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Niche construction and optimal foraging theory in Neotropical agricultural origins: A re-evaluation in consideration of the empirical evidence

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ABSTRACT

The various theoretical approaches advanced over the past 50 years to explain the origins of agriculture have prompted much discussion and debate. Most recently, controversy has arisen concerning the utility of two Darwinian approaches; namely, cultural niche construction (CNC) and human behavioral ecology-derived optimal foraging theory (OFT). Recent papers advocate for the primacy of cultural niche construction, calling for optimal foraging approaches to be all but disregarded in the quest to explain how and why foragers became farmers (Smith, 2015, 2016; Zeder, 2015, 2016). In particular, it is claimed that archaeological, paleo-environmental, and paleontological evidence from the Neotropics of northern South America fail to meet predictions derived from OFT theory, while predictions said to be derived from CNC-based approaches are supported (Smith, 2015, 2016; Zeder, 2015). However, a number of misreadings of the northern South America evidence are made in those discussions, while some pertinent literature is not considered. In this paper we discuss these misreadings and provide a clear re-articulation of the original data and interpretations, finding support for OFT predictions. Our re-evaluations of OFT and CNC further suggest they can, in fact, be complimentary explanatory approaches.

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1. Introduction

The fundamental importance in human history of plant domestication and human economies based on agricultural products has prompted a number of theoretical debates as to how and why human populations around the globe became farmers starting about 11,000 years ago. Current arguments center on the utility of two Darwinian theoretical approaches for explaining agricultural origins; human behavioral ecology (HBE) and its derivative optimal foraging theory (OFT) and cultural niche construction (CNC) (e.g., Gremillion et al., 2014; Coddling and Bird, 2015; Freeman et al., 2015; Smith, 2015, 2016; Zeder, 2015, 2016; Bird et al., 2016; Stiner and Kuhn, 2016; Wallach, 2016). In two recent papers Smith (2015, 2016) argues that OFT approaches should generally be

rejected and replaced by CNC explanations. In way of assessing empirical data for his arguments, he focuses on a portion of the archaeological and paleo-environmental records from northern South America, thought to be a major independent region of agricultural origins (hereafter termed plant food production [PFP] to incorporate both initial cultivation of plants and appearance of their domesticated products). As investigators who have carried out long-term research there, we find that in Smith's discussions there are several critical misreadings of the evidence, while a number of important sources aren't considered. Given the considerable importance of this region in Neotropical prehistory and its place as an early and likely independent center of agricultural origins, our aim here is two-fold: 1) to provide a more complete and arguably more accurate review of the evidence for the transition from foraging to farming, and 2) on this basis, re-evaluate the different positions taken with regard to OFT and CNC in agricultural origin research.

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2. Background: optimal foraging and niche construction theory

So that empirical evidence from Neotropical records discussed below may be best considered and understood in the light of the two theories, we first briefly review a few pertinent tenets and theoretical predictions of each with particular regard to PFP origins. More extensive discussions are available in Kennett and Winterahlder (2006), Gremillion et al. (2014), and Coddling and Bird (2015). In Piperno and Pearsall (1998) and Piperno (2006a, 2011a) the “diet breadth model” (DBM) of OFT was employed in order to posit and test some underlying reasons accounting for resource use, change, and intensification among the first farmers and their forager predecessors. The DBM uses a straightforward currency—energy—to measure the costs and benefits of alternative resource sets, and assumes that humans will have a goal of optimizing the energetic returns of their subsistence labor. One of its strengths is how it underwrites the logic of diet choice and dietary broadening or narrowing, both shown to be integral to PFP origins globally (e.g., Larson et al., 2014). Under the DBM, resource “rankings” are based on their energetic returns to labor, not simply on their actual abundances on landscapes. Those resources with the highest returns are expected to be taken when encountered, and when higher-ranked resources become less frequent or unavailable due to environmental change or human over-exploitation, lower-ranked items are taken. A result is that the diet may broaden and become less energetically efficient overall. This decrease of high-ranked resources is in OFT terms called “resource depression”.

