1492 AND THE LOSS OF AMAZONIAN CROP GENETIC RESOURCES. I. THE RELATION BETWEEN DOMESTICATION AND HUMAN POPULATION DECLINE[1,2]

CHARLES R. CLEMENT

Clement, C. R. (*Instituto Nacional de Pesquisas da Amazônia, Cx. Postal 478, 69011-970 Manaus, AM, Brasil*). 1492 AND THE LOSS OF AMAZONIAN CROP GENETIC RESOURCES. I. THE RELATION BETWEEN DOMESTICATION AND HUMAN POPULATION DECLINE. *Economic Botany 53(2): 188–202, 1999. There may have been 4–5 million people in Amazonia at the time of European contact. These people cultivated or managed at least 138 plant species in 1492. Many of these crop genetic resources were human artifacts that required human intervention for their maintenance, i.e., they were in an advanced state of domestication. Consequently, there was a relationship between the decline of Amazonian Amerindian populations and the loss of their crop genetic heritage after contact. This relationship was influenced by the crop's degree of domestication, its life history, the degree of landscape domestication where it was grown, the number of human societies that used it, and its importance to these societies. Amazonian crop genetic erosion probably reflects an order of magnitude loss and the losses continue today.*

1492 E A PERDA DOS RECURSOS GENÉTICOS DA AMAZÔNIA. I. A RELAÇÃO ENTRE DOMESTICAÇÃO E O DECLÍNIO DAS POPULAÇÕES HUMANAS. *A Amazônia poderia ter tido de 4 a 5 milhões de habitantes quando os Europeus chegaram. Estes povos cultivaram ou manejaram pelo menos 138 espécies vegetais em 1492. Muitos destes recursos genéticos eram artefatos humanos que requeriam a intervenção humana para sua manutenção, ou seja, estavam num estado avançado de domesticação. Conseqüentemente, existiu uma relação entre o declínio das populações indígenas da Amazônia e a perda de seus recursos genéticos após o contato. Esta relação foi influenciada pelo grau de domesticação do cultivo, sua história de vida, o grau de domesticação da paisagem em que foi cultivada, o número de sociedades indígenas que o utilizou, e sua importância a estas sociedades. A erosão dos recursos genéticos indígenas da Amazônia provavelmente reflete uma perda de um ordem de magnitude e as perdas continuam hoje.*

Key Words: Amazonia; landscape domestication; crop domestication; pre-Columbian demography; European contact; genetic erosion.

The crop genetic resources of the Neotropics are extremely rich and varied. They represent one of the greatest pre-Columbian Amerindian achievements and continue to benefit humans around the world (Harlan 1992:235). At least 257 species were cultivated in the Americas when Columbus arrived in 1492 (León 1992), several of which are staples today in various parts of the world, e.g., maize (*Zea mays*), potato (*Solanum tuberosum*), and cassava (*Manihot esculenta*). Many of these crop genetic resources are human artifacts and depend upon humans for their continued existence. During the centuries immediately after European contact, human populations in the Americas were drastically reduced, with as many as 90–95% of the people killed by European diseases or resisting the conqueror's attempts to enslave them (Denevan 1992b; Dobyns 1966). Amazonia occupies half of South America but, because of lack of data, is often neglected when discussing American crop origins and diversity, while attention is focused on the better studied Andes (Pearsall 1992). In this paper, I hypothesize that this lack of attention is not due to a paucity of indigenous crop plants in pre-Columbian times, but is partially the result of the post-Columbian demographic collapse in the Amazon basin and the

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[2] Dedicated to the memory of Paulo Sodero Martins, 1941–1997, fellow student, researcher and professor of South American crop domestication, origins and biogeography.

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adjacent lowlands in northern South America. A companion paper discusses the biogeography of crop diversity at contact.

American prehistory is now the subject of ample debate generated by new, sometimes controversial research findings. Genetic analyses (e.g., Bonatto and Salzano 1997a,b) suggest human arrival in the Americas well before 12 000 years before present (BP), the date most widely accepted until recently (Cavalli-Sforza, Piazza and Menozzi 1994). The earliest humans in South America are now thought to have been broad-spectrum hunter-gatherers (Dillehay et al. 1992), and occupied parts of Amazonia very early (Roosevelt et al. 1996). The oldest pottery yet reported was recently found along the eastern reaches of the Amazon River, dated to 7–8000 BP (Roosevelt et al. 1991). Pottery is generally associated with a shift to sedentary lifestyles (Meggers 1988), necessary for intensive agricultural development. In the millennium before contact, some human societies built earthworks in various parts of lowland northern South America. These earthworks were designed to control water for crop production (Denevan 1966; Denevan and Zucchi 1978), or as habitation mounds (Roosevelt 1993), suggesting high local human population densities or long gestation periods or efficient societal organization to supply the labor for their construction.

When Francisco de Orellana descended the Amazon River in 1542, he reported high population densities along the Amazon River floodplains, the *várzeas* (Carvajal 1894; Denevan 1992b), although the reliability of this report is questioned (Galloway 1992 and Gheerbrant 1992, cited by Meggers 1993–5). Denevan (1992a) emphasizes, however, that "high" is relative to other parts of Amazonia, not to the Andes, MesoAmerica or some Caribbean islands. Given the long occupation and the possibility of advanced societies (Roosevelt 1993), one would expect to find a rich crop genetic heritage, as occurs in other areas with long occupation and/or advanced societies (Harlan 1992:52; Hawkes 1983:67; Vavilov 1992a,b).

