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Primate archaeology 3.0

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Abstract

The new field of primate archaeology investigates the technological behavior and material record of nonhuman primates, providing valuable comparative data on our understanding of human technological evolution. Yet, paralleling hominin archaeology, the field is largely biased toward the analysis of lithic artifacts. While valuable comparative data have been gained through an examination of extant nonhuman primate tool use and its archaeological record, focusing on this one single aspect provides limited insights. It is therefore necessary to explore to what extent other non-technological activities, such as non-tool aided feeding, traveling, social behaviors or ritual displays, leave traces that could be detected in the archaeological record. Here we propose four new areas of investigation which we believe have been largely overlooked by primate archaeology and that are crucial to uncovering the full archaeological potential of the primate behavioral repertoire, including that of our own: (1) Plant technology; (2) Archaeology beyond technology; (3) Landscape archaeology; and (4) Primate cultural heritage. We discuss each theme in the context of the latest developments and challenges, as well as propose future directions. Developing a more "inclusive" primate archaeology will not only benefit the study of primate evolution in its own right but will aid conservation efforts by increasing our understanding of changes in primate-environment interactions over time.

KEYWORDS
ephemeral technology, evolution of material culture, non-technological traces of behavior, primate cultural heritage

1 | INTRODUCTION

As members of the primate order we share multiple traits with the other ~500 primate species (Rowe & Myers, 2017). However, unlike any other primate, our survival depends on the use of tools and our culture is ingrained in every aspect of our lives (Koops et al., 2022; Rolian & Carvalho, 2017). Thus, why, when, and how these traits arose and became established in the hominin lineage are key questions of interest in human origins research. One way to address these questions is by using a comparative framework such as the one proposed by the new field of primate archaeology (Carvalho et al., 2008; Haslam et al., 2009, 2017; Luncz et al., 2015; Stewart et al., 2011). This approach extends the use of archaeological methods, commonly only applied to the study of humans, to all technological primates, enabling the investigation of the origins of hominin technology through a comparative perspective (Carvalho & Almeida-Warren, 2019; Haslam et al., 2017). Nevertheless, primate archaeology has a caveat, in that it has (with very few exceptions, see Hernandez-Aguilar et al., 2007 or Stewart et al., 2011) largely focused on stone tool use, paralleling the archaeology of human origins which is heavily based upon the analysis of lithic artifacts (Haslam et al., 2009; Pascual-Garrido & Almeida-Warren, 2021). While

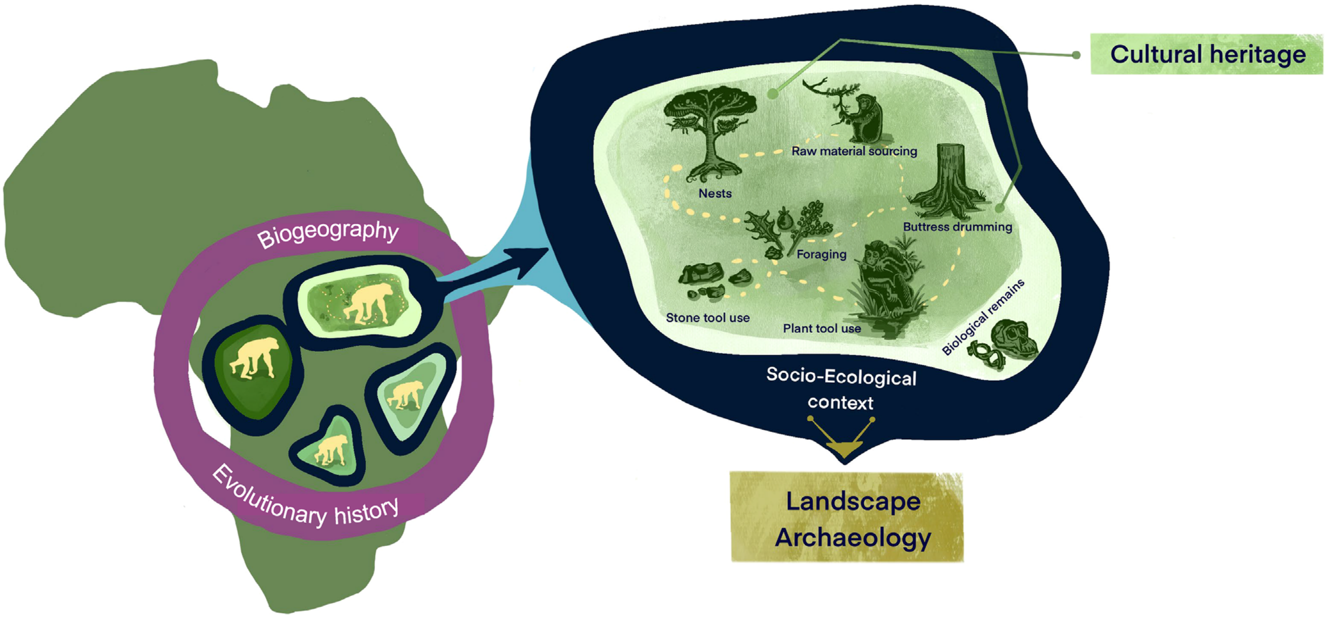

FIGURE 1 Uncovering the full potential of primate archaeology. Promising novel areas of research include: Plant technology; Archaeology of non-technological behaviors; Landscape archaeology; and Primate cultural heritage. Complementary research fulfilling these areas will open the way to better understand the evolutionary history and biogeography of non-human primate populations and their technological repertoires. (Illustration by Elodie Freymann).

valuable comparative data have been gained through an examination of nonhuman primate tool use and its material record (Falótico et al., 2019; Haslam et al., 2016; Mercader et al., 2007), focusing on one single aspect of nonhuman primate lives provide limited insights. It remains to be explored to what extent the full range of modern nonhuman primate activities may produce identifiable archaeological traces. Here, we propose four areas of investigation which we consider have not yet received sufficient attention, and which may be crucial to uncovering the full archaeological potential of nonhuman primate behavioral repertoires: (1) Plant technology; (2) Archaeology beyond technology; (3) Landscape archaeology; and (4) Primate cultural heritage (Figure 1). We discuss each theme in the context of the latest developments and challenges, as well as propose future directions.

