

RESEARCH ARTICLE

Human Niche Construction and Population Growth in Pre-Columbian Amazonia

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The use of Niche Construction Theory in archaeological research demands that we establish empirically how human-constructed niches acted as legacies that shaped the selection pressures affecting past human populations. One potential approach is to examine whether human demography changed as a result of the continued use of landscapes enduringly transformed by past societies. This paper presents proxies for Amazonian population growth during the late Holocene and discusses their significance within the broader context of landscape legacies resulting from cumulative anthropic environmental alteration during pre-Columbian times.

Introduction

Niche Construction Theory is clearly relevant to understand the role that natural and anthropic landscape transformations have had in shaping the long-term trajectories of human societies (Arroyo-Kalin 2016; Boivin et al. 2016; Laland, Odling-Smee and Feldman 2000). Indeed, the human species is regarded as the ultimate niche constructor (Smith 2007), one that has 'self-imposed' a sliding range of selection pressures over time through migration, dispersal, habitat selection, and environmental modification (Laland, Odling—Smee and Myles 2010). Niche Construction theory, which finds its primary empirical foundation in ecosystem engineering (Jones, Lawton and Shachak 1997), references beaver dams and ant nests as classic examples of constructed niches. However, it also insists that the evolutionarily-significant modified niche is not *per se* the physical environment modified by organisms. Rather the selection landscape is co-constructed by organisms that have altered environments enduringly, such that the latter serve as ecological inheritance for future generations (Odling-Smee, Laland and Feldman 2003). The distinction between organism-led ecosystem alteration and selection pressure-modifying aspects of niche construction (Odling-Smee et al. 2013) can potentially confound the adoption of a niche construction perspective among archaeologists interested in the built environment and human-modified landscapes. While anthropic landscapes and the built environment are human analogues to coral reefs, beaver dams, and ant nests, regarding them from the perspective of niche construction theory demands that we establish empirically how they acted as environmental legacies that shaped selection pressures for past human populations.

Niche Construction Theory considers that perturbations to existing environments

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A consideration of pre-Columbian anthropic landscape transformations in the Amazon basin sheds important light on the preceding questions. In what follows I will first contextualise and summarise key points of our current knowledge regarding pre-Columbian societies of Amazonia. I will specifically emphasise the varied ways in which pre-Columbian populations of the late Holocene enduringly transformed the landscapes they inhabited, bequeathing ecological legacies that affected the fitness of both niche constructors and subsequent

inhabitants of specific locales. This fitness enhancement, as we will see, extends to some plant populations that were consumed or otherwise used by past human populations. Next, I will examine whether we can ascertain follow-up responses to these niche construction activities in the form of fluctuations in human demography. As I will argue below, the answer is a resounding 'yes'. The most evident implication is that these forms of ecological inheritance, resulting from modes of pre-Columbian human niche construction and whose legacies are still in evidence today, helped to modulate late Holocene demography prior to recent European colonisation.

Pre-Columbian Amazonian Societies of the Late Holocene

The Amazon basin is one the most linguistically- and ethnically-diverse regions of the planet. Indigenous languages – which number around 300 - can be grouped into at least six large language families, over twelve smaller language families, and more than a dozen linguistic isolates. Some of the larger language families (Tupi, Arawak, and Carib) are present in five or more separate geographical regions (Dixon and Aikhenvald 1999). Surprisingly, however, linguistically diverse indigenous groups living thousands of kilometres apart share constellations of highly distinctive cultural features, including common or analogous livelihoods, material culture, musical traditions, and cosmological understandings. Early Amazonian scholars, such as Max Schmidt (1917), Erland Nordenskiöld (1930) and Alfred Metraux (1928), felt this reflected the ancient expansion of specific populations that had broadcast languages, crafts, agricultural practices, and ceremonial modes across the region. By the mid 20th century, however, this 'civilisational' model had been all but replaced by strong environmental determinism, which characterised pre-Columbian Amazonia as a 'counterfeit paradise' in which relatively mobile lifestyles and low population densities where and had been the norm (Meggers 1971).