A rich crop genetic heritage and associated crop management practices were probably major instruments for "the remarkable success of the indigenous population in enhancing the subsistence potential of one of the world's most unpredictable and ecologically complex regions . . ." (Meggers 1992a:38). In this paper I hypothesize that a significant portion of this heritage was lost when the indigenous human populations were nearly eradicated. Due to the lack of physical evidence, i.e., the crop genetic diversity itself, this paper defines landscape and plant domestication and relates them to genetic erosion when human populations disappear; lists the crop species probably present at contact and categorizes them with respect to their degree of domestication; and reviews estimates of Amerindian population density at contact and the extent of population decline suffered by these peoples. The synthesis of this information provides an order of magnitude estimate of the post-contact collapse of Amazonian crop genetic resources.

LANDSCAPE AND PLANT DOMESTICATION

Clear definitions of domestication are essential to understanding the rapid loss of crop genetic resources in Amazonia after European contact. Domestication of a plant or animal species is a co-evolutionary process, so one expects to find plant or animal populations that exhibit various degrees of domestication (Harlan 1992:64). Domestication of the biotic and abiotic landscape is a cultural process, where human knowledge about the consequences of environmental manipulation accumulates and becomes more comprehensive over time (Harris 1989). Consequently, it is important to define both plant and landscape domestication and some categories within each that are important for the present discussion. As Harris (1989) emphasizes, domestication is a continuum of human investment in selection and environmental manipulation, so its subcategories are merely constructs that imperfectly reflect the real world. It is also important to remember that indigenous peoples frequently practice(d) all forms of landscape domestication at the same time (Harris 1989; Rindos 1984:153) and that they do not always distinguish domesticated from wild plants the way I do here (V. M. Patiño, pers. com., 1994).

PLANT DOMESTICATION

Plant domestication is a co-evolutionary process by which human selection on the phenotypes of promoted, managed or cultivated plant populations results in changes in the population's genotypes that make them more useful to humans and better adapted to human intervention in the landscape. As Darwin (1882) pointed out, human selection may be either unconscious or directed (Heiser 1988). For plant domestication to take place, however, there must be selection and management to cause differential reproduction and survival, contrary to Rindos' (1984: 154) definition that includes co-evolution without human selection. The degree of change in the targeted population can vary:

1. Wild

A naturally evolved population whose genotypes and phenotypes have not been modified by human intervention.

2. Incidentally Co-Evolved

A population that volunteers and adapts in a human disturbed environment, possibly undergoing genetic change, but without human selection. This definition corresponds approximately to Rindos' (1984:154) "incidental domestication." Many weeds are examples of incidentally co-evolved species, which can also enter the domestication process if humans start to select for their useful traits and start to manage or cultivate them (Harlan 1992:90).

3. Incipiently Domesticated

A population that has been modified by human selection and intervention (at the very least being promoted), but whose average phenotype is still within the range of variation found in the wild population for the trait(s) subject to selection. The variance of this average is probably smaller than that of the original wild population, however, as selection has started to reduce genetic variability. This definition corresponds roughly to Rindos' (1984:158) "specialized domestication."

4. Semi-Domesticated

A population that is significantly modified by human selection and intervention (at the very least being managed) so that the average phenotype may diverge from the range of variation found in the wild population for the trait(s) subject to selection. The variance of this phenotypic average may be larger than that of the wild population, because the phenotypic variation now includes both types that are common in the wild population and types that are novel. Underlying genetic variability [e.g., isozyme variation (Doebley 1989)], however, continues to decrease because fewer individuals meet the selection criteria and are therefore included in the next generation. The plants retain sufficient ecological adaptability to survive in the wild if human intervention ceases, but the phenotypic variation selected for by humans will gradually disappear in the natural environment.

5. Domesticated

A plant population similar to (4) but whose ecological adaptability has been reduced to the point that it can only survive in human-created environments, specifically in cultivated landscapes (Harlan 1992:64). Genetic variability is generally less than in (4) because of increased selection pressure and loss of ecological adaptation. If human intervention ceases, the population dies out in short order, depending upon its life history, stature and the type of vegetation that invades the abandoned area. In clonally propagated crops, a single genotype may be the domesticate, but also is lost soon after it is abandoned.

5a. Landrace

A domesticated (or occasionally semi-domesticated) population selected in a cultivated landscape within a restricted geographical region with high phenotypic variability and relatively high genetic variability.

5b. Modern Cultivar

A highly selected and modified plant population or clone adapted exclusively to intensive monocultures with much reduced phenotypic and genetic variabilities.

Landscape Domestication

Landscape domestication is a conscious process by which human manipulation of the landscape results in changes in landscape ecology and in the demographics of its plant and animal populations, resulting in a landscape more productive and congenial for humans (Chase 1989; Harris 1989; Yen 1989). The intensity of manipulation may vary widely:

1. Pristine

A landscape in which humans have not manipulated plant or animal populations. It is unlikely that there was much pristine landscape in Amazonia at contact, nor is there today (Balée 1989; Denevan 1992c; Smith 1995).

2. *Promoted*

In this category desirable plant populations and individuals are encouraged through minimal forest clearance and expansion of the forest fringes (Groube 1989). Even though there may have been a low level of human intervention, the biotic components of this landscape may remain modified long after humans have abandoned the area.

3. *Managed*

In this category the abundance and diversity of food and other useful plant populations may be further encouraged through partial forest clearance, expansion of the forest fringes, transplanting of desirable individual plants or planting of individual seeds, addition of amendments to enhance plant growth, and reduction of competition from non-useful plants (Alcorn 1989; Anderson and Posey 1989; Groube 1989). Groube (1989) further divides this class into "forest management" and "forest gardens." Again, the biotic components of this landscape may also remain long after humans have abandoned the area and may account for several of Balée's (1989) anthropogenic forest types, e.g., some palm, bamboo, liana forests, and forest islands.