2 | PLANT TECHNOLOGY

Primate archaeology continues to mirror the study of human prehistory, in that it is mostly reliant on stone tools (Haslam et al., 2017). However, given that plant-based technology is the most common, and arguably, the most diverse and complex form of primate tool use—as well as the only form involving (intentional) tool manufacture (Luncz, Arroyo, et al., 2022; Rolian & Carvalho, 2017)—the opportunity to focus on organic records is perhaps an even more important asset of studying primate technology.

Non-industrialized human societies and nonhuman primate species use plant materials for implements far more often than bones or stone (Marlowe, 2010; Rolian & Carvalho, 2017). It is therefore unlikely that our early ancestors overlooked the potential value of this material, with plant tools likely being part of the most ancient technological repertoires (Hardy, 2018; Hardy et al., 2020; Panger et al., 2002). Given the limited archaeological evidence for perishable materials before the emergence of anatomically modern humans (~400–300 thousand years ago), testing this hypothesis remains challenging (but see Wadley et al., 2020 for novel discoveries in cave contexts and Luncz, Braun, et al., 2022 for novel methods to allow identification of damage on wooden tools). However, the extensive use of plant tools by nonhuman primates offers an overlooked opportunity to investigate the social, environmental, and cultural drivers of plant-based technology (Koops et al., 2014), thus expanding interpretations of ancient tool use (Luncz, Braun, et al., 2022; Panger et al., 2002). Interestingly, if we consider archaeological contexts where plant remains have survived, fiber artifacts outnumber stone tools by a factor of 20 to 1, while, under anaerobic conditions, 95% of all recovered artifacts are made from wood or fiber (Adovasio et al., 2007). This broadly coincides with the use of tools by wild chimpanzees, in which plant implements constitute the bulk of their technical repertoire, with proportions ranging between 11%–18% for stones compared to 78%–83% of plant-based materials (Reader, 2004). As such, most of the technology used by chimpanzees today, like most ancient human technologies (Hardy, 2018), would not enter the archaeological record (McGrew, 2010).

However, in certain (usually anoxic) circumstances, plant material can last for hundreds of thousands of years (Goren-Inbar, Werker, et al., 2002; Wadley et al., 2020). Plant use-residues persisting as by-products on inorganic tools, such as cashew nuts cracked by capuchin monkeys (Falótico et al., 2019) or plant fibers used by Neanderthals for cordage manufacture (Hardy et al., 2020), can last for tens of

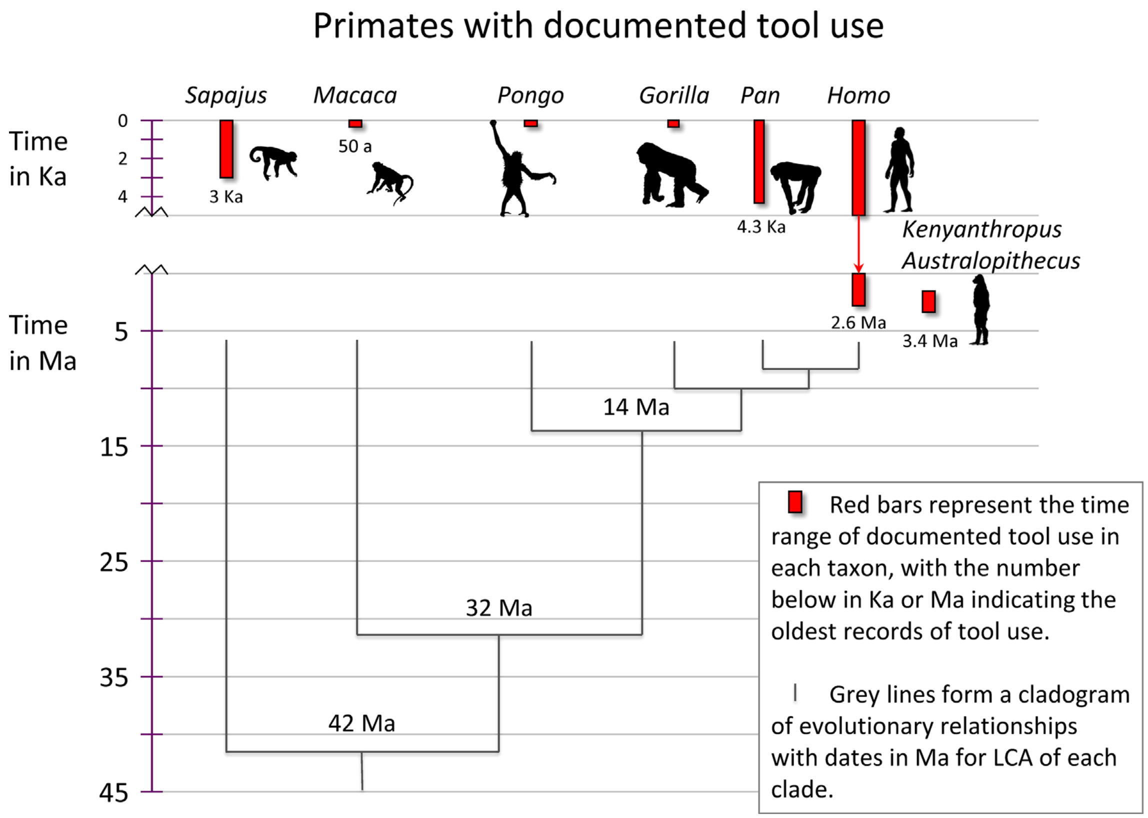

FIGURE 2 Timeline of the currently known archaeological evidence for nonhuman primate tool use and cladogram of evolutionary relationships (credit: René Bobe & Susana Carvalho).

