JASs Journal of Anthropological Sciences Open Access
Research articles Vol. 104 (2026), pp. 1 - 24 e-pub ahead of print doi. 10.4436/JASS.10401

Reexploring drivers of technological variation through the complex landscapes of cultural evolution

James Clark[1,2], **Lucy Timbrell**[3,4], **Sarah E. Paris**[2,5] & **Gonzalo J. Linares-Matás**[2,6]

1) *Corpus Christi College, University of Cambridge, Trumpington St., Cambridge, CB2 1RH, UK*

2) *McDonald Institute for Archaeological Research, University of Cambridge, Downing St., Cambridge, CB2 3ER, UK*
e-mail: jc2012@cam.ac.uk

3) *Human Palaeosystems Group, Max Planck Institute of Geoanthropology, Kahlaische Str. 10, 07745, Jena, Germany. https://orcid.org/0000-0003-1229-554X*

4) *Department of Archaeology, Classics and Egyptology, University of Liverpool, 12-14 Abercromby Square, Liverpool, L69 7WY, UK*

5) *Palaeoanthropology, Institute for Archaeological Sciences, Eberhard Karls University of Tübingen, Tübingen, Germany. https://orcid.org/0000-0002-7447-8766*

6) *Emmanuel College, University of Cambridge, St Andrew's St., Cambridge, CB2 3AP, UK. https://orcid.org/0000-0002-0429-7636*

Summary - *Despite a number of issues in its collation, the dataset published by Oswalt et al. (1976) remains a key resource for operationalising cross-cultural technological variability and understanding the socioecological drivers of cultural change in small-scale societies. At the same time, however, it has not been comprehensively explored using up-to-date contextual metrics of subsistence, climate, and demographic structure in each population. In this paper, we present a novel evolutionary framework for understanding technological change in both modern and past populations, according to the complex fitness landscapes of cultural evolution present in different environments. We then use this framework as a lens to explore the drivers of toolkit composition and complexity among hunter-gatherer populations to assess how they relate to the adoption of particular behavioural strategies. We suggest a hierarchy of interlinked influences on the nature of technology: resource distributions exert the most proximate influence on their character, but demography (especially the size of seasonally-aggregated groups) and climate (especially seasonality and inter-annual predictability) are themselves critical in constraining technological possibilities. Finally, we argue that landscape knowledge is crucial in driving access over time to the highest-return technological strategies that are possible in any given environmental context.*

Keywords - *Technological complexity, Cultural fitness landscapes, Behavioural ecology, Demography, Seasonality and inter-annual variability, Landscape knowledge.*

Introduction

Understanding how social and environmental systems influence cultural dynamics in modern and past hunter-gatherer populations remains a major focus of research in archaeological and anthropological studies. Previous work has highlighted that cultural diversity in human societies is the product of multiple interacting processes, incorporating both environmental conditions and traditional knowledge. Conscious formation of identity and long-term tradition are suggested to play an important role in non-subsistence based activities and material culture, such as musical instruments (Wengrow and Graeber 2022; Padilla-Iglesias et al. 2024), while ecological patterns likely play a larger role in driving variation in foraging toolkits (Collard et al.

2006, 2011). While these domains are interrelated, here we attempt to explore technological patterns in food-getting technology readily explained by socioecological correlates.

There is substantial debate surrounding measurement of technological variability, and particularly its 'complexity'. Oswalt et al. (1976) pioneered an attempt to quantify these concepts in ethnographic societies, developing the concept of foraging tool "technounits". These "technounits" refer to the number of individual components combined in a single "subsistant" (foraging tool), explicitly operationalising 'complexity' through modularity. This approach has received varied criticisms since its publication, including of the dataset itself, the way it conceptualises "complexity" (e.g. Hoffecker and Hoffecker 2018), its applicability to the archaeological record (e.g. Perreault et al. 2013), and its underappreciation of "complexity" in certain tool sets.

Nonetheless, authors have repeatedly returned to the Oswalt et al. (1976) dataset (Torrence 1983; Shott 1986; Collard et al. 2005; Read 2008; Hoffecker and Hoffecker 2018), because it remains one of the most useful cross-cultural datasets for understanding hunter-gatherer behavioural variability. Past examinations have extensively used regression models to assess the relative influence of both demography and climate on technological complexity and have been used to support the primacy of both population size (e.g. Kline and Boyd 2010) and ecological risk (e.g. Collard et al. 2005, 2011, 2013; Read 2008, 2012). At the same time, however, without a careful consideration of how variables might be horizontally, or vertically related, such regression models risk false negatives by controlling for mediating or moderating relationships—especially with the small dataset of Oswalt et al. (1976). Other studies have utilised both modelling and experimental approaches to this question (e.g. Henrich 2004; Grove 2009; Powell et al. 2009; Derex et al. 2013; Kempe and Mesoudi 2014; Derex and Boyd 2016), but some argue these often involve unrealistic assumptions about the nature of human populations (e.g. Vaesen et al. 2016; Read and Andersson 2020).

These debates highlight the importance of a solid interpretative framework for contextualising discussions of complexity, as well as the crucial role played by selecting the appropriate statistical tools. We argue that a reassessment of Oswalt et al.'s (1976) dataset through the lens of modern cultural evolutionary theory can provide greater interpretative power than ever before, alongside more accurate covariates. In this paper, we present a novel evolutionary framework applicable to both the archaeological record and modern populations (Clark and Linares-Matás 2024; Timbrell 2024). This centres on the idea of complex adaptive landscapes of cultural evolution, and the different technological strategies that can be deployed in response to socioecological factors. We then present an updated synthesis of the technological data from Oswalt et al. (1976), with corresponding subsistence, climatic, and demographic data derived from the d-Place database (Kirby et al. 2016). Our work highlights new interpretations of the dataset, with a diverse range of hierarchically-related factors influencing the character and complexity of the toolkit.

Evolutionary framework: the complex landscapes of cultural evolution

Theoretical basis

We use the concept of 'complex landscapes of evolution' to explore the cultural response(s) of populations to ecological and demographic change (Clark and Linares-Matás 2024; Timbrell 2024). Key definitions related to this concept are shown in Table 1. Developed originally in genetics, this framework was proposed by Wright (1932) as part of his 'shifting balance theory' to capture how populations that are confronted with various local fitness states, varying dynamically through space and time, adapt to local optima. These may or may not be the same as the global fitness optima across the space of possible adaptations. Once a population has begun to adopt a specific trait, it may then be difficult to shift to another trait ('peak'), even

***Tab. 1** - Definitions of key concepts related to the 'complex landscapes of cultural evolution'.*

CONCEPT	DEFINITION
Fitness Landscape	A hypothetical space that models the range of possible genotypic, phenotypic, or cultural traits for a given population, as well as the relative fitness returns of those traits.
Behaviour Space	The range of all possible behaviours available to a population
Behavioural Peaks	Individual behavioural strategies that confer higher than average fitness within the behaviour space
Local Optima	Behavioural strategies that are confer higher than average fitness within a given environment but are not the strategy returning the highest possible fitness
Global Optima	The behavioural strategy with the highest possible fitness returns for a given environment
Behavioural Troughs	Individual behavioural strategies that confer lower than average fitness within the behaviour space

if it provides greater fitness. This constitutes a form of phylogenetic constraint, because moving between peaks often involves a decrease in fitness via a fitness valley, which selection acts against. Abrupt demographic or ecological changes can cause disruption to the nature of the fitness landscape, perhaps leading to redundancy of a local optimum to which a population has adapted. These "flattened" landscapes can lead a population to extinction, or dramatic biological change. Migrants that come into contact with other populations may also help move populations from lower to higher fitness peaks through the exploration of genotypic space.

Recently, archaeological studies have adopted the idea of 'complex landscapes of evolution' to describe analogous cultural phenomena in relation to diverse social and physical environments (Kuhn 2006; Lombard and Parsons 2011; Timbrell 2024). In this framework, the ecological characteristics of an environment shape the range of potential behavioural responses viable to a population, with the rate of adaptation to local behavioural peaks influenced by a number of factors. For example, increases in population size (Powell et al. 2009; Henrich et al. 2016), density (Grove 2016), and interconnectivity (Powell et al. 2009; Grove 2016, 2018) have all been proposed to facilitate cultural change, as has environmental risk (Torrence 2001; Collard et al. 2011, 2013). As pointed out by Grove (2018), there is no reason to treat these as mutually exclusive, as they can each independently influence the fitness landscape, as can their interaction.

We suggest that the 'complex (cultural) landscapes of evolution' framework can be complemented by human behavioural ecology, in which individuals make foraging decisions to maximise a particular currency variable (e.g. nutritional return rates or social prestige), according to their relative costs and benefits, and the relevant constraints (Hawkes et al. 1982; Foley 1985; Stephens and Krebs 1986; Winterhalder and Smith 1992; Ferraro 2007; Kelly 2013; Linares-Matás and Clark 2022). At the most proximate level, hunter-gatherers always respond to resource distributions (Clark and Linares-Matás 2024), with the number of adaptive solutions (i.e. peaks) within 'behaviour space' likely associated with the carrying capacity of the environment—both resource density *and* diversity (Lieberman 1993; Grove 2018). Building upon the cultural evolutionary model of Deffner and Kandler (2019), we propose that the height of peaks in a cultural fitness landscape can be defined according to how *specialised* adaptive solutions (i.e. a toolkit) are for a specific environment. Specialised toolkits tend to have tools with high 'fit' to individual activities, producing the greatest returns for those tasks. Often these tools are more complex, as they must be highly curated to perform well. Conversely, generalised tools can be used in a diversity of activities, but their returns in each task are lower than a specialised tool form. These may facilitate the occupation of lower fitness peaks that are less sensitive to change. Deffner and Kandler (2019) suggest that specialised toolkits should be favoured in stable environments, whereas environmental shocks should be followed by an increase in technological generalisation—though specialisation should then return in the face of renewed stability.