4. *Cultivated*

This category involves the complete transformation of the biotic landscape to favor the growth of one or a few selected food plants and other useful populations, through forest clearance and burning, localized or extensive tillage, seedbed preparation, weeding, pruning, manuring, mulching, and watering in any combination (Harlan 1992:64). The biotic components of this very artificial landscape do not survive long after human abandonment because the changes that favor the growth of the human selected populations also favor the growth of weeds and the invasion of other secondary forest species; however, it takes a long time to return to a natural state. The abiotic transformations practiced in this landscape often survive for long periods, e.g., the earthworks in various parts of lowland northern South America, such as the Llanos de Mojos (Denevan 1966) or the Llanos del Orinoco (Denevan and Zucchi 1978).

4a. *Swidden/Fallow*

This category is the combination of classes (4) and (3), in that order. The swidden is a cultivated landscape, which yields well for a few years but becomes progressively more difficult to weed and tend as soil fertility decreases. Useful weeds and volunteer or transplanted shrubs and trees are managed at progressively lower intensities until a managed secondary forest results (the fallow) (Denevan and Padoch 1987). This is the most visible sequence of indigenous landscape domestication in Amazonia today (Roosevelt 1989), but may have been less prevalent before the introduction of metal axes (Denevan 1992d). The managed fallow remains long after humans have abandoned it and may account for several of Balée's (1989) anthropogenic forest types, e.g., Brazil nut (*Bertholletia excelsa*), bacuri (*Platonia insignis*), cacao (*Theobroma cacao*), and pequi (*Caryocar brasiliense*) forests [see also Frikel (1978)].

4b. *Monoculture*

This is a cultivated landscape dominated by only one food plant or other useful populations. Species quasi-monocultures [e.g., initially dominated by cassava or maize] are common in new swiddens on the *terra firme* (the non-flooded surfaces of Amazonia) and on the *várzeas* (Roosevelt 1989), and probably existed before contact also.

The phrasing of the above definitions attests to my belief that there is a strong relationship between landscape and plant domestication in the Americas. Wiersum (1997), in fact, defined "co-domestication" of crops and landscapes, which may be the best view of this relationship. There are, however, examples of advanced landscape domestication, verging upon cultivation, without domesticated plants, such as by the Australian Aborigines (e.g., Chase 1989). Furthermore, wild plants can be cultivated without being domesticated (Harlan 1992:64). The inverse is not true, however: domesticated plants, as defined above, cannot be abandoned in unmanipulated landscapes because they have lost their ecological adaptations to natural environments (Harlan 1992:64).

Consequently, when Amazonian landscapes modified by humans were abandoned after European contact, the domesticated plant populations that occurred in them either died out, suffered their own population (and genetic) contraction, or regressed to the wild genotype while also becoming rarer. These changes depended upon the degree of population domestication and

TABLE 1. THE SEQUENCE OF CROP GENETIC EROSION (IN YEARS AFTER ABANDONMENT) IN AMAZONIA DEPENDED UPON DEGREE OF DOMESTICATION AND CROP LIFE HISTORY AND STATURE.

	Annual	Semi-perennial	Perennial
Full domesticate	1–3	2–10	10–30
Semi-domesticate	2–10	5–20	20–100
Incipient domesticate	5+	10+	300+

life history (herbaceous annuals and semi-perennials; woody perennial shrubs and trees) of the species in question. The time frames are conjectural, but may be estimated based upon life histories (Table 1). Little research has been done on this subject, but the shorter time frames are subject to testing through observation of swidden abandonment. One example is the pejibaye (*Bactris gasipaes*), a domesticated palm, that stops fruiting in second-growth forest when the canopy closes over the palm's crown 10–15 years after abandonment, thus effectively eliminating the population's long-term survival (Clement 1990).

CROP GENETIC RESOURCES OF AMAZONIA

León's (1992) list of cultivated American crops was assessed to identify those that were probably in Amazonia at contact. Some Andean crops are included, if they commonly occur below 1000 m above sea level and if there is evidence that they were grown in the lowlands, although their distribution in the lowlands was generally limited. Patiño's (1963, 1964) analysis of the early Spanish chronicles from northern South America provided the major key for this assessment. Neither source, however, deals specifically with incipiently domesticated crops. For this category, Balée (1988, 1989), Cavalcante (1991), Frikel (1978) and Lévi-Strauss (1950) were useful. A preliminary and somewhat subjective [for lack of data and occasional difficulty of distinguishing wild from incipiently domesticated crops (Lévi-Strauss 1950)] listing of domesticated, semi-domesticated and incipiently domesticated crops is presented in Appendices 1, 2 and 3, respectively.

There were probably at least 138 crops, in 44 botanical families, cultivated, managed or promoted in Amazonia at contact. This is about 50% of the total for the Americas. Among the 52 domesticates, 14 are fruit or nut trees or woody vines (27%); among the 41 semi-domesticates, 35 are trees or woody vines (87%); and among the 45 incipiently domesticated species, all but one are fruit and nut trees. Overall, 68% of these Amazonian crops are trees or woody perennials. In an ecosystem characterized by forest, a predominance of tree crops is not surprising. This predominance may be an artifact of abandonment, however, as domesticated annuals are expected to disappear more rapidly than perennials (Table 1).

How many crops are not on these lists? Certainly a considerable number, but there is no way of determining how many. *A priori,* I had expected the list of domesticates (Appendix 1) to be shorter than that of the semi-domesticates (Appendix 2) and much shorter than that of the incipient domesticates (Appendix 3), because only about 200 of the 3000 crops used by humans worldwide were domesticated (Hawkes 1983:6). While some species may be misplaced, there is certainly a lack of less derived species on these lists.