thousands of years. Chimpanzee plant technology lasts for much less time, the longest known so far comprises of still-living twigs and branches in chimpanzee nests, which last for a few years (Stewart et al., 2011). Given that wood is one of the most common terrestrial fossils encountered in the geological record (Falcon-Lang, 2011), and fossilized wooden fragments have been identified in archaeological sites in the same sediments as stone artifacts and hominin fossils (Bamford, 2005, 2017), fossilized wooden tools and the signatures associated with their use (Luncz, Braun, et al., 2022), if they exist, could be detectable in the archaeological record. Current investigations of technological industries that extend further than 3 million years ago remain limited to the records produced by stone tools (Harmand et al., 2015, but see Archer et al., 2020 for an alternative view). Unless we go beyond lithic assemblages, the fundamental role plants played in these early periods and how it is reflected in the archaeological record will continue to be eclipsed.

Although nonhuman primate plant tools remain the most complex and diverse form of technology, its use has been reported for only a few species (Musgrave & Sanz, 2018). Wild chimpanzees (*Pan troglodytes*), orangutans (*Pongo* sp.), and bearded capuchin monkeys (*Sapajus libidinosus*) habitually use plant materials to manufacture tools which they commonly modify before use (Falótico & Ottoni, 2014; Mannu & Ottoni, 2009; van Schaik et al., 1996; Whiten et al., 1999). Wild bonobos (*Pan paniscus*) habitually use plant tools though their breadth of use is limited in comparison to that of common chimpanzees, and mainly restricted to non-foraging contexts (e.g., leaf umbrellas) (Samuni et al., 2022). Anecdotes of plant tool use have been reported for wild western gorillas (*Gorilla gorilla*) (Breuer et al., 2005) and black lion tamarins (*Leontopithecus chrysopygus*) (Kaisin et al., 2020). Among nonhuman technological primates, only chimpanzees typically make and use a plant toolkit in everyday life (McGrew, 2004), making them central to the first studies of perishable material culture. So far, these have focused on tools and nests. The study of wooden tools has been particularly revealing about the breadth of information that could be gained from focusing on discarded artifacts at tool use sites (Hernandez-Aguilar et al., 2007; McGrew & Collins, 1985), documenting new forms of ape technology through the material record and demonstrating the importance of an archaeological perspective in the study of ephemeral technologies (Hicks et al., 2019; McGrew et al., 2003). More recently, archaeological methods have been extended to examine the raw material procurement for plant tools by wild chimpanzees (Almeida-Warren et al., 2017; Pascual-Garrido, 2018, 2019), suggesting the possibility that a perishable-to-lithic behavioral *continuum* may have begun long before the emergence of stone technology and perhaps as early as the *Homo*-*Pan* last common ancestor (Pascual-Garrido & Almeida-Warren, 2021). Moreover, given that the use of perishable implements is shared among all extant great apes, it is possible that plant technology may date as far back as their earliest divergence in the Miocene (Figure 2). Likewise, the study of nests through this novel approach has challenged former interpretations of early hominin sites (Hernandez-Aguilar, 2009; Sept, 1992; Stewart et al., 2011), emphasizing the role that the re-use of sleeping locations may have played in the ranging patterns of our earliest ancestors (see Section 4).

But primate archaeology also encapsulates ethoarchaeology, which studies the relationship between animal behavior (ethology) and the resulting material record (McGrew et al., 2003). Similarly to ethnoarchaeology, which focuses on the material traces of modern human behavior (mostly non-industrialized societies; Beck, 2015; Gifford-Gonzalez, 1991), ethoarchaeology seeks to develop analogues between modern processes and ancient products, to help reconstruct behavioral patterns and ancient lifeways that cannot be easily derived from fossil and archaeological artifacts alone (Bandini et al., 2022). Such an approach has been extensively applied in the study of nonhuman primate stone tool use such as chimpanzee nut cracking (Arroyo et al., 2016; Benito-Calvo et al., 2015; Carvalho et al., 2008; Proffitt, Haslam, et al., 2018; Schick & Toth, 1993), macaque use of pounding tools and axe-hammers to access encased food such as shellfish, sea almonds, and oil palm nuts (Gumert et al., 2009; Haslam et al., 2013; Proffitt, Luncz, et al., 2018), and capuchin stone-tool-aided feeding repertoires, which are argued to be the most diverse among nonhuman primate species (Falótico, Siqueira, et al., 2017; Luncz et al., 2016; Mannu & Ottoni, 2009; McGrew et al., 2019). In fact, it has been the recent ethoarchaeological work on capuchins that has provided some of the most valuable clues for understanding the stone behaviors that may have led to the emergence of lithic technologies in the hominin lineage (Bandini et al., 2022; McGrew et al., 2019). A recent study by Arroyo et al. (2021) which analyzed wild bearded capuchin pounding tools used for different activities, was able to detect function-specific use-wear patterns on tool surfaces. Furthermore, some of the tools (mostly those used for digging) lacked macroscopic modifications, indicating that digging behaviors might be under-represented, and overlooked, in the archaeological record. Individuals from the same population have also been observed to unintentionally produce sharp-edged flakes by pounding stones directly against each other, some of which resemble Oldowan flakes (Proffitt et al., 2016). Similar evidence has now also been uncovered from wild macaque nut-cracking sites, challenging the intentional origin of lithic tool production and illustrating potential behavioral precursors to systematic stone knapping (Proffitt et al., 2023).