This framework has important implications for how we consider ecological risk as a driver of technological change. In environments with stable (predictable) resources year-on-year, there is time to specialise to the highest adaptive peaks with the greatest returns. The pressure towards such adaptation is exacerbated in environments with low resource diversity, as isolated peaks can form in an otherwise smooth fitness landscape—the consequences of failure are much higher when there are fewer possible resource bases to which adaptation can occur. This suggests resource risk can support more complex toolkits and faster adaptation. At the same time, when inter-annual variability is high, the predictability of returns from specialised strategies in any given year is lowered. Generalised strategies, however, show continued predictability as they can continue to provide returns from a wider diversity of resources, even when one resource is less available. Demographic variables relate to these strategies as they influence the extent and scale of exchange in technological know-how, therefore determining the total amount of information stored in a population and the capacity for innovation (Whallon 2006). Together, these factors condition the exploration of possible 'behaviour space' within the fitness landscape, and how populations subsequently adopt certain cultural traits (Timbrell 2024). For example, Lombard and Parsons (2011) suggest that the loss of bow and arrow technology in South Africa following the Howiesons Poort Middle Stone Age industry likely represents a period of demographic or ecological disruption, with populations responding by decreasing technological investment as part of a distinct behavioural strategy.

These variables share a bidirectional influence on "landscape knowledge", that is, the extent to which a population is aware of the availability, distribution, and predictability of individual resources within their unique range. This includes information regarding the spatial and temporal distributions of specific resources and, if applicable, their nutritional returns, harvesting requirements, and external processing requirements (Clark and Linares-Matás 2020, 2023). The ability to adapt to significant ecological risk reflects an understanding that the behavioural solutions available in a given environment are limited, as well as an expansive knowledge of the available foodstuffs and how these can be best accessed over time and space, which is dependent on knowledge-sharing within and between populations. Previously, we have argued that high levels of accumulated landscape knowledge is a critical baseline for increases in technological complexity, as it is the mechanism through which returns on further investment become more predictable (Clark and Linares-Matás 2020, 2023, 2024). Substantial technological investment without knowledge of the landscape through time would make populations highly susceptible to falling into a 'fitness valley', whereby behavioural solutions that once incurred high fitness become maladaptive.

Empirical predictions

Here, we formulate testable hypotheses through which to assess the Oswalt et al. (1976) dataset:

1) At any given moment, environmental conditions shape an ecosystem's resource distribution, and therefore the adaptive landscape for technological response. Where there are fewer peaks available in the fitness landscape, the risk of failure in resource acquisition is higher, placing pressure on adaptation towards a fewer number of viable strategies. There is a greater diversity of possible behavioural responses in areas with greater resource density and diversity.

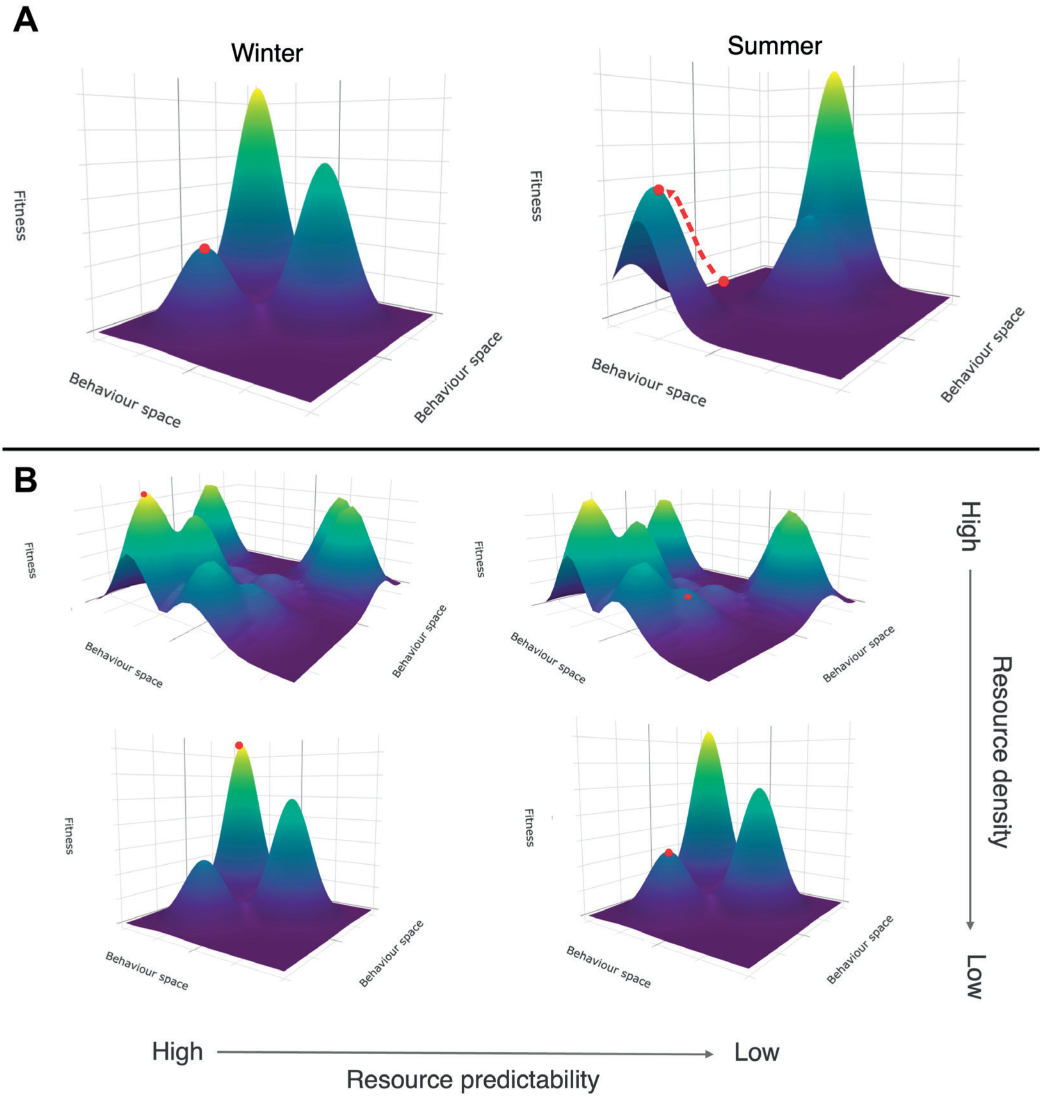

***Fig. 1** - Depiction of the 'Cultural landscapes of evolution' model in response to seasonal and inter-annual change. The figures show n-dimensional 'behaviour space' covering the range of potential behavioural responses, with peaks in the landscape where individual strategies would constitute increased fitness. The colour gradient is to enhance legibility of the relative height of peaks. Figure 1A: Hypothetical seasonal switching between lower fitness adaptive peaks. Figure 1B: Depiction of how technological fitness is linked to resource predictability and availability.*

2) The potential behavioural strategies with greatest fitness usually result from optimal exploitation of higher-value resources, which are, however, more likely to fluctuate in availability by season (Clark and Linares-Matás 2023). Highly seasonal environments lead to a particularly dynamic fitness landscape, with local optima changing between

seasons. This may necessitate switching of adaptive optima within years, with groups most likely to adopt technological solutions for each season closest to their existing knowledge. In the example of Figure 1A, the fitness landscape changes in this way between seasons, so that peaks available at one point in the year do not represent increased fitness across the year. Toolkits adapted to a local optimum in winter (red point) therefore do not incur similar levels of fitness in summer and fall into a fitness valley. This leads to technological change towards a new adaptive peak (red dotted line). Lower seasonality would alternatively lead to a relatively stable fitness landscape, with groups retaining solutions that are adaptive throughout the year.

3) High inter-annual predictability facilitates investment in technologies that maintain high fitness each year. We hypothesise that predictable environments with lower resource density are where the selection pressure for highly specialised and adapted technological responses will be felt greatest. This is depicted in Figure 1B, where the fitness landscape changes according to both resource density and predictability. Resource density determines the number of different adaptive peaks, while resource predictability determines the differential stability of these peaks through time, whereby high peaks are much less stable between years than lower peaks that focus on more widely available resources. The highest peaks with the greatest fitness should be occupied in resource predictable environments, with a greater range of options when there is high resource density. When inter-annual predictability is low, however, there is repeated reconfiguration of peaks, thus making it maladaptive to invest in highly complex solutions due to the risk of suddenly lowered returns, and entry to a fitness valley. Groups in unpredictable environments should, therefore, develop more generalised technologies to occupy a more stable set of adaptive bases, even if that entails not reaching the highest levels of return.

4) The structure of populations influences the technological response of hunter-gatherers by facilitating or constraining exploration of 'behaviour space'. We propose that populations at higher density, higher mobility, and/or higher interconnectivity have higher capacity for innovation (Powell et al. 2009; Grove 2018), facilitating the adoption of 'complex' technological solutions at higher fitness peaks in stable periods, or movement between peaks after environmental change. Conversely, groups with lower density, mobility, and/or interconnectivity may be less able to respond to changes in the fitness landscape, and thus may have less complex, more generalised, technology.

Materials and Methods

Oswalt et al.'s (1976) dataset

Population sample. The dataset of hunter-gatherers compiled by Oswalt et al. (1976) incorporated four populations from "desert", "tropics", "temperate", "arctic", and "subarctic" biogeographic zones. The resulting subset of 20 populations is shown in Table 2, with the total dataset and discussion of its limitations included as Supplementary Information. A further distinction was made between "desert" to "tropics" populations on one hand and "temperate" to "arctic" ones on the other, on the basis of perceived similarities in temperature and seasonality regimes; the latter being cooler and more seasonal. We also note that Oswalt et al. (1976) does not include data related to material transport, which is likely to have influenced the nature of technological adaptation and landscape use (see Supplementary Information). It is likely having such data would add an interesting variable to the different analyses presented here, but it would not change the individual bivariate relationships presented, nor the challenges of multivariate analyses with the present dataset (see section "Multivariate analyses").