That some have disappeared since contact can be shown, however. Carvajal (1894:56) commented that, at one point between the Madeira and Tapajós Rivers they "found a lot of maize, and also a lot of oats, with which the Indians made bread" (my translation). As Patiño (1964: 99) wrote, "we don't know what 'oats' this species was." It is not cultivated among the Amerindians and Amazonian peasants anywhere in Amazonia today. At the mouth of the Amazon River, recent archeological excavations have yielded large quantities of a rice-like grass (*Leersia hexandra*) (Roosevelt 1991:25), which may have been the 'oats' mentioned by Carvajal. She mentions early records of apparent *Leersia* cultivation on Marajó Island shortly after the arrival of the Portuguese, but there is not enough information to determine if it was domesticated to any degree (hence its placement in Appendix 3), although Roosevelt's analysis is not yet complete. Another possibility is *Oryza glumaepatula,* found along *várzea* lake margins at high density (P. S. Martins, pers. com., 1995), although the early Spanish and Portuguese explorers would probably have recognized it as 'rice,' rather than as 'oats.'

Species diversity is only one aspect of crop genetic diversity, the other is infra-specific diversity. This is where genetic erosion was probably most serious, but it is also the most difficult to quantify. Each indigenous society and village probably valued crops somewhat differently, depending upon local preferences and the genetic variability available to them. Consequently, the selection and propagation effort devoted to each may have been different. For example, *Heliconia hirsuta* is a minor root crop found among a few indigenous societies in Colombian Amazonia today. Very little variability has been observed in the modern populations. How much existed at contact will never be known. The South American sapota (*Quararibea cordata*) is a similar story. At the opposite extreme is cassava, whose variability is continuing to be amplified today. Among the inhabitants of the Vaupés River, NW Amazonia, for example, nearly 100 distinct cultivars of bitter and sweet cassava were recorded at one village (Chernela 1983). Ethnobotanists frequently record 20–50 cultivars per village in western Amazonia and slightly lower numbers elsewhere. A complex system of landraces of pejibaye exists in Amazonia, with most genetic diversity in the northwest (Clement 1988; Mora Urpí 1992). Many major crops and widespread minor crops should show patterns of genetic diversity similar to that of cassava and pejibaye if they were intensively cultivated and selected in numerous areas with different microecological variation and biotic pressures.

As with species diversity, there exists some evidence that infra-specific diversity has disappeared since contact. Patiño (1964:147–148) mentions that the maize that existed along the Amazon River at contact has been replaced by coastal Brazilian maize during recent centuries. Goodman's (1976) map of the distribution of South American "Coroico" maizes includes part of the middle Solimões and western Amazon Rivers and regions to the south, but does not extend up or down river to areas where maize was reported by Carvajal (1894) and other chroniclers [see Patiño (1964)]. Amazonian maize is poorly known today (M.M. Goodman, pers. com., 1994), because of lack of comprehensive collections.

Estimates of Post-Contact Amazonian Population Loss

Gaspar de Carvajal (1894), the chronicler of the first European descent of the Amazon River in 1542, reported dense Amerindian populations along the Amazonian *várzeas* and adjacent *terra firme*. By the time European naturalists arrived in the region 200–300 years later, these populations had disappeared and Carvajal's account was discredited. The subject of Amazonian population density and associated level of cultural complexity is hotly contested today (Meggers 1993–5).

Meggers (1992b) offered the lowest recent estimate (1.5–2 million people in the Amazon Basin proper), based upon an average density of 0.3 persons/km^2. Meggers based her estimate on the *terra firme*'s low carrying capacity and the riskiness of *várzea* cultivation. At the other extreme is Myers (1988), who estimated 10 million in the Upper Amazon alone (essentially Amazonian Peru and Ecuador, and far western Brazil). Extrapolated to the rest of Amazonia, this suggests more than 30 million, or more than 4 persons/km^2, higher than the modern population.

Denevan (1996) recently lowered his earlier estimates (1992a,b) of 5–6 million in the Amazon Basin proper and 6–8 in lowland northern South America to 3–5 in the Basin and 5–7 in northern South America. His 1992 analyses included then current hypotheses of carrying capacity and pre-historic subsistence and agricultural technologies used in the various Amazonian ecosystems, and allowed for severe decline from disease and slavery, while cautiously accepting early historical accounts. His 1996 analysis emphasized the patchiness of human distributions, caused both by the patchiness of environments, especially suitable bluffs along the major rivers (Denevan 1992d), and by possible buffer zones between the larger societies, especially along the main rivers. Denevan provided estimates for each of Amazonia's various ecosystems. Amongst the most important were the *várzeas,* with estimated densities of up to 10 persons/km^2, possibly locally to 28 persons/km^2 on the Solimões and the Amazon Rivers; of 2 persons/km^2 in the Llanos de Mojos but possibly 28 persons/km^2 around the earthworks; of 9.5 persons/km^2 along the Brazilian coast south of Amazonia; of 0.3 persons/km^2 in the *terra firme* interfluvial forests; and 0.5 persons/km^2 overall.

Areas with high population densities are most important when considering crop genetic diversity. To support such densities, social organization must be more elaborate than at low density. As a corollary, agricultural and other subsistence technologies must be intensified (Roosevelt

1991:5, 1993), although they may less sustainable. The intensification implies greater crop genetic diversity, because the intensified agricultural systems must be able to withstand pest and disease pressures. The relationship between diversity and agricultural intensification in premodern tropical and sub-tropical societies is essential to understanding why so much crop genetic diversity is found in this geographic area. Pre-modern societies in the tropics had few means of controlling pest and disease outbreaks other than genetic diversity, intercropping and swidden rotation (Altieri 1995:112–113), except in the floodplains where the annual flood cycle acts to reduce pest and disease populations in most years, just as winter cold or annual drought acts to reduce these populations in temperate regions.