Nevertheless, comparable research is limited, and in some cases virtually lacking for other types of percussive behaviors which are widespread among chimpanzee communities (Harmand & Arroyo, 2023), such as the use of embedded stone anvils to open hard-shelled *Strychnos* fruits (van Lawick-Goodall, 1968), chimpanzee pestle pounding (Yamakoshi & Sugiyama, 1995), and baobab (*Adansonia digitata*) smashing (Marchant & McGrew, 2005). Likewise, the potential knowledge that may be gained by applying similar approaches to the study of nonhuman primate non-percussive plant technologies has not been yet fully investigated (Koops et al., 2015; Lonsdorf et al., 2004; Möbius et al., 2008; Schöning et al., 2008; Sousa et al., 2009). For example, by retrieving the artifacts left behind by known individuals after a tool session, it is possible to identify who contributes to the palimpsest and observe the site formation process in real time (Carvalho et al., 2011). Furthermore, it enables the examination of individual variation in these activities (Estienne et al., 2017). Technological variation across chimpanzee populations is well established (Dutton & Chapman, 2015; Sanz et al., 2014; Whiten et al., 2001), with corresponding differences in their behavioral record (Bessa et al., 2022; Koops et al., 2015; Luncz et al., 2018; Pascual-Garrido, 2019). Tool use varies across communities of the same population as a result of different environmental affordances (Koops et al., 2014; Uehara, 1982) or different cultural knowledge (O'Malley et al., 2012; but see Koops et al., 2023; Whiten, 2022 for an extensive update and comment on culture in nonhumans). Variation across individuals within a community may result from differing ontogenetic interactions, in particular between mothers (and older siblings) with offspring (Estienne, Cohen, et al., 2019; Estienne, Robira, et al., 2019; Lamon et al., 2017; Lonsdorf, 2006; Musgrave et al., 2016). Disentangling how each of these factors contributes to the patterns of variation seen in nonhuman primate populations is perhaps one of the biggest challenges that remains ahead. Future ethoarchaeological studies should also take into account biological sex and age, both of which are particularly relevant for tools used in foraging, where sex differences have been reported and technical skills are developed and then mastered at a certain age (Boesch & Boesch, 1984; Falótico & Ottoni, 2014; Fox et al., 2004; Gumert et al., 2011; Lonsdorf, 2005; McGrew, 1979; Musgrave et al., 2020; Pruetz & Bertolani, 2007).

Another aspect of perishable technologies which has largely been overlooked is the analysis of the physical and mechanical properties of the various types of raw material used for tools or nests (Carvalho, 2021; d'Errico & Backwell, 2021; van Casteren et al., 2012). Chimpanzees exhibit strong population-specific material preferences for the manufacture of tools which vary according to the task (Sanz & Morgan, 2007). They will, for example, select plant species and materials for termite-fishing tools (Almeida-Warren et al., 2017; McBeath & McGrew, 1982), trim the tip of branches to produce pointed hunting tools (Pruetz & Bertolani, 2007), or fold and chew leaves or moss into sponge-like bundles to collect water (Lamon et al., 2018; Lapuente et al., 2017; Sousa et al., 2009). The selection and modification of these materials requires notable technical skill and will likely affect their efficiency, durability and, consequently, the performance of the tool-user and the energetic payoffs (Lamon et al., 2018; Mackworth-Young & McGrew, 2014; but see Izar et al., 2022 for a recent update from capuchin stone tool use). Yet, we still do not know if/what material characteristics are being selected (except van Casteren et al., 2012), nor if/how this knowledge is passed on—that is, through social learning (Hobaiter et al., 2014; Lamon et al., 2017; Musgrave et al., 2020; but see Koops et al., 2023; Whiten, 2022 for comments on alternative proposals). While tool use and manufacture in chimpanzees is also determined by age and manufacture methods (Humle et al., 2009; Musgrave et al., 2020; Nishie, 2011; Sousa et al., 2009), the influence of raw materials on efficiency remains unstudied. Different techniques may be used (Kalan et al., 2020), which could make a particular material more efficient or prey more easily obtainable. Likewise, differences in prey behavior and energetic/nutritional value

(O'Malley & Power, 2014) may determine the adoption of certain techniques (Schöning et al., 2008).

The study of wear patterns and starch residues on stone artifacts left at nonhuman primate activity sites has helped establish a new framework with which to interpret human archaeological assemblages (Arroyo et al., 2016, 2021; Benito-Calvo et al., 2015; Caruana et al., 2014; Falótico, Spagnoletti, et al., 2017; Mercader et al., 2007; Proffitt, Haslam, et al., 2018). Yet, there is a dearth of equivalent research on perishable tools (Haslam, 2014; Heaton & Pickering, 2006; Luncz, Braun, et al., 2022). Residue studies could be applied to a variety of tools reported to be used to access starchy foods, honey, or animal prey (Fowler & Sommer, 2007; Hernandez-Aguilar et al., 2007; Pruetz & Bertolani, 2007). Many taxa of edible insects have the capacity to yield unique biochemical residues that can be left on the surface of tools, thereby enabling the identification of tools and the target prey (Lesnik, 2018). For instance, termites, which are habitually targeted by wild chimpanzees with the use of plant tools (McGrew, 1992a) have a distinctive carbon isotope signature depending on their diet, ranging from C3 to pure C4 (Lesnik, 2014; Sponheimer et al., 2005). Likewise, the recovery of DNA from discarded artifacts can be used to identify tool users (Stewart et al., 2018) and gather relevant information regarding individual preferences for tool types, frequency of tool site visits, as well as possible maternal influences in tool forms (Lonsdorf et al., 2004). Wear patterns on tool ends can help to clarify the diagnostic features of a tool (Heaton & Pickering, 2006), and help to distinguish materials that have been used as tools from those that have not. For example, wear patterns are particularly useful for distinguishing between hard woods selected and/or modified for use as digging sticks and probes, including those used by humans (Heaton & Pickering, 2006; Nugent, 2006; Sanz & Morgan, 2007). Documenting these signatures, and developing the analytical methods to do so, will not only expand on what we know about the use of ephemeral materials, but will enable their identification, if they preserve, in the archaeological record.