In this account, Amazonia's linguistic diversity was a compounded outcome of demographic stress resulting from past climate change, along with migration of, and social interaction between, different pottery-making peoples (Meggers 1975; Meggers and Evans 1983).

Renewed attention to pre-Columbian population growth and links to archaeological and linguistic evidence re-surfaced in the late 1960s, when scholars of the so-called 'revised' account argued that large populations had existed in Amazonia prior to the demographic collapse instigated by European colonisation (Denevan 1970). Donald Lathrap's (1970) provocative and highly influential reconstruction of pre-Columbian history argued that archaeological ceramic styles and the broad spatial distribution of prominent language families was to be understood as evidence for past population expansion and growth. In his account, the ancestors of the large groups reported by early European sightings had farmed the rich alluvial soils of large rivers, grown demographically, competed for land, and expanded outwards from central Amazonia via the river network.

More recent research (Heckenberger and Neves 2009; Rostain and Jaimes Betancourt 2017) has cast doubt on the prominence of floodplain agriculture and on the centripetal geography of Lathrap's reconstruction. However, it has also offered strong empirical support for many of the core elements of the 'revised' account. For instance, excavation of large archaeological sites with abundant pottery remains has demonstrated that a trend towards large sedentary settlements along the Amazon river may have started as late as the late first millennium BC. These occupations would have dominated the riparian landscape of the Amazon river and main tributaries during the first millennium AD and up to the first half of the second millennium AD (Heckenberger and Neves 2009; Moraes and Neves 2012; Neves et al. 2014). Archaeobotanical, zooarchaeological, and isotopic evidence suggests inhabitants of these settlements gathered and cultivated tree fruits, cultivated domesticated seed and tuber crops, and captured the rich aquatic fauna associated with riparian environments (Hermenegildo et al. 2017; Hilbert et al. 2017; Prestes-Carneiro et al. 2016; Mayle and Iriarte 2014; Morcote-Rios et al. 2013; Shock 2014).

The 'Landscape Twist': Niche Construction in pre-Columbian Amazonia

Amazonia's 'revised' accountalso incorporates a number of insights about human ecology that were initially developed by geographers, ethnobiologists, and anthropologists. In a rainforest biome that epitomises ideas about 'pristine nature' (Denevan 1992), these observations highlighted the ways in which current Amazonian indigenous populations act as ecosystem engineers (Posey 1985) and inhabit anthropic landscapes with timedeep histories of alteration (Balée 1989). Archaeological and ecological research has built on these insights to produce a striking account of long-term human niche construction.

The myriad species – among them numerous palm species and fruit trees - that are or were targeted for their edible parts or other economic uses during pre-Columbian times (Clement 1999b; Piperno and Pearsall 1998) were undoubtedly managed through an equally varied set of practices of environmental alteration (Arroyo-Kalin, Clement and Fraser 2008). These would have included a fire-intensive and spatially-restricted version of slash-and-burn agroforestry (Arroyo-Kalin 2012: Denevan 2004), a form of crop cultivation that at centennial time scales would have left measurable anthropic impact on local plant diversity (Saldarriaga 1994) and soils (Arroyo-Kalin 2010a). Ethnographic literature also shows other significant practices of environmental alteration: clearance associated with settlement implantation; the making of doorstep orchards or 'house gardens'; the management of natural and human-made forest gaps and old settlements for planting foodstuffs; and the promotion, tending, and/ or harvesting of clumps of edible and useful

plant species, domesticated or otherwise (Clement 1999a). Historical Ecological studies document the continued existence of anthropic stands of edible or useful plants. effectively highlighting them as centuriesold biotic legacies of the above practices (Junqueira, Shepard and Clement 2011, Levis et al. 2017). These studies show the role of past societies in enhancing the alpha diversity of specific locales (Balée 2006). These anthropic patches would have originated from more sedentary inhabitation (Balée 1992) or resulted from repeated seed discard by recent nomadic populations (Politis, 1996). Not only do these studies document the effects of human niche construction on other species but also highlight the relevance of legacy effects for human societal trajectories: many of these are used or managed by current populations, who sometimes acknowledge them as outcomes of previous events of inhabitation (Balée 2010). Recent archaeobotanical and palaeoecological research focusing on establishing whether these forms of environmental alteration existed in the past shows how past imprinting of vegetation by human activity took place within a complex landscape history involving climate change (Carson et al. 2014; Watling et al. 2017).