In general, advanced agricultural societies accumulate crop genetic resources, both creating and importing them, as part of their agricultural intensification. This is the major reason that several of Vavilov's (1992a,b) centers of crop genetic diversity are related to complex societies (Hawkes 1983:67), e.g., in the Americas, the Inca and pre-Inca civilizations are associated with the Peru/Bolivia center, and the Maya and Aztec civilizations with the MesoAmerican center. As paleoethnobotanical research expands in South America, the longest lists of crops are from areas where good conditions exist for archaeological artifact preservation and where complex societies with high population densities and advanced agricultural technologies existed (Pearsall 1992). In Amazonia, areas with higher population density in the pre-Columbian period should also exhibit a rich crop genetic heritage but the poor environment for archaeological preservation and lack of research effort have not yielded much information to date. Consequently living biological evidence is critical, but there are few clear patterns in Amazonian crop biogeography today, except in NW Amazonia (Clement 1989). The lack of clear patterns suggests that the loss of the Amazonian Amerindian population affected the crop genetic heritage severely.

Dobyns (1966) estimated that 90–95% of the Neotropical population was lost within 100–200 years after contact. Disease was the principal agent (Dobyns 1966), but missionization, slavery and warfare contributed importantly (Hemming 1978). In Amazonia, this meant a collapse from 3–5 million to a low of about 200 000. Today there are perhaps 500 000 Amerindians in lowland northern South America (Denevan 1992b), often organized in small bands and restricted to the *terra firme,* with relatively simple agricultural and subsistence technologies. Many are already extensively acculturated. How then did this human population collapse effect crop genetic resources?

The Consequences of Population Decline

Although individual farmers are responsible for selecting and propagating crops, the village is the unit of interest because it identifies a domesticated plant population. Farmers within a village exchange germplasm and influence each others' preferences and planting strategies. There is probably less exchange between villages than within, and less still between villages of different language groups (cf. Chernela 1987), because there is simply less contact in general. Myths of crop origins in Amazonia, for example, sometimes acknowledge the prowess of a farmer for stealing germplasm from a neighboring society (J. Chernela, pers. com., 1986), which would not be necessary if there was easy exchange. Consequently, the fate of the village determined the fate of its crop genetic resources during the post-contact population collapse.

The larger indigenous Amazonian societies consisted of numerous villages. Those that dominated the *várzeas* may have had many large and numerous small villages, while those restricted to the *terra firme* may have had only small villages. It is possible that the 90–95% population decline resulted in an equal loss of village units, although village members would attempt to escape from disease epidemics or slave raids, rather than stay and risk dying (Denevan 1992a).

Loss in human numbers was quickly reflected in a loss of crop diversity at the village site as the forest reclaimed the landscape (Table 1). Balée (1992) presented the example of the Guajá of eastern Amazonia, who regressed from village horticulturalists to nomadic hunter-gatherers that depend upon the fallows of other societies or managed forests left by predecessors. In the process of regression, their repertory of crops diminished rapidly to only a few crops with short life histories.

Given the extent of population loss, I feel that it is reasonable to hypothesize that 70–80% of the pre-contact village groups either disappeared completely, or were severely reduced and then absorbed by other groups, or regressed to a non-agricultural state. The major *várzea* societies, such as the Omagua on the Solimões River, disappeared almost completely (Roosevelt 1993). It is this low level of human survival in such important areas as the Omagua that is responsible for the tantalizing hints of a richer crop genetic past.

Although there is no direct evidence of how the loss of the human population was reflected in the loss of genetic resources, a synthesis of the information and ideas presented here permits an order of magnitude estimate. Genetic erosion after contact depended not only upon population decline but upon the degree of domestication of each crop, its life history, the agroecosystem in which it was cultivated or managed, and the number of crops maintained by each human society. I think that it is safe to assume that the Amazonian crop genetic heritage at contact was at least an order of magnitude greater than it is today. Unfortunately, even its current magnitude is poorly known for most crops, the partial exceptions being *Bactris gasipaes, Elaeis oleifera, Hevea brasiliensis* and *Theobroma cacao,* because they were extensively prospected during the early 1980s by Brazilian institutions.

Modern Crop Genetic Erosion

After the post-contact decline of Amazonian Amerindians, their populations stabilized and then expanded again, to about 500 000 today (Denevan 1992b). The number of societies continues to decline, however (Burger 1987; Clay 1990). During this century, the acculturation of the remaining Amerindians has accelerated, caused by the immigration of northeastern Brazilians to tap rubber during the late 19th century boom, the attempts by governments to occupy the region after World War II through directed colonization, and the spontaneous colonization that accompanied various infrastructure projects of the 1960–90 period (Hecht and Cockburn 1990).

After the Brazilian revolution of 1964, the government decided that Amazonia must be occupied by 'Brazilians.' This was and remains an issue of 'national security' (Hecht and Cockburn 1990:104–141). The first major initiative was the Trans-Amazon highway system, which started the era of reliance on roads, rather than Amazonia's extensive network of navigable rivers. This highway system made its strongest impact on eastern and southern Amazonia. In central Amazonia, the creation of the Free Zone of Manaus in 1967 had the greatest impact, as financial resources were funneled towards establishing industries in Manaus, rather than supporting trade between the hinterlands and the city. As traders stopped working, the interior of this vast region was essentially abandoned by government, and peasants started to migrate to Manaus and other urban centers. The 1970s saw the initiation of other large infrastructure projects, such as the Tucuruí Hydroelectric Dam, the encouragement of cattle pasture expansion, and the definition of PoloAmazonia's development targets. In the 1980s, Rondônia and Acre were opened by paving the Cuiabá-Porto Velho highway. By the late 1980s, Amazonia had become a focus of world attention because of the fires that accompanied deforestation (Hecht and Cockburn 1990:52–54). All these initiatives resulted in localized extinction of biodiversity and continued acculturation of the original Amazonians and their descendents.