3 | ARCHAEOLOGY BEYOND TECHNOLOGY

So far primate archaeology has largely focused on the study of technological traces. Yet, human archaeology encapsulates the study of all evidence of past people—from their material culture to the organic remains of individuals and the food they have consumed, as well as the physical and chemical traces resulting from their activities. Thus, to truly parallel the breadth of human archaeology and culture, it is paramount that primate archaeology extends toward the investigation of non-technological behaviors which may also leave an archaeological signature. Reports on bark peeling (Lapuente et al., 2020; Nishida, 1976), stone throwing (Kühl et al., 2016), and tree buttress drumming (Babiszewska et al., 2015; McGrew et al., 2003), suggest that these activities may leave conspicuous and durable traces through scarification and the development of use-wear. With the implementation of innovative diagnostic techniques to identify damage on robust wooden implements (Luncz, Braun, et al., 2022), such signatures, under the right taphonomic conditions, could be identifiable in the archaeological record. Contexts such as this have been documented in several sediments near Plio-Pleistocene archaeological sites (Bamford, 2017; Goren-Inbar, Sharon, et al., 2002). Other promising subjects for primate archaeological research include bedding and nest construction (Baldwin et al., 1981; McGrew, 2021; Stewart et al., 2011), well-digging (McGrew et al., 2007; Péter et al., 2022), tortoise smashing (Pika et al., 2019), crab processing (Koops et al., 2019), and underground storage organ processing (Truppa et al., 2019; Figure 3). Similar traces are already well-documented in our more recent history. For example, First Nations communities in British Columbia have been extracting pine cambium as a subsistence resource since at least 1790 CE (Prince, 2001). While the practice is less common today, the process involves stripping the bark off living pine trees leaving visible scars which can remain identifiable for at least 200 years (Prince, 2001). Going further back in time, we find evidence that early *Homo sapiens* used leaf bedding ~77,000 years ago (Wadley et al., 2011), with the earliest evidence of grass bedding dating back to 200,000 years ago following recent discoveries in South Africa (Wadley et al., 2020). This indicates that optimal conditions and particular depositional environments can preserve such traces for very long periods of time. Such results are challenging the widely accepted view that it is impossible to recover traces of similar behaviors prior to the emergence of anatomically modern humans.

Aquatic resources have also been identified in a number of paleolithic deposits from Neanderthal and Middle Stone Age (MSA) shell middens (Will et al., 2019; Zilhão et al., 2020), to ornamental shell beads recovered from MSA sites (Vanhaeren et al., 2013), and 1.95 million years (Ma) old traces of tortoise and fish consumption (Braun et al., 2010). Nevertheless, evidence of aquatic resource exploitation remains extremely rare and is yet to be identified in hominin records prior to 2 Ma. While this may be in part due to preservation bias, research has rarely focused on these resources and the contexts in which they can be found (e.g., ancient coastal environments, flooded habitats). It is also likely that we simply lack the knowledge base to identify them. Thus, studying the signatures and taphonomy of these behaviors in nonhuman primates will help identify similar behaviors in our ancient past (Habermann et al., 2019).

One of the main strengths of primate archaeology is that it provides data that can be directly compared to the hominin record, and there are various techniques that could contribute to that. Dental microwear is one of these techniques. Teeth constitute a direct interface between organisms and their environment (Cuozzo et al., 2012). As such, dental microwear analysis can be used to reconstruct an animal's feeding ecology (Teaford & Glander, 1991; Teaford & Runestad, 1992; Teaford & Walker, 1984), and be used as a comparative model for fossil dentition (McGrew, 2001). But unlike rare and isolated fossil remains, extant primates can help to better understand the interaction between dental microwear and feeding ecology as the ecological context is generally known. Likewise, microwear analysis of the dentition of myrmecophagous mammals, suggests that their faunivory produces a distinct pattern (Strait, 2014), while dust

FIGURE 3 (a) Bark stripping traces produced by chacma baboons (*Papio ursinus*) in Gorongosa National Park, Mozambique (Photo credit: Jana Muschinski); (b) Tree buttress drumming use-wear (outlined in white) created by chimpanzees (*Pan troglodytes verus*) in the Nimba Mountains, Guinea (Photo credit: Maegan A. Fitzgerald); (c) Digging hole left by *Sapajus libidinosus* after USO extraction in Fazenda Boa Vista, Brazil (Photo credit: Valentina Truppa; EthoCebus Project); (d) Discarded crab carcass (circled in white) at a chimpanzee (*Pan troglodytes verus*) crab processing site in the Nimba Mountains, Guinea (Photo credit: Kathelijne Koops).

accumulated on plant foods consumed by wild chimpanzees leaves recognizable tooth wear (Schulz-Kornas et al., 2019). Understanding the intra- and inter-specific variation of tooth wear patterns in nonhuman primates and how this corresponds to their known diets and environment is a crucial first step for reconstructing the paleoecology and diet of extinct hominins (Percher et al., 2018; Ungar et al., 2008).

Stable isotope analysis is becoming the standard in research of primate diets, dietary variability, and habitat use (Crowley, 2012; Phillips & O'Connell, 2016; Sandberg et al., 2012). Biological remains used for isotopic analysis, some recoverable from the archaeological record, include hair, feces, bone, collagen, and enamel (McGrew, 2014; Sponheimer et al., 2009). Because these remains can be collected without habituation of the study groups to researcher presence, stable isotope analysis is increasingly used as a non-invasive method to broaden insights into primate feeding ecology (Crowley et al., 2014; Wessling et al., 2019). To date, stable isotope analyses have been conducted on taxonomically and geographically diverse groups of primates including strepsirrhines in East Africa and Madagascar (Loudon et al., 2007; Schoeninger et al., 1998), platyrrhines in Central and South America (Schoeninger et al., 1997), cercopithecoids in Africa and Asia (Codron et al., 2006; O'Regan et al., 2008), and hominoids in Africa (Schoeninger et al., 1999; Sponheimer et al., 2005). For chimpanzees, which constitute the bulk of published stable isotope data within hominoids, the carbon isotope values have been used to evaluate the degree of canopy cover and the proportion of C_3 versus C_4 diet, while nitrogen isotope values reflect the degree of faunivory (Sandberg et al., 2012; but see also Lüdecke et al., 2022 for new nitrogen isotope applications to hominin diet). Paired with local plant isotopic baselines, this can be used to reveal dietary isotopic signatures across ape populations, chart isotopic landscapes, and be a useful reference for paleodietary reconstructions in fossil hominins and extinct nonhuman primates (Oelze et al., 2016; Wessling et al., 2019).