The 'landscape twist' continues: many late Holocene archaeological settlements are characterised by the presence of anthropic soils known as Amazonian Dark Earths (Arroyo-Kalin 2017a). The best-known examples are terras pretas de índio, which are dark-coloured and chemically enhanced soils with abundant pre-Columbian pottery remains. Terras pretas are believed to have formed as organic inputs – excrements, bone, organic matter, and combustion residues associated with kitchen middens, house gardens, dwelling structures, and other practices, concentrated and were churned into the soil mantles of intensively occupied land surfaces, i.e. these soils can be regarded as signature evidence for dense pre-Columbian settlement (Arroyo-Kalin 2014; Schmidt et al. 2014). The oldest examples of these soils probably push back to the middle Holocene (Miller 1992). However, a pattern of regionally widespread formation seems to begin as early as the end of the 1st millennium BC. Certainly by the mid to late first millennium AD, many rivers of eastern Amazonia show multiple locales where expanses of these soils were forming. Significantly, occupations associated with the latter phase are frequently recorded at the very locales where these soil expanses started to form in previous centuries (Arroyo-Kalin 2017b). A related type of anthrosol are terras mulatas, which are less chemicallyenhanced soils that in some cases surround patches of terras pretas. Terras mulatas have been interpreted in different ways: as legacies of as legacies of repeated burning around large settlements (Sombroek 1966); as former outfields associated with the settlements signalled by terras pretas (Andrade 1986; Arroyo-Kalin 2012; Denevan 2004); or as soil enrichment with overall lower black carbon/less burning associated with intrasettlement activity (Hecht 2003; Mora 2003, Schmidt et al. 2014; Walker 2011). A chronology for these anthrosols is less clear: one well-dated example is buried by mounds associated with defensive structures that were built no later than the late 1st millennium AD (Neves and Petersen 2006). Terras pretas and terras mulatas constitute expressions of anthropic soil modification that ultimately reflect the palimpsest-like character and legacy effects of past human occupations (Erickson 2003). They are prized to this day by Amazonian farmers because of their fertility, which leads to higher yields of staple lowland cultivars such as Manihot esculenta (cassava) and facilitates the cultivation of acid-intolerant or pest-sensitive crops, such as Zea mays (maize) (Clement, Mccann and Smith 2003; Fraser, Junqueira and Clement 2011; German, 2003; Lins et al. 2015; de Souza et al. 2017). Their enhanced fertility touches upon long-standing discussions about Amazonia's ability to sustain large populations against presumed inherent limitations of the soil mantle for agricultural intensification (Denevan 2012; Meggers 1954; Smith 1980).