Technological variables. Oswalt et al. (1976) quantified technology in each population according to the overall number of tools ("subsistants"),

Tab. 2 - Summary of hunter-gatherer populations collated by Oswalt et al. (1976) and further analysed here.

SOCIETY	LATITUDE	LONGITUDE	HABITAT CLASS (OSWALT et al. 1976)	NUMBER OF SUBSISTANTS	MEAN NUMBER OF TECHNOUNITS
SV Paiute (Kidutokado)	41.50	-120.06	Desert	39	2.49
Aranda	-23.7	133.76	Desert	16	2.63
Naron	-21.64	21.61	Desert	12	3.33
OV Paiute (Mono Lake)	38.11	-118.45	Desert	28	3.82
Tiwi	-11.59	130.87	Tropics	11	1.27
Ingura (Anindilyagwa)	-14.00	136.62	Tropics	13	2.46
Chenchu	16.25	78.97	Tropics	20	2.75
Andamanese	13.32	92.89	Tropics	11	4.64
Tasmanians	-41.38	145.21	Temperate	11	1.36
Klamath	42.62	-121.50	Temperate	43	3.51
Tlingit	57.00	-133.59	Temperate	28	4.32
Twana	47.55	-123.16	Temperate	48	4.94
Caribou Inuit	64.33	-96.20	Subarctic	34	3.47
Nabesna	63.44	-143.12	Subarctic	25	4.2
Ingalik (Deg Xit'an)	61.82	-157.75	Subarctic	55	5.38
Tanaina (Dena'ina)	61.74	-150.45	Subarctic	40	5.60
Copper Inuit	68.58	-106.61	Arctic	27	4.52
Iglulik Inuit	69.45	-81.51	Arctic	42	5.36
Tareumiut	71.24	-156.78	Arctic	35	5.86
Angmagsalik (Tasiilaq)	65.64	-37.64	Arctic	33	6.12

their complexity (see below), and their typological assignment. This latter variable represents a categorical distinction between "instruments" (hand-manipulated tools), "weapons" (designed to maim or kill edible species), "tended facilities" (constraints on species' movement that require people to be present), and "untended facilities" ('constraints on species' movement that do not require people to be present). Instruments were broadly related to acquisition of stationary foodstuffs (mostly plants, but also shellfish and other stationary creatures), while each of the other three categories were broadly associated with the harvest of mobile animals and fishes (Oswalt et al. 1976).

Oswalt et al. (1976) define tool "complexity" according to the number distinct material components of the artefact ("technounits"), as well as a capacity to change state (attached-detached, open-closed) during use. We chose not to use the latter measure, nor the related metric of Hoffecker and Hoffecker (2018)—the number and proportion of multiple-state artefacts—for the following reasons. First of all, the measures have only a binary set of outcomes, which may mask how complex tools are in relation to each other. Secondly, the raw number of multiple-state artefacts as the marker of complexity used by Hoffecker and Hoffecker (2018) will inevitably correlate with the overall number of tools in the toolkit (r = 0.784, p < 0.001 amongst the populations they examine that are also present in the Oswalt et al. [1976] dataset). Thus the raw number of these artefacts does not produce a straightforward measure of their complexity. Finally, when you use the proportion of multiple-state artefacts in an assemblage, there is still a substantial association with the average number of technounits (r = 0.697, p < 0.001) as defined by Oswalt et al. (1976). Therefore, as Hoffecker and Hoffecker (2018) themselves acknowledge, the two complexity metrics are broadly comparable.

Population and climatic variables. Data regarding the diets, demography, and environments of each population were collated from Binford (2001) through d-Place (Kirby et al. 2016). Demographic variables collected were: population density, the distance moved in a year, the number of moves in a year, and the maximum size of aggregated camps or villages. Following Grove et al. (2023), we also calculated a distance/frequency index (distance moved in a year/number of moves), referred to as the DFI. The corresponding environmental variables studied were: mean monthly precipitation, mean monthly temperature, mean monthly net primary productivity (NPP), monthly precipitation variance, monthly temperature variance, monthly NPP variance, precipitation predictability, temperature predictability, and NPP predictability. The predictability values are calculated from Colwell's (1974) models of inter-annual variability, which combine "constancy" (how stable a variable that is broadly invariant within a year is between years) and "contingency" (how stable a variable that is seasonally distributed is between years). These are therefore explicitly measures of *temporal* predictability in resource availability.

Oswalt et al. (1976) provide data on the relative dietary contributions of "immobile", "terrestrial mobile", and "aquatic mobile" foodstuffs in each society. The reason for these divisions was that immobile foodstuffs were thought to have a common technological basis (instruments), while the complexity of the remaining tool categories (weapons, tended facilities, and untended facilities) was thought to be higher when exploiting aquatic resources (fish or marine mammals). While these dietary estimates were declared valid for Inuit groups, they were described as "reasonable guesses" for the other populations in the dataset, and so are not considered accurate enough here. Instead, using d-Place (Kirby et al. 2016), we have incorporated Binford's (2001) measurements of "gathering", "hunting", and "fishing" as percentage dietary contributions. It is important to note that these metrics are not the same as Oswalt et al.'s (1976) categories, which, for example, grouped together plants and stationary animals as "immobile" foodstuffs. Nonetheless, the metrics are more or less comparable, with correlations between the "immobile" and "gathering" (r = 0.856, p < 0.001), "terrestrial mobile" and "hunting" (r = 0.504, p = 0.023), and "aquatic mobile" and "fishing" (r = 0.760, p < 0.001) variables all highly significant.

Data analysis and availability

All analyses were carried out in RStudio 2023.12.1.402 running R 4.3.3 (Posit Team 2023; R Core Team 2024). As a result of the risk of false negatives described in the introduction, we carried out our analysis in two stages. The first involved a series of bivariate Pearson's Correlation Coefficients using base "stats" commands, alongside some partial correlations carried out using the package "ppcor" (Kim 2015). We explicitly chose to start with these simple tests to identify variable associations without *a priori* assumptions of outcome, and to ensure variables were not ruled out from our discussion by controlling for related variables. Subsequently, we used significant predictors of toolkit size and complexity as inputs to a path analysis which uses multiple regression to test a specified hierarchical relationship between variables. According to the logic of the model we presented in section "Evolutionary framework: the complex landscapes of cultural evolution",

Tab. 3 - Relationships between different technological variables in the dataset. Instr. = Instruments, TUs = Technounits, Weap. = Weapons, TF = Tended Facilities, UF = Untended Facilities. $^\dagger p<0.1$, $*p<0.05$, $**p<0.01$, $***p<0.001$. NS = Not Significant.

VARIABLE	%INSTR.	MEAN INSTR. TUS	%WEAP.	MEAN WEAP. TUS	%TF	MEAN TF TUS	%UF	MEAN UF TUS	TOTAL N
%INSTR.	—	—	—	—	—	—	—	—	—
MEAN INSTR. TUS	NS	—	—	—	—	—	—	—	—
%WEAP.	NS	NS	—	—	—	—	—	—	—
MEAN WEAP. TUS	NS	**0.538***	NS	—	—	—	—	—	—
%TF	NS	NS	**-0.730*****	NS	—	—	—	—	—
MEAN TF TUS	NS	NS	NS	0.437†	NS	—	—	—	—
%UF	**-0.737*****	NS	NS	NS	NS	**0.633****	—	—	—
MEAN UF TUS	-NS	NS	NS	0.431†	NS	**0.548***	**0.627****	—	—
TOTAL N	**-0.629****	NS	NS	NS	NS	**0.560****	**0.665****	**0.547***	—
MEAN TOTAL TUS	**-0.593****	**0.467***	NS	**0.841*****	NS	**0.710*****	**0.547***	**0.738*****	**0.625****

climatic variables were considered the most ultimate drivers of technological characteristics, with demography and diet also a function of climate (see Figure S7). A full description of the procedure can be seen in the Supplementary Information. All figures were produced using the package “ggplot2” (Wickham 2016). All data are available as a supplementary file to this manuscript.

Results

Summary of dataset

There is enormous variability between populations in the proportion of each of Oswalt et al.’s (1976) tool types, as illustrated in Figure S4. Each population displays some deployment of instruments, weapons, and tended facilities, while untended facilities are absent amongst the Andamanese, Chenchu, and Tiwi. Instruments are notably rare among the Tareumiut and Nabesna, but are broadly uncommon in arctic and subarctic populations. Instruments are also the least (or joint least) complex tool type by average technounits in 14/20 populations, but are the most complex in 2 of the remaining 6 (Figure S5). In 10 populations, weapons are the most complex tool type, compared to untended facilities in 7, and tended facilities in 1. Descriptions of dietary composition, demography, and climatic context for each population, as well as the relationships between these variables, are shown in the Supplementary Information.