DNA studies add time-depth and insights on the behavioral history of living primates. Methods of non-invasive genotyping using shed hair, feces, or chewed-up food wadges are currently used to examine paternity, mating patterns, and community structure (Constable et al., 2001; Fontsere et al., 2022; Stewart et al., 2018). They can be employed to estimate the longevity of individual primate communities (Langergraber et al., 2012) and reconstruct past population sizes, interbreeding events, and kin relationships (Constable et al., 2001; de Manuel et al., 2016; Fontsere et al., 2022; Gumert et al., 2019; Prüfer et al., 2012; Santander et al., 2022; Scally et al., 2012). Furthermore, analysis of fecal samples can also reveal the DNA of imperceptible species consumed (i.e., insects), thus, providing a more complete picture of primate diets beyond what is visible to the naked eye (Ozga et al., 2019; Phillips & Lancelotti, 2014; Pickett et al., 2012).

Primate archaeology should also take advantage of the latest archaeological advances. Soil analysis, including the study of biomarkers, diatoms, environmental DNA, and phytoliths, are becoming ever more commonplace in modern human archaeology (Neumann et al., 2016; Salisbury et al., 2022; Stone & Yost, 2020). Combined with micro-archaeology (Salisbury et al., 2022; Weiner, 2010), this research can reveal previously overlooked behavioral traces, and provide greater ecological resolution.

4 | LANDSCAPE ARCHAEOLOGY

In order to fully understand how material records for a nonhuman primate species form, it is necessary to study the species behavior and the resulting physical evidence as part of its ecosystem, which includes the physical environment as well as its interactions with other plants and animals, whether as food sources, competition, or predators. Given that early hominins would have navigated similarly complex, multi-faceted, landscapes (Almeida-Warren et al., 2022; Bobe & Carvalho, 2019; Carvalho & Beardmore-Herd, 2019), establishing these ecological relationships is crucial for reconstructing patterns of landscape use and determining how these may have changed through time. This requires the study of archaeological traces at a landscape scale, in relation to other archaeological assemblages, activity areas, and broader environmental factors such as vegetation composition and distribution, climate, hydrology, and geology (Almeida-Warren et al., 2022).

Such landscape archaeology approaches were introduced to human origins research in the 1970s by Glynn Isaac to better understand why lithic assemblages varied in size and composition, and what this could reveal about early hominin behavior (Foley, 1981; Isaac, 1981b; Isaac & Harris, 1976; Stern, 1991). This research spurred the development of the first models for the interpretation of early hominin lithic assemblages, landscape-use, and resource exploitation strategies (e.g., Behrensmeyer, 2011; Blumenschine et al., 2012; Blumenschine & Peters, 1998; Rogers et al., 1994). Nevertheless, with archaeological evidence almost exclusively composed of time-averaged lithic deposits, the behavioral processes underlying the formation of early hominin sites remain debated (Braun, 2012; Plummer, 2004; Schick & Toth, 2006).

The first nonhuman primate contributions to this research examined the distribution of chimpanzee nests as daily debris-generating activities with potential to elucidate patterns of early hominin landscape use and the origins of human shelter (Hernandez-Aguilar, 2009; Sept, 1992; Stewart et al., 2011). These studies found repetitive reuse of nesting sites, resulting in a patchy, clumped distribution, similar to the distribution of archaeological materials at early hominin sites. Patterns normally associated with social changes, such as food sharing and division of labor (Isaac, 1978), were not necessary to produce such patterns across the landscape. Furthermore, the use of sleeping sites by *Pan* has been proposed to be analogous to the transport of food to tree-shaded places offering refuge to early hominins, and therefore may be a precursor to hominin-specific landscape features such as carcass processing sites (Hernandez-Aguilar, 2009). Thus, the study of chimpanzee "living" archaeological sites across their home ranges provides clues to factors that may have influenced early hominin tool use and discard across the landscape (i.e., niche construction; Stewart et al., 2011).

Subsequent research has uncovered links between nesting locations and a range of ecological parameters such as tree species and canopy architecture, as well as surrounding topography, vegetation types, and fruit availability (Badji et al., 2018; Basabose & Yamagiwa, 2002; Furuichi & Hashimoto, 2004; Hernandez-Aguilar et al., 2013; Hernandez-Aguilar & Reitan, 2020; Ndiaye et al., 2018). Collectively, these findings show that the distribution of nest sites is non-random, but also that their ecological correlates are not universal (Koops et al., 2012; Stewart & Pruetz, 2020).

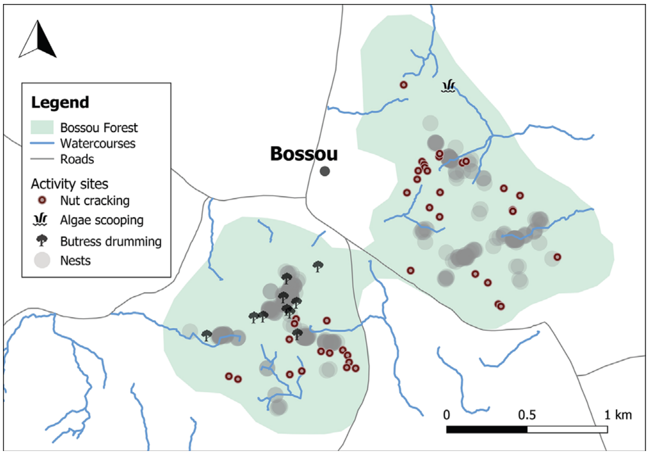

FIGURE 4 Behavioral traces of Bossou chimpanzees (*Pan troglodytes verus*) (Guinea) across the landscape featuring nut-cracking sites, nesting locations, drumming trees, and algae scooping (Map credit: Katarina Almeida-Warren).