Lastly we can examine an impressive array of pre-Columbian forms of landscape engineering that also modified local geomorphologies lastingly in widely-separated regions of the Amazon basin. These anthropic landforms are associated with settlements that range in scale from small villages to proto-urban aggregations. Among them are rectangular and circular bank-and-ditch features, variously interpreted as special-purpose ceremonial sites or defensive features around settlements. These are found along a wide arc connecting the Brazilian state of Acre and the headwaters of the Xingu River, as well as the middle Amazon and lower Madeira (Heckenberger, Petersen and Neves 1999; Moraes and Neves 2012; Schaan 2011). Also recorded in the flooding savannah landscapes of the Guianas and Llanos de Mojos are vast areas with different types of raised or drained fields (Rostain 2017). Archaeological investigations also reveal an even broader variety of earth mounds, including the ubiquitous presence of mounded rubbish middens; raised house platforms within settlements of the middle and lower Amazon region, the lower Madeira river, the upper Xingu river, and the Ecuadorian Amazon; and settlement mounds constructed in seasonally-flooding sayannah environments of the Guianas, Llanos de Mojos, and Marajó Island (Prümers 2017). To these features can be added constructed causeways, waterways, water reservoirs, fish ponds and traps in different regions of the Amazon basin (Erickson 2008; Lombardo and Prümers 2010; Schaan 2011; Stenborg et al. 2014). Overall, the great majority of these earthworks date from the early centuries of the first millennium AD to the time of European colonisation. Their size, ubiquity, enduring qualities, and chronology highlight how many of them shaped anthropic environments that were subsequently inhabited and managed (Arroyo-Kalin 2016; Erickson 2006).

Late Holocene Demographic Fluctuation in pre-Columbian Amazonia From the preceding overview, it cannot be doubted that sedentary inhabitation dur-

From the preceding overview, it cannot be doubted that sedentary inhabitation during the late Holocene pre-Columbian times lastingly modified the landscape in multiple

regions of the Amazon biome. However, the very extent and scope of this historical process remains to be specified in detail, particularly as it relates to pre-Columbian demography (cf. McMichael et al. 2012; Woods, Denevan and Rebellato 2013). Most discussants of this hotly debated topic have drawn on ethnographic and ethnohistorical sources, specified benchmark population densities, and -in some cases- calibrated these vis-à-vis specific habitats' productivities. Final estimates on the 'eve of European contact' have varied widely. Summarising others' and his own approach to the matter, geographer William Denevan (2014: 215) has recently stated that "now Denevan (. . .) says lestimating demography before European colonisation] can't be done with any meaningful result (. . .) On the other hand, I have some perspective (. . .). [It] gives me confidence that the Indian population in 1492 was indeed at least five to six million for Greater Amazonia and at least 3 to 4 million for Amazonia. Considering terra preta densities, the total for the former could have been eight to ten million. (. . .) There were large areas with fewer people, but there were also locations with many, many more."

Most archaeologists would agree that establishing actual numbers of people in the past is indeed very difficult (Chamberlain 2006). However, recent analytical and methodological innovations based on the compilation of large archaeological datasets offer increasingly more robust proxies for overall demographic fluctuation over time (Shennan et al. 2013). I present here preliminary results of analysis of the R Amazon database being developed at UCL Institute of Archaeology, which compiles radiocarbon dates from published archaeological sites from across the Amazonian biome. Analysis of 1,700 radiocarbon dates from archaeological sites located at least 1km apart permits exploring variation in summed calibrated probability distributions (SCPD). Because variation in SCPD is a proxy for occupational density per unit of space (1 km radius), it can be assimilated to demographic fluctuation in pre-Columbian times. Fig. 1 presents a SCPD

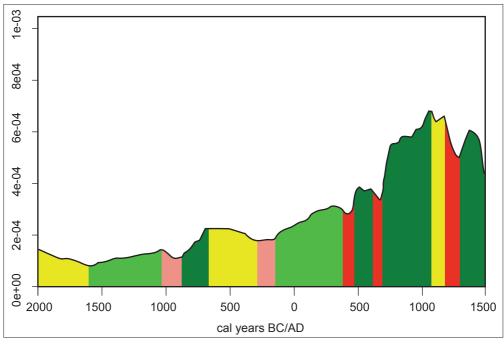


Figure 1: SCPDs for un-normalised radiocarbon dates plotted in fifty-year bins for the entire Amazon biome. Green shows moments of population growth (dark green = rapid growth); yellow shows moments of population decline; red shows population decline (dark red = sharp decline).

curve for the entire Amazon biome during the second half of the late Holocene. In its simplest outline, the plot shows an important increase in population during the early part of first millennium BC, followed by slow decline and then growth starting just before 0 AD and peaking before 500 AD. This is followed by sharp decline, rapid increase, and sharp decline in population starting around or after 500 AD, after which sharp population growth is observed. This trend peaks early in the second millennium AD with a potential bust and ensuing boom in the final centuries before European colonisation. In order to interpret this demographic fluctuation proxy we need to draw from the broader knowledge about past societies that Amazonian archaeology provides.