Technological diversity and complexity

Relationships between the numbers of each tool type involved in food acquisition and their average number of technounits from Oswalt et al. (1976) are displayed in Table 3, where p<0.1 (full details can be seen in Table S2). We find a positive relationship between the absolute number of foraging tools in the cultural repertoire and the

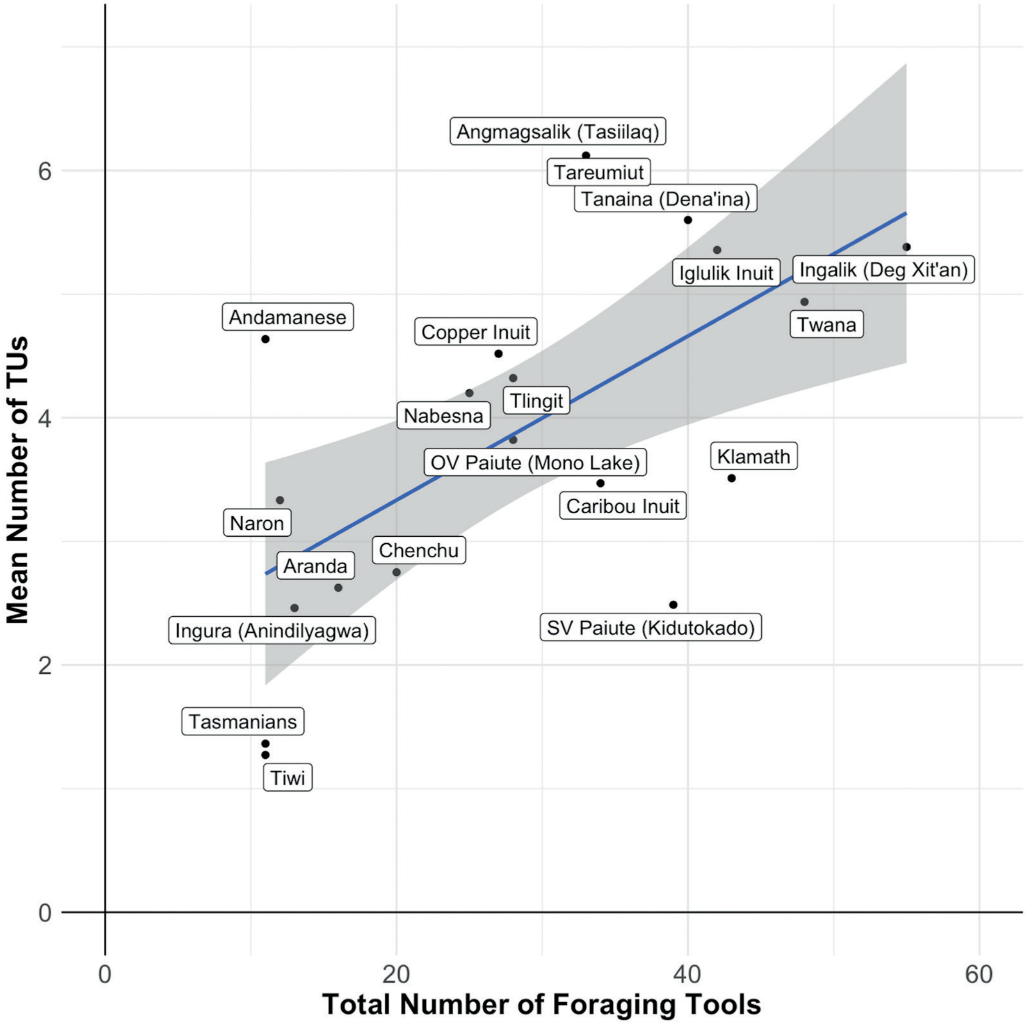

***Fig. 2** - Relationship between number of tools in the foraging toolkit and the mean number of TUs for each tool.*

average number of technounits for each of those tools across societies (r = 0.625, p = 0.003). This is shown in Figure 2. The relationship is similar to Oswalt et al.'s (1976) documented relationship between the *total* number of technounits in an assemblage and the number of foraging tools, but the number of technounits was not standardised by the size of the toolkit.

Table 3 shows that overall toolkit complexity is associated with a reduced proportion of instruments and an increased proportion of untended facilities, as well as increased complexity within each of the four tool categories (especially among weapons, tended facilities, and untended facilities). Complexity of instruments is associated with the complexity of weapons but not of either type of facility, with the average number of technounits within weapons showing a slight influence on the number for each form of facility. The complexity of tended and untended facilities is clearly

***Tab. 4** - Relationships between technological variables and dietary components. TUs = Technounits, TF = Tended Facilities.* $^{\dagger}p<0.1$, $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$. *NS = Not Significant.*

VARIABLE	% GATHERING	% HUNTING	% FISHING
% Instruments	0.744***	NS	-0.589(0.006)**
Mean TF TUs	-0.446*	NS	NS
% Untended Facilities	-0.647**	NS	0.409†
Total n	-0.579**	NS	0.439†
Mean Total TUs	-0.525*	NS	0.481*

related, while the complexity of both tended and untended facilities also clearly increases when there are more untended facilities being deployed. These data suggest that more closely related tool types may have more transferable knowledge that increases the complexity of each form.

An increased total number of tools in the toolkit is related to a lower proportion of instruments, an increased number of untended facilities, and more complex tended and untended facilities. The proportion of tended facilities is clearly negatively associated with the proportion of weapons, suggesting a trade-off in technological strategies, which is also seen in the negative relationship between the proportion of instruments and the proportion of untended facilities.

Diet and technology

The notable relationships between dietary variables and Oswalt et al.'s (1976) technological variables are shown in Table 4, with the full results shown in Table S3. The results suggest that, overall, increases in the proportion of gathering reduce the number of tools in the toolkit, as well as their average complexity, whereas increases in fishing produce a greater total number of tools, and a more complex toolkit. Increases in gathering significantly increase the proportion of instruments in the assemblage (which are significantly decreased by fishing), decrease the proportion of untended facilities (which are increased by fishing), and decrease the complexity of tended facilities. Hunting has no relationship with the character of the toolkit. These data reaffirm that instruments are most closely related to gathering behaviours, and are perhaps preferred when plant availability is greatest. Other technological behaviours are less clearly associated with hunting and fishing, probably because both are variously responsible for the nature of the other tool categories in different populations.

Demography and technology

The notable relationships between demographic and technological variables are shown in Table 5, with full information shown in Table S4. Population density is associated with an increased proportion of instruments in the assemblage—likely because both are supported by environments with increased plant availability—and a decrease in the proportion of untended facilities—probably due to an increase in hunting and especially fishing in areas where the environment does not support plant productivity. Instruments are also complex where populations are more dense. Increases in DFI are associated with a reduced proportion of instruments and an increased proportion of untended facilities, which are similarly explained: fewer moves of greater distance are made in low productivity environments where plant distributions are restricted, with more hunting and fishing instead required. Moreover, groups that practise lower residential mobility (and therefore have higher DFI) may be more likely to engage in the provisioning of places (*sensu* Clark and Barton 2017; see also Kuhn 1992) through untended facilities monitored by logistical task groups deployed from residential

Tab. 5 - Relationships between technological variables and demographic information. TUs = Technounits, TF = Tended facilities, UF = Untended facilities.†p<0.1, *p<0.05, **p<0.01, ***p<0.001. NS = Not Significant.

VARIABLE	**LOG (POP. DENSITY)**	**LOG (YEARLY DISTANCE)**	**YEARLY CAMP MOVES**	**DFI**	**LOG (MAXIMUM AGGREGATED SETTLEMENT)**
% Instruments	**0.661****	NS	NS	**-0.635****	-0.407†
Mean Instrument TUs	**-0.453***	NS	NS	NS	NS
% Tended Facilities	NS	0.393†	NS	NS	NS
Mean TF TUs	NS	NS	NS	NS	**0.654****
% Untended Facilities	**-0.546***	NS	NS	**0.493***	0.413†
Mean UF TUs	NS	NS	-0.463†	NS	NS
Total n	NS	NS	NS	0.423†	NS
Mean Total TUs	NS	NS	NS	NS	**0.548***

bases (Binford 1980). This may also be reflected in a generally increased size of the toolkit where DFI is higher in the present dataset. The number of yearly camp moves potentially being negatively associated with the complexity of untended facilities may be most parsimoniously explained by the fact that populations who do not stay in the same place for long are less able to monitor these apparatuses, and therefore have less to gain from investment in them.

The only demographic association with technological complexity is seen through the size of the maximum aggregated settlement. Increases in the sizes of these seasonal settlements are associated with an increased complexity of tended facilities, a potential increase in the number of untended facilities, a potential decrease in the number of instruments, and an overall increase in average complexity across the toolkit. To reinforce the influence of raw camp size over camp density, the increased complexity of tended facilities ($r_{partial}$ = 0.471, p = 0.042) and the whole toolkit ($r_{partial}$ = 0.447, p = 0.055) largely remain when controlling for log population density. The increased proportion of untended facilities does not remain when controlling for log population density ($r_{partial}$ = 0.247, p = 0.308) but the reduced proportion of instruments does ($r_{partial}$ = -0.453, p = 0.051).

Climate and technology

The notable relationships between climatic variables and technological outcomes are shown in Table 6, with full data in Table S5. There is a strong correspondence between different environmental variables, especially between precipitation, precipitation seasonality, temperature, and (inverse) temperature seasonality and their relationships with different technological variables. This again suggests that distinct behavioural strategies are being followed in different environments, whereby those with greater plant availability show greater use of (less complex) instruments, while those with reduced plant availability see greater focus on other tool forms and/or investment in the complexity of one or more tool categories. NPP and its seasonality follow these variables in many places, but exert independent influence on the proportion of weapons in an assemblage, especially in the relationship between

Tab. 6 - Relationships between technological variables and climatic characteristics. Instr. = Instruments, TUs = Technounits, weap. = Weapons, TF = Tended facilities, UF = Untended facilities, Precip. = Precipitation, Temp. = Temperature, NPP = Net Primary Productivity. $^{\dagger}p<0.1$, $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$. NS = Not Significant.