More recently, primate archaeology has started to investigate the relationships between ecological factors and the distribution of nonhuman primate stone tool assemblages (Carvalho & McGrew, 2012). Emerging research has found that chimpanzees in Bossou (Guinea) select their nut-cracking sites based on the availability of nut trees, the presence of raw materials, food abundance, and proximity to sleeping sites (Almeida-Warren et al., 2022) (Figure 4). Analogous resources, such as dependable foods, raw materials for stone tool manufacture, and sheltered places, have also been hypothesized to have shaped spatial patterns of early hominin tool-use, being featured in several models of hominin landscape use (Isaac, 1981a; Rogers et al., 1994; Rose & Marshall, 1996; Sept, 2011). One study demonstrated that the technological landscape of Bossou chimpanzees shared affinities with the "favored places" model proposed by Schick (1987), in which hominin tool sites were hypothesized to represent resource rich areas that attracted a variety of activities, with sites being used more frequently and intensively in locations with higher resource abundance (Almeida-Warren et al., 2022). Landscape archaeology approaches have also recently been applied to examine assemblage variability in nut-cracking behaviors by long-tailed macaques in the abandoned Ao Lobi Bay oil palm plantation (Thailand), where assemblage density and composition were found to correlate with the mechanical properties of raw materials and the distribution of food sources (Reeves, Proffitt, Malaivijitnond, et al., 2023). Together, these studies are elucidating the role that behavioral ecology likely played in shaping the early hominin archaeological record (Almeida-Warren et al., 2022; Reeves, Proffitt, Almeida-Warren, et al., 2023).

Other research has integrated the use of agent-based modeling, to examine long standing questions about the transport mechanisms that generated the long-distance displacement of tools from their original source, as described for some Oldowan records (Reeves et al., 2021). Inspired by chimpanzee nut-cracking in the Taï forest (Côte d'Ivoire), this model examined whether long-distance displacement of tools could be produced by repeated chimpanzee-like small-scale (<200 m) transport events. This model has provided a proof-of-concept that under certain ecological conditions, long-distance transport is not necessary to generate landscape-scale archaeological patterns akin to early hominin assemblages and could have simply resulted from short-distance redistribution of tool material over hundreds to thousands of years (Wynn & McGrew, 1989). A recent follow up study has added further detail to these findings, showing that while landscape-scale tool displacement can emerge from a chimpanzee model of tool transport, the number of transport events (and therefore total distance), is contingent on the use-life of the tools themselves (Reeves, Proffitt, Almeida-Warren, et al., 2023). When the simulation replaced chimpanzee pounding tools with hominin cores, characterized by their smaller size and shorter use-life, the average resulting accumulated distance dropped by nearly two thirds. This research has demonstrated that while there are structural similarities between chimpanzee and hominin patterns, long-distance transport may have been of adaptive significance for the establishment of core and flake technology in the genus *Homo* (Reeves, Proffitt, Almeida-Warren, et al., 2023).

Nevertheless, primate archaeology studies remain limited, in that they focus on single aspects of material evidence (e.g., nests, stone tools), missing the opportunity to incorporate other factors which could elucidate the ecological and social dynamics of landscape use (e.g., the use of caves by extant primates as per Pruetz (2007), or chimpanzee biogeography as per Wessling et al., (2020). This should include the spatial and temporal distribution of resources, population sizes, home ranges, and, importantly, non-technological activities (see previous Section 3). Such a holistic landscape approach will require the adaptation of methods from landscape archaeology that can be applicable to living populations with dynamic archaeological contexts. Furthermore, extending this line of research to other technological primates, will help build a broader perspective on the relationships between technology, behavior, and environment across primate species with different evolutionary histories. For example, populations of Burmese long-tailed macaques (*Macaca fascicularis aurea*) that use stone tools for extracting marine resources have been recognized as important models for understanding the role of coastal environments in human evolution (Gumert & Malaivijitnond, 2012). Studying the distribution of marine-processing sites of these primates within the broader ecological and behavioral landscape could provide important insights into the landscape-use patterns and artifact accumulation of coastal-foraging hominin populations (Almeida-Warren & Pascual-Garrido, 2023). This could prove particularly crucial if we aim to test the important paleoanthropological hypothesis regarding a coastal origin for the first hominins and the use of coastal areas during critical periods of environmental variability (Joordens et al., 2019; Kingdon, 2003; but see also Bobe et al., 2020).

The study of extant nonhuman primates also provides an important approach to examine temporal changes in activity patterns and the associated spatial and temporal distribution of behavioral signatures. For many nonhuman primate populations certain tool use practices occur seasonally: termite fishing by chimpanzees at Gombe occurs mainly in the early wet season (van Lawick-Goodall, 1968), while nut cracking by chimpanzees at Bossou is most frequent during the early dry season (Yamakoshi, 1998). Likewise, capuchin nut cracking occurs primarily during the dry season and early wet season (Spagnoletti et al., 2012). Yet, little is known about how these seasonal changes may affect the temporal and spatial distribution of behavioral traces. Similarly, studying populations with different technological repertoires could reveal how the presence or absence of certain behaviors may result in different signatures across the landscape. The diversity of Early Stone Age assemblages, combined with the spatio-temporal overlap of several hominin species, is providing increasing evidence that the earliest technological industries are likely to be the product of multiple hominin species (Braun, 2013). Nevertheless, it has not yet been possible to attribute different archaeological signatures to the species that produced them. Primate archaeology continues to be in a unique position to offer new insights into the full scale of hominin cultural diversity and potentially species-specific archaeological signatures.

