc varieties in their fields by combining clonal propagation with sexual reproduction. The deft mingling of clonality and sexuality is the genius of Amerindian management of manioc populations. It truly represents "the perspicacity and intensity of science of everyday life embodied in ethnobiological knowledge" (Hunn 2006, 178). While much of

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11. By enriching Boster's (1984*b*, 1985, 1996) model with new findings on indigenous classifications of bitter and sweet manioc varieties, incorporated self-seeding plants, and wild relatives of manioc, this research has shed new light not only on indigenous perception of diversity but also on indigenous constructions of what a variety is (see also Emperaire 2001; Sambatti, Martins, and Ando 2001; Hamlin and Salick 2003).

12. According to Ellen Basso (personal communication, April 29, 2008), such representation is not characteristic of Alto Xingu manioc cultivators.

the seed and seedling ecology of the wild ancestors has been transferred unmodified to domesticated manioc, domestication has produced at least one striking evolutionary change: it has transformed the seedling's regeneration strategy, reflected in its morphology, from one more adapted to tolerating environmental risks in the wild ancestor to one more adapted to maximizing growth rate in relatively resource-rich agricultural habitats (Pujol et al. 2005*b*). Manioc seems well adapted to long-fallow slash-and-burn agriculture on poor soils, as practiced by many contemporary Amerindians whose domestication actions are deeply informed by ethnobiological representations. By reproducing manioc and its diversity, indigenous cultivators reproduce distinct social relations and cultural meanings. And by humanizing nature through the cultivation and domestication of manioc, they work at creating a "manioc civilization" whose historical ecology we are slowly beginning to unravel through ethnobiology (Ellen 2006), an integrative approach that goes beyond the complementarity of genetics and archaeology as advocated by Zeder et al. (2006) and others. The challenge in writing this history is heightened by the fact that contact with Europeans in the late fifteenth century caused population losses and crop genetic erosion of a magnitude so far unparalleled in human history. As this research has shown, if the diversity of many cultivars was substantially reduced by conquest (Clement 1999), the infraspecific diversity of manioc was not, as it has been, and continues to be, re-created through the dynamic interactions between the plant's biology and people's traditional knowledge and management of the plant.

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