Discussion

We can explore a number of alternative scenarios to explain sharp but punctuated human population growth during the late Holocene. Does this pattern indicate the initial adoption of plant cultivation practices in the region? This scenario seems unlikely given both the ancient history of plant management in Amazonia and the fact that different domesticated crops - maize, cucurbits, manioc, cacao, and potentially domesticated rice - were present already by the end of the mid Holocene in different regions of the tropical lowlands (Bush et al. 2000; Bush, Piperno and Colinvaux 1989; Hilbert et al. 2017: Morcote-Rios et al. 2013: Piperno and Pearsall 1998; Shock et al. 2013; Zarrillo 2012). Can we then reject the role of agriculture, propose that ethnographic crop use patterns are largely artefacts of European colonisation, and explain population growth as a primary outcome of the exploitation of aquatic resources (Moraes 2015; Neves 2007)? On the one hand, a pattern dominated by opportunistic agroforestry (Neves 2013) seems inconsistent with continued population growth. On the other, both in Amazonia

(Schaan 2008) and beyond (e.g. Ames 1994; Benfer 2007) there are important examples that show how sedentism and population growth arose from an aquatic resource base. However, we should draw an important lesson from Widmer's (1988) insightful study of the Calusa chiefdom in southern Florida: where agricultural and aquatic potential are juxtaposed, adaptations tend to incorporate both livelihoods through mixed economies or specialised exchange. In the Amazon basin, both are evident today in the upper Negro River basin, were highly ritualised exchange of different types of produce including manioc for fish - permits resource complementarity among communities who lack access to specific resources (Arroyo-Kalin 2010a: 486).

Whilst the Amazon biome is a very large region that would have accommodated multiple adaptations (Steward 1948), complementarity rather than fluidity between foraging, fishing, arboriculture, and crop cultivation seems far more consistent with constant population growth during the early centuries of the first millennium AD. The sharp growth in overall population documented after 500 AD, in contrast, is largely either diagnostic of strong immigration or indicative of a demographic transition resulting from intensification of food production. As mentioned previously, agricultural intensification based on floodplain cultivation (Lathrap 1970) staggers as a model: large settlements are by no means exclusively associated with rivers that aggrade extensive floodplains nearby. In contrast, we have seen that the formation of altered soil substrates, coupled with deliberate soil modification resulting from fire-intensive and spatially concentrated practices of cultivation (Arroyo-Kalin 2010a; Denevan 2004), produce a specific ecological inheritance that would have had distinct effects for subsequent inhabitants of the same locales. As a whole, these places were implanted in geographies that had different strategic value, had variable access to fish resources, and presented access to different degrees of soils fertility. What they all came to share as common features are the fact that they were cleared of thick forest growth, their soils were enduringly enriched by human practices, and – after abandonment – they came to host stands of formerly managed useful or edible trees as well as crop-enriched seed banks. These features not only made them attractive for re-occupation but also rendered them into crucial niches where domestication of fruit trees adapted to open vegetation (e.g. *Bactris gasipaes* – peach palm) and cultivation of crops poorly adapted to nutrient-poor, low pH soils (e.g. Zea mays) could have taken place. To put it succinctly, rather than to understand these expanses simply as epiphenomena to intense occupations or expanding populations, we might consider them as the crucial substrates that permitted productive intensification and attendant population growth during the first millennium AD (Arroyo-Kalin 2010a; Denevan 2004).1