VARIABLE	ENVIRONMENTAL BASELINE			ENVIRONMENTAL SEASONALITY			ENVIRONMENTAL PREDICTABILITY		
	LOG (PRECIP.)	TEMP.	LOG (NPP)	LOG (PRECIP.)	LOG (TEMP.)	LOG (NPP)	PRECIP.	TEMP.	NPP
%Instr.	**0.613****	**0.799*****	**0.512***	**0.681*****	**-0.769*****	0.246	-0.353	**0.800*****	**-0.741*****
Mean Instr. TUs	**-0.553***	**-0.595****	**-0.749*****	**-0.475***	**0.531***	**-0.585****	NS	**-0.484***	**0.704*****
%Weap.	NS	NS	-0.427†	NS	NS	**-0.512***	NS	NS	NS
Mean Weap. TUs	NS	**-0.486***	**-0.613****	NS	**0.451***	-0.433†	NS	-0.434†	**0.534***
Mean TF TUs	NS	-0.393†	NS	NS	NS	NS	**0.500***	-0.406†	NS
%UF	NS	**-0.619****	NS	**-0.547***	**0.629****	NS	**0.533***	**-0.713*****	0.395†
Mean UF TUs	NS	NS	NS	NS	NS	NS	NS	**-0.574***	NS
Total n	NS	**-0.651****	NS	-0.441†	**0.703*****	NS	NS	**-0.734*****	**0.529***
Mean Total TUs	NS	**-0.678****	**-0.512***	**-0.450***	**0.583****	NS	NS	**-0.633****	**0.596****

NPP seasonality and the proportion of weapons in the toolkit.

Temperature predictability seems to have a profound impact on the toolkit, as it is broadly associated with an increased proportion of instruments, decreased instrument complexity, decreased weapon complexity, decreased tended facility complexity, fewer untended facilities, decreased untended facility complexity, fewer tools in the toolkit, and decreased average tool complexity overall. Increased precipitation predictability is associated with increased complexity of tended facilities and an increased proportion of untended ones, while increased NPP predictability is associated with fewer instruments, more complex instruments, more complex weapons, perhaps more untended facilities, more tools in the toolkit, and overall increases in complexity. These patterns seem related to a strong inverse correlation between temperature predictability and NPP predictability (r = -0.822, p = 8.69e-06), with populations in more northerly latitudes seeing low temperature predictability but high NPP predictability.

A schematic of the influences of both seasonality and predictability variables on technology are displayed in Figure 3. These highlight that seasonality and predictability appear to play largely inverse associations with each variable, as temperature in particular is more predictable in environments where its log-transformed seasonality is lower (r = -0.972, p = 8.218e-13). Precipitation seasonality often shows inverse relationships with NPP predictability, but often not with rainfall predictability. This would suggest that NPP, but not always rainfall, is more predictable (though predictably lower) where rainfall seasonality is lower. Indeed, log-transformed monthly precipitation variance is more strongly associated with NPP predictability (r = -0.828, p

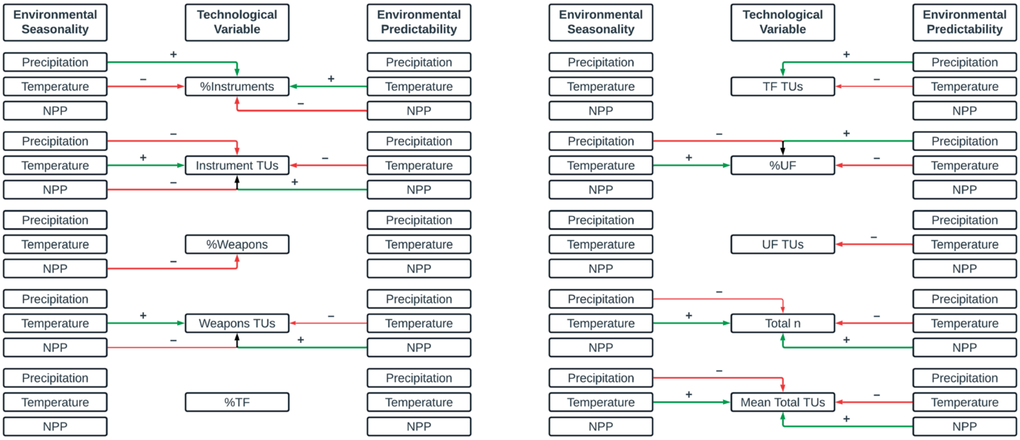

***Fig. 3** - Schematic of relationships between seasonality and predictable variables and each of the technological variables. Green lines denote positive associations, and red lines denote negative associations. Thick lines denote p < 0.05, and thin lines denote 0.1 > p > 0.05.*

= 6.652e-06) than it is with rainfall predictability (r = -0.520, p = 0.019).

Multivariate analyses

Path analyses for each technological variable are documented in the Supplementary Information, with the independent variables only those that reached significance in the bivariate analyses. These tests show quite poor fit for the small samples available in the present dataset, resulting in some spurious findings for different outcome variables, including significant findings in the opposite direction to those expected. For example, the proportion of the diet attributed to gathering becomes *positively* associated with toolkit complexity, as does precipitation seasonality, while temperature seasonality becomes *negatively* associated. These trends are extremely hard to interpret in the face of the raw data and a continued negative relationship between mean monthly temperature and the mean number of technounits in the path analysis. In this context, we believe such findings are likely statistical artefacts, and re-emphasise the difficulty with interpreting complex multivariate analyses of small datasets. This makes simple relationships and a strict interpretative framework crucial for investigating the drivers of technological complexity.

Discussion

Defining complexity

We reiterate that the Oswalt et al. (1976) dataset is imperfect, both in terms of the sample and in the operational definition of "complexity". Defining complexity according to the number of composite units subsumes substantial variability within the category of "1 technounit", which has major implications for the broader application of this framework. Firstly, as long as the artefacts are made of a single component, this broad grouping equalises the use of natural objects ("naturefacts" in the terminology of Oswalt et al. 1976) and those modified by humans ("artefacts"), as well as between objects used for ad hoc versus planned purposes more broadly (Binford 2001). This rather does a disservice to the material complexity of even chimpanzees, whose tools would almost always be defined by a single technounit, yet they can create some tool forms by selecting and modifying raw materials through multiple stages to fit specific tasks (e.g. Suzuki et al. 1995), and they can combine individual components to make more complex tool systems (e.g. Boesch 2003). Use of tools in this way is clearly distinct to more simplistic manipulations of material, such as in the use of leaves for water dipping (e.g. Goodall 1986; Boesch and Boesch 1990; Whiten et al. 1999).

Nonetheless, technounits clearly downplay the technological sophistication of present, recent, and ancient humans to a much greater extent than they do to chimpanzees.

For example, rudimentary "spears" used by Fongoli chimpanzees, torn from trees and modified with teeth (Pruetz and Bertolani 2007; Pruetz et al. 2015), are not analogous to the elongated wooden spears made on highly selected and modified wooden materials by human populations across the world (see Milks 2020 for a review). Similar objects are also seen in the archaeological record, including the 300,000-year-old wooden tools from Schöningen, which recently were shown to reflect elongated and complex *chaînes opératoires* with defined end goals (Leder et al. 2024). All of these forms would nonetheless be classified as a single technounit by Oswalt et al. (1976), as they share manufacture on a single material form with no composite additions. These technounit counts have been misused to claim an overlap in material complexity between chimpanzee and modern human toolkits (McGrew 1987), which creates the potential for overly simplified narratives of human evolution.

On the other hand, Hoffecker and Hoffecker's (2018) focus on the binary presence of "multiple state artefacts" in foraging toolkits may mask even more variability than technounits, grouping together everything from chimpanzee material to relatively simple components of modern human toolkits as non-complex. In our opinion, therefore, the quantitative nature of Oswalt et al.'s (1976) technounits makes them a much better starting point for preliminary investigations of technological variability, certainly within ethnographic human populations where issues of 'missing elements' are less pertinent. Future studies will be better served by defining complexity units according to how many steps are involved in their operational sequences (Perreault et al. 2013; Paige and Perreault 2024), or how many discrete behavioural procedures constitute their manufacture and the structure of these actions (Muller et al. 2017; Fajardo et al. 2023; Kozowyk et al. 2023), allowing for more robust comparisons between populations, species, and over evolutionary timescales. Moreover, understanding how these different measures of complexity relate to each other will remain an important avenue of research.

Scales of analysis

Previous authors have extensively discussed the drivers of technological change in modern and past populations with the view to better understanding change in the ethnographic and archaeological record, drawing attention to either demographic and ecological variables, with little attention to their interaction (though see Grove 2018; Timbrell 2024). This is what we have aimed to address in this study, using the complex landscapes of cultural evolution as a lens through which to explore Oswalt et al.'s (1976) dataset. The importance of this interpretive framework is highlighted by the aforementioned difficulties with multivariate analyses, which can produce inconsistent findings with the small dataset of technological complexity in hunter-gatherer populations. In the context of our evolutionary model, we emphasise that, at the most proximate level, it is resource distributions through space (and the relative contributions of different resources to the diet) that hunter-gatherers are adapting to, and that other variables exert influence at different scales (Clark and Linares-Matás 2024). All being equal, diversity and stability of these resource distributions through time determines what types of toolkits are the most adaptive in a given environment and the level of investment worth putting into their development and adoption. Hunter-gatherer populations acquire and apply technological knowledge in response to these environmental factors, with demography determining the conditions of its accumulation, and thus innovation and diffusion.

Diet. The most direct associations with complexity can be seen in the relative contributions of gathering, hunting, and fishing to hunter-gatherer diets. This is a rather coarse division of food acquisition, but it suggests that hunting is most stable between populations, with increased amounts of gathering reducing average tool complexity, and increased amounts of fishing increasing it. This is driven partly by an increase in the use of instruments (the simplest tool form according to Oswalt et al. 1976) when collecting plant foods, compared to more untended facilities (some of the most complex tool forms) when focusing on fish. Weapons and tended facilities are important across the hunting and fishing spectrum. This reliance on more complex technologies underlines that an increased focus on hunting and fishing necessitates a tradeoff in greater technological—and time—investment, to access the optima they offer on the fitness landscape. At the same time, even the comparatively simple instruments appear to be more complex when the whole assemblage is more complex, which is also true of the other three tool types. Similarly, the complexity of both types of facility is interrelated. These findings highlight two key things: a) the relative appearance of specific types of cultural solution are intrinsically related to the foodstuffs being consumed, and b) that technological knowledge is transferable between domains, especially when they are closely related. Both of these points were emphasised by Oswalt et al. (1976, p. 189) when examining inter-population variability, but they did not have the data to examine higher-level influences.