Further integration of longitudinal ecological and behavioral data from long-term study sites remains another critical step in extending the scope of nonhuman primate archaeological research. Environmental variability played a leading role in the evolution of early hominin technologies and diversity (Bobe & Carvalho, 2019; Potts, 2012; Potts et al., 2020). Similarly, local habitat variability, as well as environmental change, have been proposed to affect the breadth, development, and loss of technical and cultural behaviors in nonhuman primates (Hockings et al., 2015; Kalan et al., 2020; Luncz et al., 2017). Investigating long-term spatio-temporal patterns of tool use, together with social, behavioral, and ecological changes, will help identify the mechanisms behind variations in landscape use and the spatial distribution of behavioral signatures over time (Kalan et al., 2020).

5 | PRIMATE CULTURAL HERITAGE

The study of nonhuman primate material culture began more than six decades ago when Jane Goodall first observed the manufacture and use of tools by wild chimpanzees to fish for termites at Gombe Stream National Park in Tanzania (Goodall, 1964). Since then, field studies conducted over decades in east, west, and central Africa have yielded impressive findings in chimpanzee cultural objects, revealing regional and local variations argued to mirror culturally transmitted practices in humans (Boesch et al., 2020; McGrew, 1992b; Whiten et al., 1999). With the establishment of new field sites, tool use behaviors previously unknown for certain communities such as ant fishing by Issa chimpanzees living in Tanzania (Wondra et al., 2016), as well as new tool types, such as the brush-tipped fluid probes (Lapuente et al., 2017), algae fishing tools (Boesch et al., 2017), and spears to skewer bushbabies (*Galago senegalensis*) (Pruetz & Bertolani, 2007), continue to be revealed. Variation in artifacts across populations ranges from environmental to culturally related, allowing the distinction of communities and their practices based on the artifacts alone (Bessa et al., 2022; Hicks et al., 2020; Luncz et al., 2012, 2019; Pascual-Garrido, 2019; Sanz et al., 2014). In the past two decades, with the advent of primate archaeology, we have also learned that chimpanzees not only leave artifacts behind, but that all technological primates create long-lasting records of material culture across the landscape as a product of their daily activities, and that they have been doing so for thousands of years (Falótico et al., 2019; Haslam et al., 2017; Mercader et al., 2007). If we accept that chimpanzees have culture, then their material records and intangible cultural attributes can, by definition, only be termed cultural heritage.

Cultural considerations are becoming even more prevalent in discussions surrounding animal conservation (Carvalho et al., 2022), and the latest conservation plan for western chimpanzees has introduced an agenda for establishing a baseline of cultural diversity to better inform conservation strategies (IUCN, 2020).

Nevertheless, while nonhuman primate material culture is widely recognized and has been well studied for decades (Koops et al., 2018; McGrew, 1992a; van Schaik et al., 2003), little effort has been made to curate and preserve nonhuman primate artifacts and their legacy for future generations, bar a few exceptions (e.g., the chimpanzee plant artifacts curated for public display by Norman McBeath at the Scottish National Museum, Edinburgh, and the Oxford University Natural History Museum, Oxford). Many nonhuman primates are under severe threat from human activities (Estrada et al., 2017). Their tangible cultural materials resulting from daily activities are therefore in immediate need of preservation before they disappear forever. If we lose them, we will not only lose a critical resource to understand our past, but also erase a large part of our rich and diverse primate heritage. As such, primatologists should liaison with museums and other authorities (including those in countries with nonhuman primate populations) to ensure the proper curation of primate tools and design of corresponding exhibitions. Primatologists would also benefit from dialogues with heritage experts in archaeology to better integrate culture and concepts of heritage in primate conservation. It is our duty, now more than ever, to document and preserve the sites, practices, and artifacts of our extended primate family.

6 | CONCLUSION

We have seen the field of primate archaeology flourish during the last 15 years. We now have detailed records of stone tool use behaviors and a recognizable and dated archaeological record of three extant nonhuman technological primates: chimpanzees, capuchins, and long-tailed macaques. These records have provided valuable comparative data on our understanding of human technological evolution (Carvalho & Almeida-Warren, 2019; Haslam et al., 2017). One of the reasons for expanding archaeology to nonhuman primates was the need to recognize that archaeological assemblages do not pertain exclusively to humans. This acknowledgment allowed us to start investigating the different signatures left by human and nonhuman technological populations. This acknowledgment has allowed investigations of the varying signatures left by nonhuman technological primate populations and has paved the way for ground-breaking studies that have pushed the boundaries of the archaeological *status quo*. Because of primate archaeology, ideas about a nonhuman origin for ancient archaeological records, previously attributed to humans, have begun to be taken seriously after important discoveries focused on capuchin monkeys (Agnolín & Agnolín, 2022; Proffitt et al., 2016).

Given that technology constitutes only one aspect of nonhuman primate lives, it is therefore necessary to explore to what extent other non-technological activities such as non-tool aided feeding, traveling, and social behaviors or ritual displays, may leave traces that could be detected in the archaeological record. This perspective is important not only for understanding chronological changes in activity patterns and the associated spatial and temporal distribution of behavioral signatures, but also because it would be naïve to assume that only traces resulting from the use of non-ephemeral technologies can be preserved in the past records. Extinct hominins have left valuable albeit fragmentary behavioral evidence in the form of preserved artifacts. Records from the use of ephemeral technologies and other non-technological activities continue to be virtually absent in the ancient archaeological record. However, their prevalence in nonhuman primates suggests that these may have constituted the majority of early hominin everyday life. Primate archaeology is therefore in a unique position to build the foundations for the future identification of these activities in the archaeological record. Developing a more “inclusive” primate archaeology, that includes not only technological behaviors and activities, will not only benefit the study of primate evolution in its own right, but will aid conservation efforts by increasing our understanding of changes in primate-environment interactions over time.

AUTHOR CONTRIBUTIONS

Alejandra Pascual-Garrido: Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Susana Carvalho:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal). **Katarina Almeida-Warren:** Conceptualization (equal); writing – original draft (equal); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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