Piperno and Pearsall (1998) and Piperno (2006a, 2011a) applied the DBM to Neotropical PFP based on the following: 1) demonstrations from ethnographic data that energetic efficiency is a significant influence on food procurement decisions, 2) seeds and underground plant organs are typically shown to be much lower-ranked than small to medium-sized fauna, in turn lower-ranked than many large animals, and 3) paleoecological evidence for considerable climate, vegetation, and faunal changes during the Pleistocene-Holocene transition, with loss of open, savanna-type lands and their subsistence resources—including the now-extinct megafauna—in concert with expansion of tropical forests and their lower-ranked plant and animal resources, and 4) the limited but intriguing evidence that initial PFP may have been more energetically-efficient than the preceding tropical full-time foraging, providing an OFT-derived rationale for initial cultivation (see Piperno and Pearsall, 1998; Piperno, 2006a; Piperno, 2011a for complete discussions). Therefore, decreasing foraging efficiency as dietary breadth necessarily expanded to incorporate lower-ranked resources was posited as an important selection pressure acting on human food procurement strategies during the Late Pleistocene and early Holocene.

Turning to CNC theory, archaeologists are increasingly interested in its applications, for good reasons. Human environmental modification has a deep history, as studies dating back to the Paleolithic demonstrate, and humans may be expected to alter their environments with numerous practices that leave both short- and long-term ecological legacies. Moreover, topics such as subsistence intensification and PFP origins are intimately tied to how human actions often times drive environmental change, both intentionally and not. The application of CNC to PFP origin questions is more recent than with HBE and OFT. In two recent papers that explicitly discuss the Neotropics, Smith (2015, 2016) argues that CNC uniquely predicts the circumstances around which initial domestication occurred, and he puts forward a number of “test implications” said to derive from CNC logic for evaluating its efficacy when empirical evidence is considered. These are set against competing test implications said to be derived from OFT formulations.

For example, the following, operating shortly before or concomitant with PFP origins, are argued to support primacy of CNC; the opposite would support OFT: 1) little to no environmental change that would cause biomass reduction of optimum dietary resources, 2) no changes in food processing activities such as appearance of a grinding stone technology, 3) no decrease of high ranking resources, 4) evidence for CNC in way of sustained local ecosystem modification and without prior decrease in high-ranking resources, and 5) decreases in residential mobility due to a focus on rich resource areas “with abundant, predictably available resources within a relatively circumscribed area” (the OFT-supported implication would be population packing) (Smith, 2015; Zeder, 2016:339 following Smith, 2015). Numbers 1, 3, and 4 relate directly to the issue of resource depression, one of Smith's foci when comparing OFT with CNC. In contrast, therefore, to OFT-derived hypotheses that a decreased availability of high-ranked resources (i.e. resource depression) led to subsistence changes with dietary broadening shortly before and at PFP origins, energetic efficiency as a determinant of subsistence choice/change is not considered in these CNC-derived expectations, and initial domestication is predicted to occur “... within a context of stable or enhanced resource availability ...” (Smith, 2015:239). These test implications are evaluated below with regard to the empirical evidence from northern South America and Neotropics more broadly.

3. Paleoenvironments and subsistence changes in northern South America

A zone located in Colombia and labeled D1 in Piperno (2011a, Fig. 1) that is reproduced here as Fig. 1, is an area where a number of archaeological sites with early PFP evidence occur and putative wild ancestors of some crop plants are native, making it a likely center of domestication. Early PFP occupations there, located in the Middle and Upper Cauca Valley and dating from about 11,000 to 7500 BP (all ages are in calendar years BP unless noted), are characterized not only by appearance of crop and other economic plants, but also by the introduction of numerous ground stone tools for plant processing and hoes, all indicating a substantial subsistence focus on plants (Piperno, 2011a; Aceituno and Loaiza, 2014, 2015; Dickau et al., 2015 for recent reviews). Reconstructed vegetation for these occupations is tropical forest of various types depending on elevation and annual precipitation. Smith (2015, 2016), focusing on Zone D1, makes several errors in his presentation of the evidence from it that form part of his basis for his critique of OFT applications, and which need to be addressed.