Other modern Amazonian nations have followed roughly similar trajectories, with similar results. In Bolivia, Colombia, Ecuador and Peru, the poorer populations of the Andes were often encouraged to settle in the Amazonian lowlands, and governments are providing at least a part of the infrastructure necessary to further the migration. Peru and Ecuador have struck oil on the eastern slopes of the Andes and the boom has accelerated migration to those regions. In these areas, biodiversity, Amerindian cultures and crop genetic resources are disappearing rapidly, as occurs in numerous other parts of the world when modern societies displace indigenous and folk societies (Smith et al. 1992).

The late 1970s and 1980s also saw the first attempts at systematic evaluation of a few of Amazonia's crop genetic resources. Coordinated by the Brazilian National Center for Genetic Resources (CENARGEN), important collections of *Bactris gasipaes, Elaeis oleifera,* and *Hevea brasiliensis* were made. Collections of *Theobroma cacao* were made by the National Cacao Board (CEPLAC). Both the National Research Institute for Amazonia (INPA) and the Center for Agricultural Research in the Humid Tropics (CPATU) made casual collections of dozens of other species (Clement 1991; Clement, Müller and Chávez Flores 1982). Nonetheless, the germplasm saved is minuscule in comparison with the presumed erosion of the crop genetic resources of Amazonia and their wild populations and relatives caused by modern 'development.' In sum, the erosion of Amazonian crop genetic resources is presumed to have continued during the premodern and modern eras and appears to be accelerating as deforestation and acculturation proceed.

What trends are likely? Most Amazonian governments sponsor, or acquiesce to, acculturation of their Amazonian Amerindian populations, either as a conscious policy or by lack of action to protect the Amerindians from unwanted, forced contact with colonists (Treece 1990). Colombia, Ecuador and Venezuela are partial exceptions. Although several countries protect the rights of their indigenous populations on paper, few protect these rights on the ground. Recent efforts in Brazil, sponsored by the World Bank and the G-7, are aimed at changing this reality but it is still too early to measure their impact. Given the rapid expansion of non-indigenous populations, also demanding rights, land and government support, trends are unlikely to change enough to make a difference, unless governments alter their policies and enforce them.

Deforestation proceeds, although it slowed somewhat in the early 1990s due to an economic recession in many countries (Fearnside 1993). Strong systemic forces drive deforestation in Amazonia (Barbosa 1993) and are unlikely to change direction soon, although some popular movements are working to promote change. Some countries, such as Brazil, are reviewing government policies that favor deforestation, but social pressures to deforest are as yet unabated. Increasing poverty, combined with the still rapid population growth, are the major social pressures. Continued deforestation inevitably results in loss of biodiversity and associated crop genetic resources, many of which occur in formerly managed forests, now abandoned by their Amerindian creators (Smith and Schultes 1990; Smith et al. 1992).

Ex situ collections of most tropical crop genetic resources are inadequate, poorly maintained, and poorly financed because of low government priority and conflicting economic demands throughout the Third World (Fowler and Mooney 1990:201–222; Harlan 1992:239–243). Even some Brazilian collections made in the 1980s are in danger of being lost, either by institutional apathy and budgetary restrictions (e.g., *B. gasipaes*) or by biotic pressures (e.g., *H. brasiliensis*). Only a few in situ genetic reserves exist on the ground; these are focused on forest species (E. Lleras, pers. com., 1990), few of which are even incipiently domesticated. Current trends suggest that central government budgets for genetic resource conservation will continue to shrink in Amazonia, although some international efforts are expanding (e.g., the Pilot Program for the Conservation of the Brazilian Rain Forest, financed by the World Bank, the G-7, and the government of Brazil, and the Global Environment Facility (World Bank, UNDP, UNEP) has initiated a new in situ program with CENARGEN).

One promising new trend is an international (and national in some countries) interest in exotic foods and natural sources of some industrial products, especially from Amazonia (Clay 1996: v–x; Smith et al. 1992:448–460). This interest has the potential of stimulating plantations in Amazonia to supply the emerging demand, but must overcome a series of limitations in order to compete internationally (Clement 1997). Given the fragility of most regional institutions and the likelihood of continually smaller institutional budgets as Amazonian countries adapt to increased globalization, reverting the trends towards increased genetic erosion will require not only the development of numerous 'new crops' but a new focus by Amazonian research institutions—participatory plant improvement and community conservation of genetic resources (Engels 1995).

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APPENDIX 1. PROBABLY DOMESTICATED CROPS GROWN IN AMAZONIA AT CONTACT (BRÜCHER 1989; LEÓN 1987, 1992; PATIÑO 1963, 1964; PEARSALL 1992; PICKERSGILL AND HEISER 1977; SCHULTES 1984; SCHULTES AND HOFMANN 1979).