Demography. Demographic structure should subsequently follow the nutrition obtained from these diet-technology interactions, and feed-back into the knowledge base from which technology is derived. In particular, foodstuffs that provide increased nutritional density—but that are only found in an isolated area and/or need more individuals to successfully acquire (e.g. animal products)—will support a larger population for any given environment (Grove 2018). On the other hand, a focus on such resources is enforced where gathered foodstuff productivity is low (including plants, insects, honey, and shellfish, for example), and may require quite substantial (seasonal) moves. Where populations can successfully subsist on gathered resources, they may be able to maintain density over a larger area through a number of smaller groups with distinct foraging radii, more frequent moves over shorter distances, and reduced aggregation of foraging subunits. These patterns are supported in the associations between rainfall, rainfall seasonality, mean temperature, and/or reduced temperature seasonality with reduced DFI, maximum aggregated settlement size, and distance moved in a year, along with increased population density (Supplementary Information).

The findings described above highlight that access to the broadly more calorie-dense foodstuffs of animals and fish come with important tradeoffs that would favour a focus on gathered resources where these are more widely available. The scales evaluating this tradeoff are not always the same throughout the year. This is most obviously seen in the near-universal preference of hunter-gatherers towards honey—a calorie-dense but seasonal and spatially-dispersed resource—which is eagerly consumed in place of these resources almost whenever it is accessible in large quantities (e.g. Marlowe et al. 2014). For example, Turnbull's (1961) classic observations of the MButi in the Ituri Forest (Democratic Republic of Congo) describe the hunting group fissioning into smaller camps during the honey season, only to later fuse as the group returned to hunting when honey became less available. Similarly, the Hadza—as in the Kua and Ju/'Hoansi of the Kalahari Desert (Bartram et al. 1991; Lee 2013)—form larger aggregated hunting camps nearby to water sources that attract animals in the dry season, but disperse into smaller camps focused on the location of fruiting berry trees during the wet season, when they also bring more honey back to camp (Vincent 1985; Hawkes et al. 1989, 1991; Marlowe and Berbesque 2009; Marlowe et al. 2014). These patterns reflect a shifting of the complex fitness landscape at different times of the year, towards a greater number of local optima when focusing on the gathering of berries and honey, and a global optimum when having to shift towards animal resources.

The data presented here showed that at least one demographic variable, the size of the largest seasonally-aggregated camp or village, is associated with increases in toolkit complexity (due to an increase in the complexity of tended facilities, but also a reduced proportion of instruments and an increased proportion of untended facilities). This remained when controlling for the influence of overall population density. It is logical that we see greater investment in tended facilities when there are (at least seasonally) more people who can tend them. In such contexts, as argued by advocates of population size and structure as a driver of behavioural change, larger aggregations may create stronger spheres of interaction and knowledge sharing, whereby an increased encounter rate leads to new innovations that can result in increased complexity (Grove 2009, 2018). More individuals may also facilitate greater efficiency in foraging and other tasks critical for survival, creating more time for technological experimentation and investment (Kraft et al. 2021). Seasonal aggregations—reflecting 'partial connectivity' of a wider population network (*sensu* Derex and Boyd 2016)—provide populations with a greater capacity to reach global optima than those that remain in contact all year round, as fully connected groups explore inherently less of 'behaviour space'. Large seasonal aggregations may therefore lead to technological innovations that both incur higher fitness and greater resilience to environmental change and subsequent fitness landscape alterations. This provides one possible mechanism in support of hypothesis 4 within section "Empirical predictions", but more data are needed to explore this further.

Climate. At the most ultimate level, the climatic properties of the environment are what determines its resource productivity, seasonality, and year-to-year predictability, and thus the technological responses of hunter-gatherers within 'behaviour space'. A number of the associations between climatic variables and toolkit composition and complexity are logically mediated by resource acquisition and population structure. For example, toolkits are more diverse and complex in colder environments, with the most seasonal and unpredictable temperatures but most predictable NPP, reflecting the increased focus on hunting and especially fishing, and perhaps also the large seasonal aggregation of groups that come together to survive harsh arctic winters. Such seasonal reconfigurations of necessary behavioural strategies also support hypothesis 2 of section "Empirical predictions". This also strongly underlines the role of ecological risk in driving technological complexity, because the success of resource acquisition becomes paramount in areas relying on sparse mobile resources where other foodstuffs, especially plants, are not readily available (Torrence 2001; Collard et al. 2011, 2013).

Conversely, in warmer and less seasonal environments, the diversity of behavioural possibilities does not seem to necessitate diverse or complex tool use, especially due to the low ecological risk of any given strategy failing, as predicted by hypothesis 1. Increased rainfall seasonality in areas of greater carrying capacity also cyclically revitalises the ecosystem, and thus people have greater access to plant resources. Smaller, less complex toolkits with higher proportions of instruments and fewer untended facilities may allow for a diverse range of plant gathering and processing activities in more tropical areas. This is likely to influence the foraging strategy of populations in these regions towards a "forager strategy" of movement between abundant resource patches, rather than a "collector strategy" of more intensive exploitation of a single area, which has its own set of influences on ecological risk (Read 2008; Read and Andersson 2020). In these contexts, we may expect rainfall variables to have a greater influence on the toolkit in tropical areas, while temperature variables may be more important in higher or lower latitudes. At the same time, populations in these environments may experience fewer selection pressures guiding the adoption of highly specific adaptations at a single global optimum, as the adaptive landscape is highly dynamic through time. Highly complex technologies should only become adaptive when the reward or time invested in traversing a steep adaptive peak outweighs the risk of not having done so.

We have previously argued that climatic variables should be most important in patterning and/or constraining technological investment, through its influence on both resource risk and population structure, rather than influencing it directly. In particular, we emphasised that seasonality should determine how consistent the toolkit is across seasons (Figure 1A), and that inter-annual (resource) unpredictability would provide a constraint on investment, given year-to-year returns would be uncertain (Figure 1B). Viewing these climatic variables as part of a wider environmental system in the data presented here broadly conforms with these predictions presented via our evolutionary framework. The alternative explanation for the associations between various aspects of climate seasonality and predictability, and different technological variables is that more generalised toolkits were deployed as a response to more dramatic changes between seasons and years (*sensu* Clark and Linares-Matás 2024). However, this is much less plausible than the simple association between areas of increased plant availability and increased rainfall seasonality, as well as extensive evidence of hunter-gatherer responses to completely distinct seasonal conditions in tropical environments. Further elucidation of these two alternatives would require greater sampling of multiple populations from within the same climatic regime, especially those who share a greater need to respond to rainfall seasonality, rather than from across much broader areas.

Landscape knowledge and technological organisation

As per hypothesis 3 of section "Empirical predictions", assuming the increased complexity of toolkits in northerly latitudes is due to reduced plant availability, and the necessary complexity of exploiting animals and fish—alongside the high risk of failure—the predictability of resource distributions (as judged by high NPP predictability) may be particularly important in facilitating technological investment within these strategies. This predictable environmental productivity, even if predictably low, may underpin an ability to accumulate knowledge about areas that have a high knowledge threshold, often because of a limited number of behavioural optima, and would otherwise be very difficult to first occupy (Rockman 2003). In northerly, and especially sub-arctic to arctic environments, these barriers to initial occupation include the lack of widespread plant resources on which to subsist whilst understanding the processes involved in subsistence on foodstuffs of greater caloric density, the isolation and dramatic seasonal movements of these calorie-dense foodstuffs, and the lack of obvious landmarks from which initial waypoint navigation can proceed (see Rockman and Steele 2003, and papers therein). Encoding of this environmental information forms the basis for memory formation (Prezioso and Alessandroni 2023), and thus it is a critical baseline for subsequent adaptation through cumulative cultural evolution (*sensu* Tomsello 1999).

The importance of predictability in such environments is illustrated by Oswalt et al.'s (1976, p. 185-186) own summary of indigenous technologies along the American Pacific Northwest Coast: "the complexity of Northwest Coast Indian [sic.] life usually has been attributed to the abundance, predictability, and richness of salmon as food", and that "the technological forms designed by these peoples to take salmon were among their most developed subsistants". In this way, we should conceptualise the interplay between climatic context and the ability of populations to understand the temporal and spatial distribution of key resources as the driver of investment and access to optima within complex fitness landscapes. The convergence of harpoon-based technological strategies for hunting large marine mammals in western Alaska and the Tierra del Fuego in extreme South America highlight this pattern, given neither are amongst the earliest technologies in their respective regions, but represent continued patterns of landscape adaptation through time (Linares-Matás and Lim 2024). They differ, however, through their association with Holocene neoglaciation in Alaska, which increased the risk associated with resource acquisition failure. Meanwhile, their appearance in southernmost South America is not associated with any known climatic reconfiguration, only an increase in investment facilitated by landscape habituation. The continuation of cold conditions in Alaska subsequently provided the stability required to occupy novel environments and re-specialise the technological base (Linares-Matás and Lim 2024).