Smith states that in Piperno (2006a, 2011a) the D1 zone is characterized as being “generally covered by savanna/thorny scrub vegetation” during the Late Pleistocene (hereafter, LP), but then states that this characterization is contradicted in the same publications where Zone D1 is placed in forest during the LP in Fig. 7.4 in Piperno (2006a) and Fig. 1 in Piperno (2011a). He also claims, citing three papers (Gnecco, 2003; Gnecco and Aceituno, 2006; Gnecco and Mora, 1997), that environmental reconstructions of the D1 zone by others place it in “dry seasonal forests” during the LP, supposedly ruling out any open savanna/thorny scrub-dominated landscape to forest cover change during the transition from the LP to early Holocene (hereafter, EH). As discussed above in Section 2, using the DBM in light of the paleoenvironmental data, an open-land to forested vegetation change was predicted to have occurred that significantly altered energetic return rates and subsistence choices for foragers during the LP to EH transition, as higher-ranked open-land flora and fauna (including now-extinct megafauna, discussed below) were replaced by those of lower-ranked tropical forest taxa (Piperno and Pearsall, 1998; Piperno, 2006a, 2011a). Smith goes on to argue from the same three papers he cited above

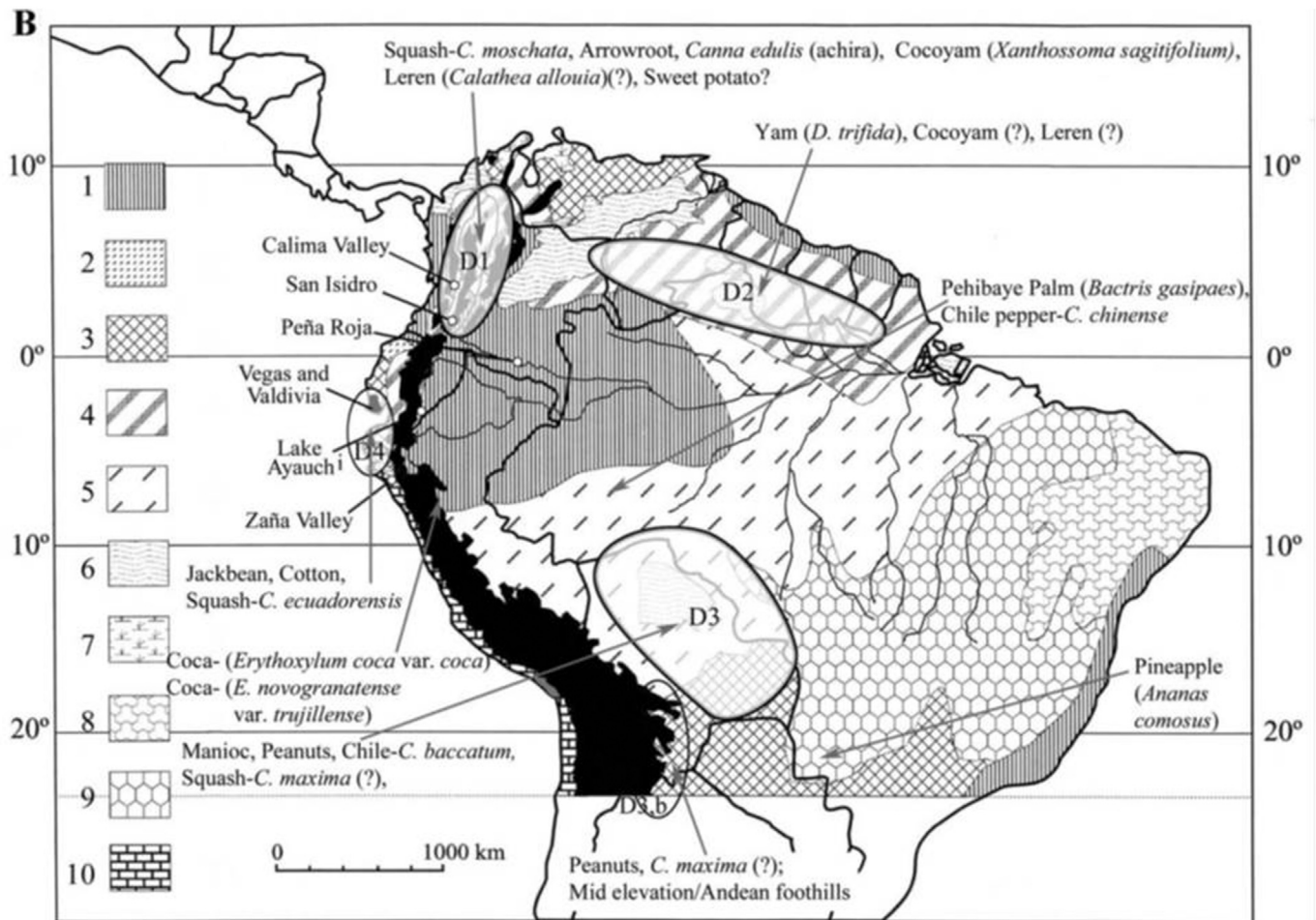


Fig. 1. Shown against a background of modern potential vegetation are: 1) areas within ovals (called zones in the text) labeled D1–D4 where it appears that more than one or two important crops originated; in some of these zones, as in D1 discussed in the text, early plant food production (PPF) is evidenced; 2) postulated domestication areas for various tropical crops in South America, denoted by arrows from a plant species; arrows point to approximate areas and are not meant to identify specific