Species	Family	Probable origin	Uses
Annona muricata L.	Anonaceae	N. S. America	fruit
Rollinia mucosa (Jacq.) Baillón	Anonaceae	Amazonia	fruit
Xanthosoma brasiliense Engler	Araceae	N. S. America	vegetable
X. sagittifolium (L.) Schott	Araceae	N. S. America	root
Crescentia cujete L.	Bignoniaceae	N. S. America	tree gourd
Bixa orellana L.	Bixaceae	S. W. Amazonia	colorant
Ananas comosus (L.) Merrill	Bromeliaceae	Brazil/Paraguay	fruit
A. erectifolius L.B. Smith	Bromeliaceae	Amazonia	fiber
Neoglaziovia variegata Mez.	Bromeliaceae	N. S. America	fiber
Canna edulis Ker.	Cannaceae	Andes/W Amaz	root
Carica papaya L.	Caricaceae	MesoAmerica	fruit
Eupatorium ayapana Vent.	Compositae	Amazonia	condiment
Spilanthes acmella (L.) Murr.	Compositae	Amazonia	condiment
S. oleracea Jacq.	Compositae	Amazonia	condiment
Ipomoea batatas (L.) Lam.	Convolvulaceae	N. S. America	root
Cucurbita maxima Duch.	Cucurbitaceae	E. Bolivia	vegetable
C. moschata Duch. ex Poir.	Cucurbitaceae	MesoAmerica	vegetable
Cyclanthera pedata Schrad.	Cucurbitaceae	N. S. America	vegetable
Lagenaria siceraria Standl.	Cucurbitaceae	Africa	gourd
Sicana odorifera (Vell.) Naud.	Cucurbitaceae	Brazil/Paraguay	vegetable
Cyperus sp.	Cyperaceae	Amazonia?	condiment
Dioscorea trifida L. f.	Dioscoreaceae	Guianas	root
Erythroxylum coca Lam.	Erythroxylaceae	Central Andes	stimulant
Manihot esculenta Crantz	Euphorbiaceae	N. S. America	root
Zea mays L.	Gramineae	MesoAmerica	cereal
Poraqueiba paraensis Ducke	Icacinaceae	E. Amazonia	fruit, oil
P. sericea Tul.	Icacinaceae	W. Amazonia	fruit, oil
Persea americana Mill.	Lauraceae	MesoAmerica	fruit
Arachis hypogaea L.	Leg. Papilionoideae	Brazil/Paraguay	seed
Canavalia ensiformis (L.) DC.	Leg. Papilionoideae	N. S. America	seed
C. plagiosperma Piper	Leg. Papilionoideae	MesoAmerica	seed
Phaseolus lunatus L.	Leg. Papilionoideae	N. S. America	seed
P. vulgaris L.	Leg. Papilionoideae	N. S. America	seed
Pachyrhizus tuberosus Spreng.	Leg. Papilionoideae	W. Amazonia	root
Gossypium barbadense L.	Malvaceae	N. S. America	fiber
G. hirsutum L.	Malvaceae	MesoAmerica	fiber
Calathea allouia (Aubl.) Lindl.	Marantaceae	Amazonia	root
Maranta arundinacea L.	Marantaceae	N. S. America	root
Bactris gasipaes Kunth	Palmae	S. W. Amazonia	fruit
Passiflora edulis Sims	Passifloraceae	N. S. America	fruit
P. quadrangularis L.	Passifloraceae	N. S. America	fruit
Genipa americana L.	Rubiaceae	N. S. America	colorant
Paullinia cupana Kunth	Sapindaceae	C. Amazonia	stimulant
Pouteria caimito Radlk.	Sapotaceae	Amazonia	fruit
Brugmansia insignis Lockwood	Solanaceae	W. Amazonia	drug
B. suaveolens Bercht. & Presl.	Solanaceae	W. Amazonia	drug
Capsicum baccatum L.	Solanaceae	Bolivia	condiment
C. chinense Jacq.	Solanaceae	W. Amazonia	condiment
Nicotiana rustica L.	Solanaceae	N. S. America	stimulant
N. tabacum L.	Solanaceae	N. S. America	stimulant
Solanum sessiliflorum Dunal	Solanaceae	W. Amazonia	fruit
Cissus gongyloides Burch.	Vitaceae	Amazonia	vegetable

APPENDIX 2. PROBABLY SEMI-DOMESTICATED CROPS GROWN IN AMAZONIA AT CONTACT (BRÜCHER 1989; LEÓN 1987, 1992; PATIÑO 1963, 1964; PICKERSGILL AND HEISER 1977; SCHULTES AND HOFMANN 1979).

Species	Family	Probable origin	Uses
Anacardium occidentale L.	Anacardiaceae	N. E. Brazil?	fruit, nut
Spondias mombin L.	Anacardiaceae	N. S. America	fruit
Annona montana Macf.	Anonaceae	Amazonia	fruit
A. reticulata L.	Anonaceae	MesoAmerica	fruit
Macoubea witotorum Schultes	Apocynaceae	W. Amazonia	fruit juice
Thevetia peruvianum Merr.	Apocynaceae	C. Andes	poison
Ilex guayusa Loes.	Aquifoliaceae	N. W. Amazonia	stimulant
Mansoa alliacea (Lam.) Gentry	Bignoniaceae	W. Amazonia	condiment
Quararibea cordata Vischer	Bombacaceae	W. Amazonia	fruit
Couepia subcordata Benth.	Chrysobalanaceae	Amazonia	fruit
Clibadium sylvestre Baill.	Compositae	N. S. America	poison
Dioscorea dodecaneura Steud.	Dioscoreaceae	Amazonia	root
Phyllanthus acuminatus Vahl.	Euphorbiaceae	N. S. America	poison
Mammea americana L.	Guttiferae	Antilles	fruit
Platonia insignis Mart.	Guttiferae	E. Amazonia	fruit, seed?
Heliconia hirsuta L. f.	Heliconiaceae	W. Amazonia	root
Cassia leiandra Benth.	Leg. Cesalpinioideae	Amazonia	fruit
Anadenanthera peregrina Speg.	Leg. Mimosoideae	N. S. America	drug
Inga cinnamomea Benth.	Leg. Mimosoideae	Amazonia	fruit
I. edulis Mart.	Leg. Mimosoideae	W. Amazonia	fruit
I. feuillei DC	Leg. Mimosoideae	W. Amazonia	fruit
I. macrophylla H.B.K.	Leg. Mimosoideae	W. Amazonia	fruit
Lonchocarpus utilis Smith	Leg. Papilionoideae	Amazonia	poison
Banisteriopsis caapi Morton	Malpighiaceae	W. Amazonia	drug
B. inebrians Morton	Malpighiaceae	W. Amazonia	drug
Bunchosia armeniaca DC	Malpighiaceae	Amazonia	fruit
Byrsonima crassifolia H.B.K.	Malpighiaceae	MesoAmerica	fruit
Maranta ruiziana Korn.	Marantaceae	W. Amazonia	root
Pourouma cecropiifolia Mart.	Moraceae	W. Amazonia	fruit
Eugenia stipitata McVaugh	Myrtaceae	W. Amazonia	fruit
Myrciaria cauliflora McVaugh	Myrtaceae	S. Brazil	fruit
Psidium guajava L.	Myrtaceae	N. E. Brazil	fruit
Astrocaryum aculeatum Meyer	Palmae	W. Amazonia	fruit
Talinum triangulare Willd.	Portulacaceae	N. S. America	vegetable
Borojoa sorbilis Cuatr.	Rubiaceae	Amazonia	fruit
Paullinia yoco Schult. & Killip	Sapindaceae	W. Amazonia	stimulant
Pouteria macrocarpa Baehni	Sapotaceae	Amazonia	fruit
P. macrophylla (Lam.) Eyma.	Sapotaceae	Amazonia	fruit
P. obovata H.B.K.	Sapotaceae	C. Andes	fruit
Theobroma bicolor H. & B.	Sterculiaceae	W. Amazonia	fruit, seed
T. cacao L.	Sterculiaceae	W. Amazonia	stimulant