In terms of how predictability relates to technological organisation, Binford (1979) drew a distinction between "personal" and "situational" gear from his observations of foraging behaviour in the Nunamiut, with the former carried by individuals in anticipation of future need, and the latter being collected or produced in response to an unexpected opportunity. Personal gear—including dressed stone cores for the release of flakes in the event of butchery—was said to be heavily curated (that is, recycled, reused, and maintained), whereas situational gear was expedient according to the availability of material. Curated tools are often also more specialised towards a specific task, but can be multi-functional tools (McCall, 2012). Kuhn (1992) elaborated on this framework for the Palaeolithic, emphasising that either individuals could be provisioned with tools—especially where their need was relatively unpredictable—or places could be provisioned with raw material and/or tools, where their need would be more predictable. Kuhn (1992) is largely referring to spatial predictability—where resources will usually be acquired from the same patches, even if acquisition was unpredictable at the day-to-day scale—whereas Binford (1979) is largely referring to temporal predictability—where resources can reliably be obtained on any given day, but from varied points across the landscape. Where both variables are high, the two models would suggest the provisioning of *either* places or individuals with curated tools (*sensu* Binford 1979), but the predominance of the former is consistent with Binford's (1979) reports of Nunamiut caching material and technology at strategic places to which they expected individuals to return. These strategies are heavily dependent on consolidated landscape knowledge that facilitates such adaptation.

In the data presented above, DFI is broadly associated with a greater overall size of the toolkit, and with an increased proportion of untended facilities. We would suggest that these patterns may be related to greater provisioning of places in areas of high spatial and temporal predictability, whereby untended facilities are more complex and could be more frequently monitored by logistical groups moving from residential bases (Binford 1979, 1980). This fits well with the findings relating to the almost all-encompassing relationships of climatic predictability, as well as the association between technological complexity and the overall size of the toolkit, which suggests applicability of knowledge bases beyond their original context. In sum, landscape knowledge is a critical mediator of the identified relationships between ecology, demography, climate, and technology, forming the basis for conscious population-level reconfiguration of behaviour. This is the difference between the existence of theoretical peaks within the fitness landscape, and the ability to climb and traverse them.

Conclusions

In this paper, we have re-analysed Oswalt et al.'s (1976) classic dataset on technological complexity in modern human hunter-gatherers, using updated dietary, demographic, and climatic variables, in order to understand the ecological and demographic drivers of technological diversity. While we acknowledge the limitations of the Oswalt et al.'s (1976) dataset and its operationalisation of complexity, we suggest it can still provide important insight into current debates surrounding the nature of technological variability in lieu of future methodological advances, especially when examining its findings through modern cultural evolutionary theory. We have interpreted our results through a novel framework focused on the complex fitness landscapes of cultural evolution, integrating previous work in behavioural ecology and models of adaptation through time, to show how different factors hypothesised to relate to technological change can each play a role in shaping the structure and nature of human behaviour. Future work must tackle issues surrounding the operationalisation of complexity in both modern and past populations, and how to compare between the two, as well as expanding the cross-cultural sample for the application of multivariate statistics.

We argue that resource distributions impose the most proximate and direct influences on the fitness landscapes, which technological adaptations can help navigate, while changes to the height and the frequency of these changes of individual fitness peaks are dictated by local climatic factors—especially seasonality and inter-annual predictability. We also re-emphasise the importance of resource risk in eliciting specialisation of toolkits in lower productivity environments, including an interlinked role for the size of seasonal population aggregations in allowing for cultural development, as well as the fundamental importance of accumulated information about the landscapes inhabited by hunter-gatherer populations. This knowledge is critical for human populations to exploit the niches theoretically available in a landscape, and optimise their environmental returns through time.

Acknowledgements

We thank Enrico Crema for advice before submission of this version of the manuscript.

Author contributions

JC conceived of the study in collaboration with all authors and collated the data. JC and LT carried out the statistical analyses. All authors contributed to the writing and review of the manuscript.

Financial support

The work of JC is supported by an Early Career Research Fellowship at Corpus Christi College, University of Cambridge. The work of LT is supported by funding awarded to the Human Palaeosystems Group by the Max Planck Society. The work of SEP is supported by the Eberhard Karls University of Tübingen. The work of GJLM is supported by a Research Fellowship at Emmanuel College, University of Cambridge. No specific additional funding was provided for this research.

Conflicts of interest

All authors declare none.

Research transparency and reproducibility

All data is available as Supplementary Information to this manuscript.

References

Bartram LE, Kroll E, Bunn HT (1991) Variability in camp structure and bone food refuse patterning at Kua San hunter-gatherer camps. In: Kroll E, Douglas Price T (eds) The Interpretation of archaeological spatial patterning, Plenum Press, New York, NY, pp. 77–148.

Binford LR (1979) Organization and formation processes: looking at curated technologies. J Anthropol Res 35:255–273.

Binford LR (1980) Willow smoke and dogs' tails: hunter-gatherer settlement systems and archaeological site formation. Am Antiq 45:4–20. https://doi.org/10.2307/279653

Binford LR (2001) Constructing frames of reference: an analytical method for archaeological theory building using ethnographic and environmental data sets, University of California, Berkeley.

Boesch C (2003) Is culture a golden barrier between human and chimpanzee? Evol Anthropol 12:82–91. https://doi.org/10.1002/evan.10106

Boesch C, Boesch H (1990) Tool use and tool making in wild chimpanzees. Folia Primatol 54:86–99. https://doi.org/10.1159/000156428

Clark GA, Barton CM (2017) Lithics, landscapes & la longue-durée – Curation & expediency as expressions of forager mobility. Quat Int 450:137–149. https://doi.org/10.1016/j.quaint.2016.08.002

Clark J, Linares-Matás G (2020) The Role of landscape knowledge networks in the early pleistocene technological variability of East Africa. Archaeol Rev Camb 35:25–44. https://doi.org/10.17863/CAM.71847

Clark J, Linares-Matás G (2023) Seasonal resource categorisation and behavioral adaptation among chimpanzees: Implications for early hominin carnivory. J Anthropol Sci 101:1–35. https://doi.org/10.4436/JASS.10006

Clark J, Linares-Matás GJ (2024) When to generalise and when to specialise? Climate change and hominin biocultural adaptability in the African early and middle stone age. Quat Sci Adv 15:100218. https://doi.org/10.1016/j.qsa.2024.100218

Collard M, Buchanan B, Morin J, et al (2011) What drives the evolution of hunter–gatherer subsistence technology? A reanalysis of the risk hypothesis with data from the Pacific Northwest. Philos Trans R Soc Lond B Biol Sci 366:1129–1138. https://doi.org/10.1098/rstb.2010.0366

Collard M, Buchanan B, O'Brien MJ (2013) Population size as an explanation for patterns in the paleolithic archaeological record: more caution is needed. Curr Anthropol 54:S388–S396. https://doi.org/10.1086/673881

Collard M, Kemery M, Banks S (2005) Causes of toolkit variation among hunter-gatherers: a test of four competing hypotheses. Can J Archaeol 29:1–19. https://www.jstor.org/stable/41103514

Collard M, Shennan SJ, Tehrani JJ (2006) Branching, blending, and the evolution of cultural similarities and differences among human populations. Evol Hum Behav 27:169–184. https://doi.org/10.1016/j.evolhumbehav.2005.07.003

Colwell RK (1974) Predictability, constancy, and contingency of periodic phenomena. Ecol 55:1148–1153. https://doi.org/10.2307/1940366

Deffner D, Kandler A (2019) Trait specialization, innovation, and the evolution of culture in fluctuating environments. Palgrave Commun 5:1–10. https://doi.org/10.1057/s41599-019-0360-4

Derex M, Beugin M-P, Godelle B, Raymond M (2013) Experimental evidence for the influence of group size on cultural complexity. Nature 503:389–391. https://doi.org/10.1038/nature12774

Derex M, Boyd R (2016) Partial connectivity increases cultural accumulation within groups. Proc Natl Acad Sci USA 113:2982–2987. https://doi.org/10.1073/pnas.1518798113

Fajardo S, Kozowyk PRB, Langejans GHJ (2023) Measuring ancient technological complexity and its cognitive implications using Petri nets. Sci Rep 13:14961. https://doi.org/10.1038/s41598-023-42078-1

Ferraro JV (2007) Broken bones and shattered stones: on the foraging ecology of Oldowan Hominins. PhD Dissertation, University of California.

Foley R (1985) Optimality theory in anthropology. Man 20:222. https://doi.org/10.2307/2802382

Goodall J (1986) The chimpanzees of Gombe: patterns of behavior, Harvard University Press, Cambridge, MA.

Grove M (2009) Hunter–gatherer movement patterns: Causes and constraints. J Anthropol Archaeol 28:222–233. https://doi.org/10.1016/j.jaa.2009.01.003

Grove M (2016) Population density, mobility, and cultural transmission. J Archaeol Sci 74:75–84. https://doi.org/10.1016/j.jas.2016.09.002

Grove M (2018) Hunter-gatherers adjust mobility to maintain contact under climatic variation. J Archaeol Sci Rep 19:588–595. https://doi.org/10.1016/j.jasrep.2018.04.003

Grove M, Hall H, Timbrell L, et al (2023) Moving far or moving often? A neglected axis of variation in hunter-gatherer mobility. J Archaeol Sci Rep 52:104266. https://doi.org/10.1016/j.jasrep.2023.104266

Gruber T, Muller MN, Strimling P, et al (2009) Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. Curr Biol 19:1806–1810. https://doi.org/10.1016/j.cub.2009.08.060

Hawkes K, Hill K, O'Connell JF (1982) Why hunters gather: Optimal foraging and the Ache of Eastern Paraguay. Am Ethnol 9:379–398.

Hawkes K, O´Connell JF, Blurton Jones NG, et al (1991) Hunting income patterns among the Hadza: big game, common goods, foraging goals and the evolution of the human diet. Philos Trans R Soc Lond B Biol Sci 334:243–251. https://doi.org/10.1098/rstb.1991.0113

Hawkes K, O'Connell JF, Blurton-Jones NG (1989) Hardworking Hadza grandmothers. In: Standen V, Foley RA (eds) Comparative socioecology: the behavioural ecology of humans and other mammals, Blackwell Scientific, Oxford, pp. 341–366.