domestication locales, and 3) archaeological and paleoecological sites with early domesticated crop remains, denoted by open circles. Areas in black are elevations above 1500 m. Vegetation zones are: 1. tropical evergreen forest (TEF); 2. tropical semi-evergreen forest (TSEF); 3. tropical deciduous forest (TDF); 4. mixtures of TEF, TSEF, and TDF; 5. mainly semi-evergreen forest and drier types of evergreen forest; 6. savanna; 7. thorn scrub; 8. caatinga; 9. cerrado; 10. desert. Originally published as Fig. 1 in Piperno 2011a with vegetation zone distributions as originally in Fig. 2.2 in Piperno and Pearsall, 1998; see Piperno and Pearsall 1998, Fig. 2.2 caption for sources used for the vegetation zone distributions.

that human populations had little need for new adaptations and exploitative strategies during the LP to EH transition, claiming that investigators working in the D1 zone considered the Pleistocene and early Holocene forests to be substantially analogous to modern dry seasonal tropical forest with regard to their relative abundances of useful animal and plant species for human exploitation (Smith, 2015, 2016).

In the first place, Figs. 1 and 7.4 that Smith refers to don't show reconstructed LP vegetation as he claims, but rather modern potential vegetation, illustrating not surprisingly that forests of different types dominate Zone D1 in the post-Pleistocene (Fig. 1 that Smith refers to is the one reproduced as Fig. 1 here). The correct figure number in Piperno (2006a) showing LP vegetation is 7.2, reproduced as Fig. 2 here. Furthermore, Piperno did not characterize the entire D1 zone as being generally covered by savanna/thorny scrub vegetation during the LP, but rather as Fig. 2 here shows, a heterogeneous zone composed of different forest types along with thorn woodland/low scrub/wooded savanna-type vegetation.