APPENDIX 3. SOME SPECIES WITH INCIPIENTLY DOMESTICATED POPULATIONS IN AMAZONIA AT CONTACT (BALÉE 1988, 1989; CAVALCANTE 1991; LEÓN 1987, 1992; LÉVI-STRAUSS 1950; PATIÑO 1963, 1964).

Species	Family	Probable origin	Uses
Couma utilis Muell.	Apocynaceae	Amazonia	fruit, latex
Hancornia speciosa Gomes	Apocynaceae	N. E. Brazil	fruit, latex
Caryocar glabrum (Aubl.) Pers.	Caryocaraceae	W. Amazonia	nut
C. nuciferum L.	Caryocaraceae	N. S. America	nut
C. villosum (Aubl.) Pers.	Caryocaraceae	C. Amazonia	fruit
Chrysobalanus icaco L.	Chrysobalanaceae	N. S. America	fruit
Couepia bracteosa Benth.	Chrysobalanaceae	C. Amazonia	fruit
C. edulis Prance	Chrysobalanaceae	Amazonia	nut
C. longipendula Pilger	Chrysobalanaceae	Amazonia	nut
Caryodendron orinocense Karst.	Euphorbiaceae	W. Amazonia	nut
Hevea spp. (various)	Euphorbiaceae	Amazonia	seed, latex
Leersia hexandra Sw.	Graminae	E. Amazonia	seed
Rheedia brasiliensis Pl. & Tr.	Guttiferae	Amazonia	fruit
R. macrophylla Planch & Triana	Guttiferae	Amazonia	fruit
Bertholletia excelsa H. & B.	Lecythidaceae	E. Amazonia	nut
Lecythis pisonis Camb.	Lecythidaceae	Amazonia	nut
Grias neubertii MacBride	Lecythidaceae	W. Amazonia	fruit
G. peruviana Miers	Lecythidaceae	W. Amazonia	fruit
Hymenaea courbaril L.	Leg. Caesalpinioidae	Amazonia	starchy fruit
Campsiandra comosa Cowan	Leg. Mimosoideae	N. W. Amazonia	fruit
Inga spp. (numerous)	Leg. Mimosoideae	Amazonia	fruit
Lonchocarpus nicou (Aubl.) DC.	Leg. Papilionoideae	Amazonia	poison
Lonchocarpus urucu Smith	Leg. Papilionoideae	Amazonia	poison
Eugenia uniflora L.	Myrtaceae	S. America	fruit
Psidium acutangulum DC.	Myrtaceae	Amazonia	fruit
P. guineensis Sw.	Myrtaceae	N. S. America	fruit
Acrocomia aculeata (Jacq.) Lood	Palmae	E. Amazonia	oily fruit
Astrocaryum murumuru Mart.	Palmae	E. Amazonia	oily fruit
Elaeis oleifera (H.B.K.) Cortés	Palmae	N. S. America	oily fruit
Euterpe oleracea Mart.	Palmae	E. Amazonia	oily fruit
Jessenia bataua (Mart.) Burret	Palmae	N. S. America	oily fruit
Mauritia flexuosa L. f.	Palmae	N. S. America	oily fruit
Maximiliana maripa Drude	Palmae	E. Amazonia	oily fruit
Oenocarpus bacaba Mart.	Palmae	Amazonia	oily fruit
O. distichus Mart.	Palmae	E. Amazonia	oily fruit
Alibertia edulis A. Rich ex DC.	Rubiaceae	Amazonia	fruit
Melicoccus bijugatus Jacq.	Sapindaceae	C. & N. S. America	fruit
Talisia esculenta Radlk.	Sapindaceae	W. Amazonia	fruit
Manikara huberi (Huber) Standl.	Sapotaceae	Amazonia	fruit, latex
Pouteria spp. (numerous)	Sapotaceae	Amazonia	fruit
Sterculia speciosa K. Sch.	Sterculiaceae	Amazonia	fruit
Theobroma grandiflorum Schum.	Sterculiaceae	E. Amazonia	fruit
T. speciosum Willd.	Sterculiaceae	Amazonia	fruit
T. subincanum Mart.	Sterculiaceae	Amazonia	fruit
Erisma japura Spruce	Vochysiaceae	N. W. Amazonia	fruit