Archaeological evidence is at least compatible with this scenario. Among Amazonian specialists there exists a virtual consensus that the broad regional expansion of specific ceramic traditions around 0 AD signals the growth of the Arawak language family (Arroyo-Kalin 2010b; Heckenberger 2008; Neves et al. 2014; Zucchi 1991). Evidence for population growth at this time, therefore, is best regarded as evidence for demic diffusion along the waterways of the Amazon basin, which also promoted intensive inter-regional interaction (see also Hornborg 2005). Fish abundance may have pulled the boat, so to speak, as early Arawak speakers expanded along the river network. However, their livelihoods probably also relied on the cultivation of multiple carbohydrate-rich domesticated crops and ancient practices of fruit tree management (Arroyo-Kalin 2012; Arroyo-Kalin et al. 2008). As is strongly suggested by ethnographic practices in the northwest Amazon and the Guianas, and by similar proto-words in northern and southern branches of the language family (Brown et al. 2013), manioc cultivation was probably crucial to their success. As a crop demanding the reproduction of savannahlike conditions for its cultivation - an agroecosystem that would have strongly encouraged intensive burning – it might have also instigated the inception of patterns of ecosystem engineering that left enduring environmental legacies for subsequent inhabitants along the waterways of the basin (Arroyo-Kalin 2010b; Neves et al. 2014).

Subsequently, towards 500-800 AD, archaeological evidence appears to suggest a 'domino effect' that instigated the expansion of different non-Arawakan populations to different regions of the Amazon biome (Brochado and Lathrap 1982; Evans and Meggers 1968; Lathrap 1970; Moraes and Neves. 2012: Rostain 2012: Tamanaha and Neves 2013). This basin-wide re-arrangement, apparently triggered by climate-change related factors (Arroyo-Kalin et al. in prep.), appears to mark the expansion and elaboration of other populations that recolonised previously-modified locales and which proceeded to further alter them. Sharp population growth recorded from then and until the early part of the 2nd millennium AD appears to signal productive intensification. Whilst more archaeobotanical evidence is still required to assess this scenario, we can remember that Roosevelt (1999) suggested this process might be related to the intensification of maize cultivation, which is consistent both with evidence from areas in the periphery of the Amazon basin (Iriarte and Dickau 2012) and with recent isotopic evidence (Hermenegildo et al. 2017). Competition for and defence of human-constructed niches appears to mark the latter history of different regions of Amazonia, as signalled by the implantation of ditches and palisades from around 1000 AD (Heckenberger 2005; Moraes and Neves 2012; Neves and Petersen 2006).

Conclusion

On the eve of contact, Amazonian livelihoods reliant on plant management and cultivation were probably an amalgamation of ancient patterns of fruit tree management and farming of carbohydrate-rich domestic crops (Arroyo-Kalin, Clement and Fraser 2008). In Amazonia, where fish abundance is strongly conditioned by water chemistry,

alluvial geomorphology, and the upstream or downstream position of a given locale within a tributary network (Denevan 1996; Moran 1995), tethering of habitation sites to locales with abundant aquatic protein can explain why many, but certainly not all, large settlements are concentrated along watercourses. Undoubtedly both variables intersected as pre-Columbian processes of demic diffusion in the late Holocene instigated intense environmental alteration which, bequeathed as environmental legacies, contributed to productive intensification. We can rephrase these points from the perspective of Niche Construction theory as follows: in the late Holocene, cumulative anthropic landscape modifications in Amazonia enduringly altered the 'selection landscape' and contributed to increased population growth. Use of competition for the control of these attractive humanconstructed niches ensued. Thus, landscapes enduring transformed in Amazonia - niches constructed by human populations over the long term – emerged as selective landscapes in their own right.

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Competing Interests

The author has no competing interests to declare.

Notes

Some students believe their wasteful reuse to build habitation mounds and their tendency to be rapidly invaded by weeds constitute strong arguments against their recycling into cultivation substrates during pre-Columbian times. My own geoarchaeological research has not yet been able to establish conclusively whether settlement-related anthropic soils were re-used for cultivation before recent times (Arroyo-Kalin, 2017a).

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