The three papers cited by Smith to argue that none of Zone D1 was in more open vegetation during the LP (Gnecco, 2003; Gnecco and Aceituno, 2006; Gnecco and Mora, 1997) refer to the

archaeological sites San Isidro and Peña Roja (the correct title for Gnecco and Mora, 1997 is "Late Pleistocene/early Holocene tropical forest occupations at San Isidro and Peña Roja, Colombia" not the citation Smith lists). Neither documents LP vegetation (it was not the intent of the papers) as San Isidro was occupied at the terminal Pleistocene/early Holocene boundary at ca. 11,600 BP when vegetation was transitioning and Peña Roja was not occupied until 1000 years later. Smith also confuses the latter's location; it is well outside Zone D1 decidedly not in an inter-Andean valley, but rather deep in the Colombian Amazon lowlands in evergreen rain forest (Fig. 1). All investigators, including ourselves, who have worked in the regions and are familiar with their data sets agree that both sites were in tropical forest at time of occupation and probably before, but not in dry seasonal formations; rather, in wetter associations of different composition (e.g., Gnecco, 2003; Cavalier et al., 1995; Gnecco and Mora, 1997; Aceituno and Loaiza, 2015; Piperno and Pearsall, 1998, Fig. 2.4 and Piperno, 2006a, Fig. 7.2; Gnecco and Aceituno, 2006; Ranere and López, 2007).

Furthermore, an area of Zone D1 pertaining to the present day deciduous and semi-evergreen forest of the middle and southern Cauca and Magdalena Valleys receiving less than 2 m of precipitation today was reconstructed in Piperno and Pearsall (1998,