Henrich J (2004) Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses—The Tasmanian case. Am Antiq 69:197–214. https://doi.org/10.2307/4128416

Henrich J, Boyd R, Derex M, et al (2016) Understanding cumulative cultural evolution. Proc Natl Acad Sci USA 113:E6724–E6725. https://doi.org/10.1073/pnas.1610005113

Hoffecker JF, Hoffecker IT (2018) The structural and functional complexity of hunter-gatherer technology. J Archaeol Method Theory 25:202–225. https://doi.org/10.1007/s10816-017-9332-4

Kelly RL (2013) The lifeways of hunter-gatherers: the foraging spectrum, 2nd revised edition, Cambridge University Press, Cambridge.

Kempe M, Mesoudi A (2014) An experimental demonstration of the effect of group size on cultural accumulation. Evol Hum Behav 35:285–290. https://doi.org/10.1016/j.evolhumbehav.2014.02.009

Kim S (2015) ppcor: An R Package for a fast calculation to semi-partial correlation coefficients. Commun Stat Appl Methods 22:665–674. https://doi.org/10.5351/CSAM.2015.22.6.665

Kirby KR, Gray RD, Greenhill SJ, et al (2016) D-PLACE: A global database of cultural, linguistic and environmental diversity. PLoS One 11:e0158391. https://doi.org/10.1371/journal.pone.0158391

Kline MA, Boyd R (2010) Population size predicts technological complexity in Oceania. Philos Trans R Soc Lond B Biol Sci 277:2559–2564. https://doi.org/10.1098/rspb.2010.0452

Kozowyk PRB, Fajardo S, Langejans GHJ (2023) Scaling Palaeolithic tar production processes exponentially increases behavioural complexity. Sci Rep 13:14709. https://doi.org/10.1038/s41598-023-41963-z

Kraft TS, Venkataraman VV, Wallace IJ, et al (2021) The energetics of uniquely human subsistence strategies. Science 374:eabf0130. https://doi.org/10.1126/science.abf0130

Kuhn SL (1992) On planning and curated technologies in the Middle Paleolithic. J Anthropol Res 48:185–214. https://doi.org/10.1086/jar.48.3.3630634

Kuhn SL (2006) Trajectories of change in the Middle Paleolithic in Italy. In: Hovers E, Kuhn SL (eds) Transitions before the transition: evolution and stability in the Middle Paleolithic and Middle Stone Age, Springer, New York, NY, p. 109–120.

Leder D, Lehmann J, Milks A, et al (2024) The wooden artifacts from Schöningen's spear horizon and their place in human evolution. Proc Natl Acad Sci USA 121:e2320484121. https://doi.org/10.1073/pnas.2320484121

Lee RB (2013) The Dobe Ju/'hoansi, 4th edn, Wadsworth, Belmont, CA.

Lieberman DE (1993) The rise and fall of seasonal mobility among hunter-gatherers: the case of the Southern Levant. Curr Anthropol 34:599–631. https://doi.org/10.1086/204209

Linares-Matás GJ, Clark J (2022) Seasonality and Oldowan behavioral variability in East Africa. J Hum Evol 164:103070. https://doi.org/10.1016/j.jhevol.2021.103070

Linares-Matás GJ, Lim JS (2024) "This is the way": Knowledge networks and toolkit specialization in the circumpolar coastal landscapes of western Alaska and Tierra del Fuego. J Isl Coast Archaeol 19:1–29. https://doi.org/10.1080/15564894.2021.2000073

Lombard M, Parsons I (2011) What happened to the human mind after the Howiesons Poort? Antiquity 85:1433–1443. https://doi.org/10.1017/S0003598X00062153

Marlowe FW, Berbesque JC (2009) Tubers as fallback foods and their impact on Hadza hunter-gatherers. Am J Phys Anthropol 140:751–758. https://doi.org/10.1002/ajpa.21040

Marlowe FW, Berbesque JC, Wood B, et al (2014) Honey, Hadza, hunter-gatherers, and human evolution. J Hum Evol 71:119–128. https://doi.org/10.1016/j.jhevol.2014.03.006

McCall GS (2012) Ethnoarchaeology and the organization of lithic technology. J Archaeol Res 20:157–203. https://doi.org/10.1007/s10814-011-9056-z

McGrew WC (1987) Tools to get food: the subsistants of Tasmanian Aborigines and Tanzanian chimpanzees compared. J Anthropol Res 43:247–258.

Milks A (2020) A Review of ethnographic use of wooden spears and implications for Pleistocene hominin hunting. Open Quat 6. https://doi.org/10.5334/oq.85

Muller A, Clarkson C, Shipton C (2017) Measuring behavioural and cognitive complexity in lithic technology throughout human evolution. J Anthropol Archaeol 48:166–180. https://doi.org/10.1016/j.jaa.2017.07.006

Oswalt WH, Mann G, Satterthwait L (1976) An anthropological analysis of food-getting technology, John Wiley & Sons, New York.

Padilla-Iglesias C, Blanco-Portillo J, Pricop B, et al (2024) Deep history of cultural and linguistic evolution among Central African hunter-gatherers. Nat Hum Behav 8:1263–1275. https://doi.org/10.1038/s41562-024-01891-y

Paige J, Perreault C (2024) 3.3 million years of stone tool complexity suggests that cumulative culture began during the Middle Pleistocene. Proc Natl Acad Sci USA 121:e2319175121. https://doi.org/10.1073/pnas.2319175121

Perreault C, Brantingham PJ, Kuhn SL, et al (2013) Measuring the complexity of lithic technology. Curr Anthropol 54:S397–S406. https://doi.org/10.1086/673264

Posit Team (2023) RStudio: integrated development environment for R.

Powell A, Shennan S, Thomas MG (2009) Late Pleistocene demography and the appearance of modern human behavior. Science 324:1298–1301. https://doi.org/10.1126/science.1170165

Prezioso E, Alessandroni N (2023) Enacting memories through and with things: Remembering as material engagement. Mem Stud 16:962–983. https://doi.org/10.1177/17506980221108475

Pruetz JD, Bertolani P (2007) Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. Curr Biol 17:412–417. https://doi.org/10.1016/j.cub.2006.12.042

Pruetz JD, Bertolani P, Ontl KB, et al (2015) New evidence on the tool-assisted hunting exhibited by chimpanzees (*Pan troglodytes verus*) in a savannah habitat at Fongoli, Sénégal. R Soc Open Sci 2:140507. https://doi.org/10.1098/rsos.140507

R Core Team (2024) R: A language and environment for statistical computing.

Read D (2008) An interaction model for resource implement complexity based on risk and number of annual moves. Am Antiq 73:599–625. https://doi.org/10.1017/S0002731600047326

Read D (2012) Population size does not predict artifact complexity: analysis of data from Tasmania, arctic hunter-gatherers, and Oceania fishing groups. UCLA, Human Complex Systems.

Read D, Andersson C (2020) Cultural complexity and complexity evolution. Adapt Behav 28:329–358. https://doi.org/10.1177/1059712318822298

Rockman M (2003) Knowledge and learning in the archaeology of colonization. In: Rockman M, Steele J (eds) Colonization of unfamiliar landscapes: The archaeology of adaptation, Routledge, London, p. 3–4.

Rockman M, Steele J (eds) (2003) Colonization of unfamiliar landscapes: The archaeology of adaptation, Routledge, London.

Shott M (1986) Technological organization and settlement mobility: an ethnographic examination. J Anthropol Res 42:15–51. https://doi.org/10.1086/jar.42.1.3630378

Stephens DW, Krebs JR (1986) Foraging theory, Princeton University Press, Princeton, NJ.

Suzuki S, Kuroda S, Nishihara T (1995) Toolset for termite-fishing by chimpanzees in the

Ndoki forest, Congo. Behav 132:219–235. https://doi.org/10.1163/156853995X00711

Timbrell L (2024) Ecology and demography of early *Homo sapiens*: a synthesis of archaeological and climatic data from eastern Africa. Azania 59:76–110. https://doi.org/10.1080/0067270X.2024.2307790

Tomasello M (1999) The cultural origins of human cognition, Harvard University Press, Cambridge, MA.

Torrence R (1983) Time budgeting and hunter-gatherer technology. In: Bailey G (ed) Hunter-gatherer economy in prehistory, Cambridge University Press, Cambridge, p. 11–22.

Torrence R (2001) Hunter-gatherer technology: macro-and microscale approaches. In: Panter-Brick C, Layton RH, Rowley-Conwy P (eds) Hunter-gatherers: an interdisciplinary perspective, Cambridge University Press, Cambridge, p. 73–98.

Turnbull C (1961) The forest people: a study of the Pygmies of the Congo, Simon and Schuster, New York, NY.

Vaesen K, Collard M, Cosgrove R, et al (2016) Population size does not explain past changes in cultural complexity. Proc Natl Acad Sci USA 113:E2241–E2247. https://doi.org/10.1073/pnas.1520288113

Vincent AS (1985) Plant foods in savanna environments: A preliminary report of tubers eaten by the Hadza of northern Tanzania. World Archaeol 17:131–148. https://doi.org/10.1080/00438243.1985.9979958

Wengrow D, Graeber D (2022) The dawn of everything, Allen Lane, London.

Whallon R (2006) Social networks and information: Non-“utilitarian” mobility among hunter-gatherers. J Anthropol Archaeol 25:259–270. https://doi.org/10.1016/j.jaa.2005.11.004

Whiten A, Goodall J, McGrew WC, et al (1999) Cultures in chimpanzees. Nature 399:682–685. https://doi.org/10.1038/21415

Wickham H (2016) ggplot2: elegant graphics for data analysis, Springer-Verlag, New York, NY.

Winterhalder B, Smith EA (eds) (1992) Evolutionary ecology and human behavior, Aldine de Gruyter, New York, NY.

Wright S (1932) The roles of mutation, inbreeding, crossbreeding and selection in evolution. Proceedings of the Sixth International Congress of Genetics 1:356–366.

Associate Editor, Emanuele Cancellieri