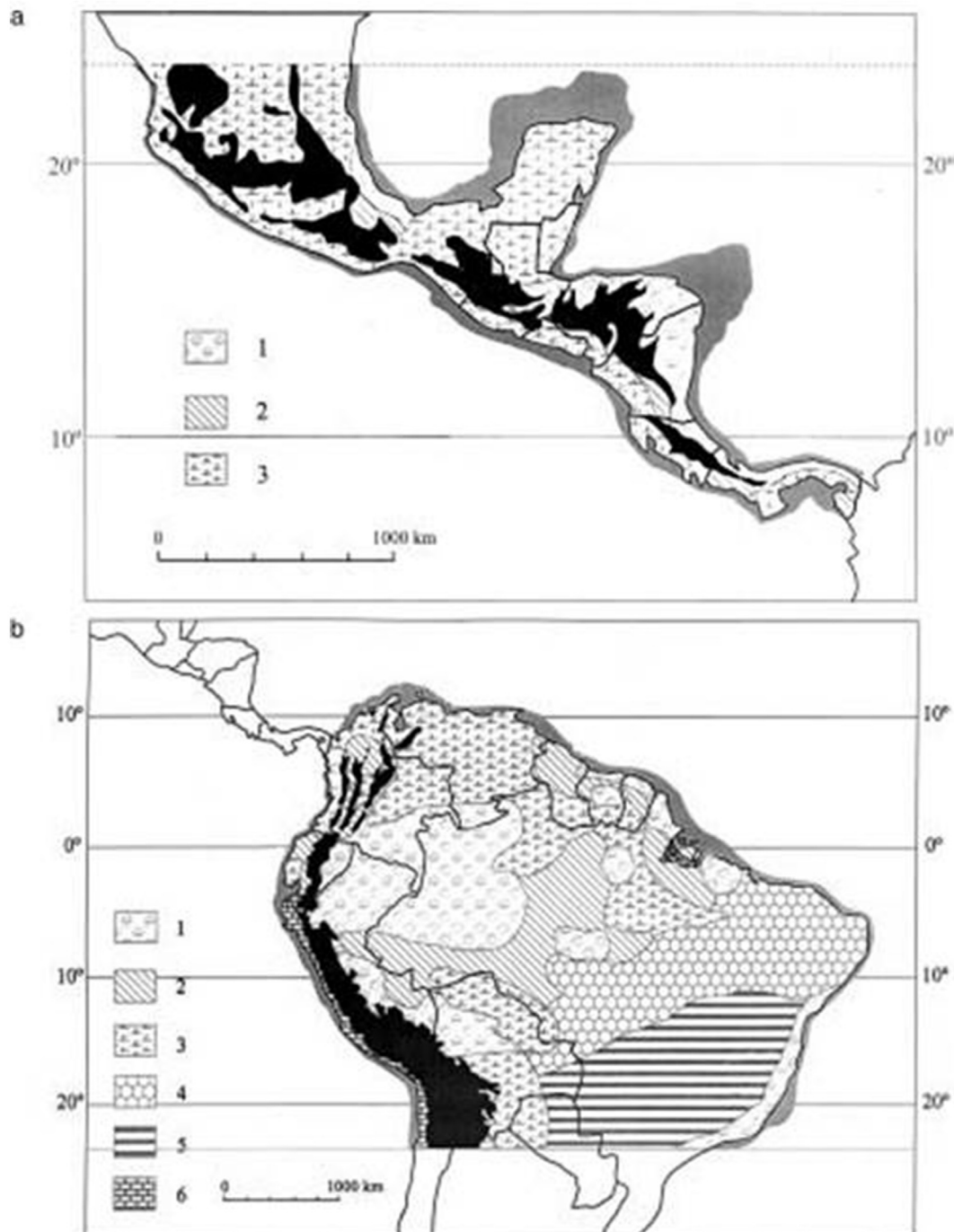


Fig. 2. A general reconstruction of (a) lowland tropical Middle and Central America vegetation and (b) South American vegetation between ca. 22,000 BP and 11,000 BP based on paleoecological information. Areas in black indicate elevations above 1500 m above sea level. Gray represents Pleistocene shoreline. Vegetation zones are: 1. Largely unbroken moist forest, often with a mixture of presently high-elevation and lowland forest elements; 2. Forest containing drier elements than characteristic today. High-elevation forest elements occur, especially in moister areas of the zone. Areas near the 2000 mm precipitation isohyet and areas with sandy soils may contain savanna woodland. The vegetation may be patchy; 3. Mostly undifferentiated thorn woodland, low scrub, and wooded savanna vegetation. Areas receiving greater than 2000 mm of rainfall today may still support a drier forest, as in 2. River- and stream-side locations support a forest; 4. Quite possibly, a drier vegetation formation than 5 (below), with fewer trees and more open-land taxa; 5. Fairly open and humid forest containing many presently high-elevation taxa (e.g., *Ilex*, *Podocarpus*, *Rapanea*, *Symplocos*) combined with elements of the modern semi-evergreen forest and cerrado. Precipitation is lower than today but northward shifts in the southern polar fronts and other factors ameliorate precipitation reduction. The modern, seasonal forest/cerrado vegetational formations of the region are not present until about 11,000 BP; 6. Desert/cactus scrub. Originally published as Fig. 2.4 in Piperno and Pearsall 1998; see that source and references in this paper for sources used for reconstructions.

Fig. 2.4) and in Piperno (2006a, Fig. 7.2) as being mostly in undifferentiated thorn woodland, low scrub, or wooded savanna vegetation (see Fig. 2 herein). This is directly supported by pollen studies indicating that dry forest elements decreased and grasses

increased rapidly about 13,800 BP as conditions became very cool and dry, and open, grass-dominated vegetation prevailed from about 12,800 until ca. 10,000 BP, when dry forest elements were advancing on the landscape (Berrío et al., 2002). Edible legumes

and other arboreal taxa characteristic of thorny scrub environments today were also more common during the 13,800–10,000 BP period. This area of Zone D1 is where early Holocene PFP occurs at sites in the Calima Valley and in many Cauca Valley locations (Fig. 1) (Piperno and Pearsall, 1998; Piperno, 2011a; Aceituno and Loaiza, 2014, 2015; Dickau et al., 2015). Smith's categorical claims that in Zone D1 there was no savanna/thorny scrub to tropical forest vegetation change during the LP to EH transition that would have affected foraging return rates and subsistence choices are incorrect.

Finally, Smith's view that there was little need for new adaptations and subsistence strategies during the LP to EH transition in the northern South American Neotropics would, if true, be surprising in view of the now decades-old evidence that the low- and middle-elevational Neotropics witnessed climatic and associated environmental changes on the order of those experienced at higher latitudes (see Piperno, 2006a; 2011a for reviews). Indeed, on the basis of data from a number of D1 Zone Cauca Valley sites we and others have investigated, we have stressed how human adaptive strategies substantially changed when the Pleistocene ended in response to significant environmental changes characterized by forest expansion, re-assortments within arboreal communities, and different resource availabilities, leading to an increased focus on plant exploitation—including the onset of cultivation—accompanied by the appearance of ground stone tools and other plant-oriented lithic technologies (sites studied include Sauzalito, El Recreo, El Jasmín, La Pochola, La Selva, Cuba, San Isidro, and others; e.g., see Piperno and Pearsall, 1998; Piperno, 2011a, b; Aceituno et al., 2013; Aceituno and Loaiza, 2014; Dickau et al., 2015). In sum, Smith's discussions of the Colombian evidence and its interpretations by researchers carrying out work there misrepresent the actual records and their interpretations.

4. Megafaunal extinctions and subsistence changes

Citing only an analysis of South American megafaunal remains by the paleontologists Barnosky and Lindsey (B&L) (2010), Smith argues that recent research indicates megafauna were all gone in northern South America 3000 years before first evidence of hunter-gatherer occupation of the region, and therefore OFT predictions for changes in resource rankings and subsistence during the EH based on an LP human exploitation of the animals before their extinction can be rejected. Smith (2015:244) quotes B&L as follows: ".... the dates analyzed suggest extinction intensity and timing may have varied across the South American continent, starting in the north long before humans ever arrived (Barnosky and Lindsey, 2010, p. 20, Fig. 8a)." Here is B&L's (2010:20) full passage: "First, taken at face value, the dates analyzed suggest extinction intensity and timing may have varied across the South American continent, starting in the north long before humans ever arrived, and becoming most intense and rapid in the southern, higher latitudes as human arrival and climate change had more dramatic effects there. Clearly, however, many more radiocarbon dates are needed to test this speculation." What B&L refer to as speculation because few data are available Smith elevates to the level of certainty.

However, what is clear to a consensus of archaeological experts on the peopling of South America is that at the site of Tibitó located on the Sabana de Bogotá in the D1 zone, a close association of dismembered and burnt megafauna (horse and mastodon) and human artifacts dated by carbon-14 studies of the burnt bone to $11,740 \pm 110$ ^{14}C yr. B.P. (about 13,600 calendar years BP) can be considered secure evidence of human exploitation of the animals (e.g., Correal Urrego, 1981; Cooke, 1998; Gruhn and Bryan, 1998; Ranere and López, 2007; López, 2008; Aceituno et al., 2013; Kornfield and Politis, 2014). Megafaunal remains were also found

in overlying strata at the site, thought to date to 13,000 to 11,500 BP on the basis of associated artifacts and palynological profiles. That the area was settled by human groups at those times is also made clear by contemporary occupations documented at the nearby site El Abra (references above). Recent work has uncovered human occupations in the Middle Cauca Valley in Zone D1 dating to 12,600 BP (Dickau et al., 2015), and although further verification is needed finds of mastodon and sloth in association with human artifacts like those at Tibitó and nearby sites are reported within Zone D1 in the Magdalena Valley lowlands (e.g., Correal Urrego, 1993; Ranere and López, 2007; López, 2008; Dickau et al., 2015). Other well-accepted northern South America megafaunal finds associated with human activity are found in Venezuela (Taima Taima and other El Jobo culture sites) (e.g., Bryan et al., 1978; Ochsenius and Gruhn, 1979; López, 2008; Navarette, 2008; Kornfield and Politis, 2014). Smith's claims that there was no human occupation in Zone D1 prior to 11,600 BP, or that megafaunal extinction could not have been a cause of substantial changes in foraging return rate in northern South America at the end of the Pleistocene are therefore not supported.

More broadly, in other regions of the Americas from Mexico to Brazil where there is evidence for a shift from open to forested landscapes over the LP to EH transition, and that have been documented or thought to have supported early PFP (Piperno, 2011a, Fig. 7.4 in Piperno, 2006a and Figs. 1 and 2 here), associations of humans with megafauna or sites containing megafaunal remains alone are evidenced, making it clear that LP foragers encountered the animals (e.g., Cooke, 1998; Ranere and López, 2007; Kornfield and Politis, 2014; Chatters et al., 2014). None of the LP human occupations contain specialized stone tools for processing plants, but rather most contain types of projectile points characteristic of those periods and not later and probably used to hunt big game. Occupations were more mobile than in the EH with less attention to, or perhaps motivation for the settling down and scheduling required to effectively manipulate and control the plant world. Multi-year archaeological site surveys and excavations in Colombia Zone D1 indicate EH occupations are much more numerous than LP examples, also pointing to population growth associated with the increasing subsistence focus on plants (e.g., Dickau et al., 2015).

5. A re-evaluation of cultural niche construction and optimal foraging theories in the neotropics

To summarize, empirical data from archaeological and paleo-environmental research are in accord with hypotheses and predictions generated from OFT to inform processes underlying PFP origins in northern Colombia and the Neotropics at large. In fact, in Smith's and Zeder's set of test implications said to be predicted from CNC (discussed in Section 2 above), Nos. 1–3 that deal with changes in the environment, availability of high-ranking resources, and food processing strategies are contradicted by the Neotropical data, instead supporting the OFT-predicted test implications including resource depression. With relation to test implication No. 4, it is difficult to envision how CNC activities would be antagonistic to OFT-met predictions of dietary broadening and subsequent resource intensification upon decline of higher-ranked resources (see below), as CNC can take place with or without previous resource depression occurring; and neither of the No. 5 propositions appear relevant since Neotropical populations, though less mobile and growing, weren't packed and the rich resource zones with abundant resources described aren't an apt fit for tropical forest ecology and consequent wild resource availability for humans (Piperno and Pearsall, 1998:39–72).

Yet all of this becomes an exercise best left undone because as most investigators involved with these issues believe, OFT and CNC

aren't competitors; they focus on different elements of human responses and Darwinian selection, and *can be complementary, informing and broadening each other* (e.g., Broughton et al., 2010; Gremillion et al., 2014; Codding and Bird, 2015; Freeman et al., 2015; Molenhoff et al., 2015; Bird et al., 2016; Stiner and Kuhn, 2016). CNC focuses on, and is more effective at, unveiling feedbacks and historical dynamics than OFT. In doing so, it can be said that CNC theory makes it possible to better understand the ecological context in which optimality is being assessed. OFT principles on the other hand may inform why niche constructors do what they do by predicting the costs of various landscape manipulations (see Gremillion et al., 2014; Freeman et al., 2015 for more discussion on these points).

What then about CNC in the Neotropics? Human environmental modification and its role in successfully adjusting early cultures to the tropical forest habitat have long been integral to study in Neotropical research (e.g., Sauer, 1958; reviews in Piperno, 2006b, 2011b). Piperno and Pearsall (1998:76) in the first modern comprehensive account of Neotropical agricultural origins and upon emergence of evidence for LP and EH human firing of forest, stated: "When humans entered the tropical forest and fired and cleared the vegetation, they unconsciously increased the reproductive fitness of many wild plants and animals most beneficial in their diets and set the stage for control of the reproduction of these plants through cultivation and domestication". This clearly describes an example of niche construction coming from OFT users before the term CNC was coined in archaeology. Indeed, there was no incompatibility exposed between OFT formulations and possible incidences of CNC. The former predicted exploitation of lower ranked resources and subsistence broadening upon post-glacial spread of tropical forest, and modifying vegetation played an important role in human adjustments to those forest resources (see Piperno and Pearsall, 1998). Obviously, the many examples of early and later human impacts on tropical forest through firing, clearing, and other alterations (Piperno, 2006b; 2011b) might be called CNC, but it will be incumbent on those who do to specify the resulting impacts on selection pressures for recipients of CNC that make it a separate evolutionary process and not simply another element of standard evolutionary theory (e.g., Scott-Phillips et al., 2014; Ellis et al., 2016). Future research will hopefully further explore links between human behavioral ecology and cultural niche construction in explaining PFP origins in the Neotropics and elsewhere.

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