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ARTICLE

A New Research Strategy for Integrating Studies of Paleoclimate, Paleoenvironment, and Paleoanthropology

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Paleoanthropologists (scientists studying human origins) universally recognize the evolutionary significance of ancient climates and environments for understanding human origins.[1–6] Even those scientists working in recent phases of human evolution, when modern humans evolved, agree that hunter-gatherer adaptations are tied to the way that climate and environment shape the food and technological resource base.[7–10] The result is a long tradition of paleoanthropologists engaging with climate and environmental scientists in an effort to understand if and how hominin bio-behavioral evolution responded to climate and environmental change. Despite this unusual consonance, the anticipated rewards of this synergy are unrealized and, in our opinion, will not reach potential until there are some fundamental changes in the way the research model is constructed. Discovering the relation between climate and environmental change to human origins must be grounded in a theoretical framework and a causal understanding of the connection between climate, environment, resource patterning, behavior, and morphology, then move beyond the strict correlative research that continues to dominate the field.

Because most paleoanthropological projects require the directed input of large teams of researchers from a variety of disciplines, one might argue that paleoanthropology is a model of how interdisciplinary research can operate. This tradition goes back to the Omo project in the 1960s[11,12] and has been book-ended by a recent National Research Council (NRC) panel report calling for improved funding directed at supporting this kind of collaboration.[13] Paleoanthropologists have approached the issue of human origins and climate and environmental change at two levels of generalization. At a general level, researchers have looked for relationships between patterns in hominin evolution and climate change. For example, it has been hypothesized that the hominin adaptation evolved in response to an increasingly unstable Plio-Pleistocene climate,[3,4,6] and that patterns of hominin speciation were driven by paleoclimate change[14] and paleoclimate change modified by tectonics.[15] Most attempts to relate climatic and environmental change to

human origins focus on explaining specifics in biology, behavior, or material culture at particular times in the past by reference to climatic and environmental changes. This has a long tradition in paleoanthropology. Some of the first attempts proposed a relationship between savannas and/or grasslands and various aspects of human evolution. Laporte and Zihlman[16] posited a relationship between grassland expansion and the origin of bipedality; that hypothesis has been a focus of paleoanthropological integration with paleoclimate and paleoenvironment ever since. For example, Vrba[17,18] suggested that the origins of *Homo* and its new suite of traits was causally linked to a shift from warm, moist, wooded conditions to cooler, drier, more grassy conditions resulting from global climate change at ~2.5 ma.

THE CORRELATIVE APPROACH TO CLIMATE, ENVIRONMENT, AND HUMAN ORIGINS

Attempts to explain or to relate hominin evolution to climate or environmental change typically rely on one or more environmental proxies, such as an isotope curve as an indicator of global ice volumes or temperature,[3,6,19] global dust curve,[2] sedimentologic profiles mirroring river runoff,[20] C_3 versus C_4 inferred ungulate diet,[21] plots of grazing versus browsing animals,[17,18] lake level changes,[15] or a variety of combined proxies.[14] Changes in these proxy variables are interpreted as indicating changes in some aspect of climate or environment. Climate can then be described as arid or wet or as having lower or higher variability or lower or higher productivity; habitat (vegetation) can be described as open or closed, or something more specific, such as "open woodland" or "edaphic grassland." Then changes are broadly described as "the environment went from x to y" in a given time period. These changes are then correlated to some contemporaneous development in hominin biology or behavior such as the origins of tool use[22]

or the appearance of anatomical traits such as large brains, modern dentition, or a lithe frame.[5]

Many of the proposed correlations between climate change and early hominin anatomical and behavioral traits were recognized long ago as a relation between increasingly open habitats and the appearance of stone tools and early *Homo*. Explanations for the correlations are absent or remain just as imprecise and underdeveloped now as they were in the past. In a review, Kingston[14] has noted that "developing adaptive or causal perspectives on the morphological and behavioral variability documented in the human fossil

We argue that correlative studies of the type that dominate paleoanthropology cannot move us forward to compelling explanatory relations between climate, environment, and hominin bio-behavioral evolution.

record requires establishing a comprehensive paleoenvironmental context." We agree. The details in Kingston's review clearly show that significant advances have been made in understanding the climate and environmental records. This work needs to continue. But why is it that the causal explanations remain no more advanced today than they were 30 years ago? We argue that correlative studies of the type that dominate paleoanthropology cannot move us forward to compelling explanatory relations between climate, environment, and hominin bio-behavioral evolution.

The problem lies in the connection, or lack thereof, between our characterizations of the climate and environment and those things that

are meaningful on a day-to-day basis to our organism of interest, in this case hominins. While Kingston's paper calls for an understanding of "shifting adaptive landscapes," it also shows that we know little about the adaptive character of any of these past landscapes; that character was driven by local characteristics (soil, geology, topography, aspect, and so on) and the changing climates that have been studied so rigorously. Hominins don't generally adapt to changes in rainfall and temperature and grass versus woodland; instead, they adapt to the costs and returns of exploiting resources, finding mates, and avoiding predators under those climate and environment conditions. As a research endeavor, the connection between those things that directly determine the fitness payoff structure for different behavioral, social, or morphological adaptations and our characterizations of climate and environment remains undeveloped and largely stagnant. The thrust of the NRC report[13] is that we need longer, higher resolution, terrestrial, regionally targeted climate and environment sequences generated in multidisciplinary projects working in concert with paleoanthropologists. These sequences then need to be correlated to the deep sea and ice core records in order to develop an understanding of how regions responded to worldwide orbitally driven climate change events. Once built, the argument goes, these high resolution sequences can then be juxtaposed against the paleoanthropological record of change in anatomy and behavior of hominins. The optimistic expectation is that insights into human origins will then somehow emerge. We agree that longer, higher resolution, terrestrial, regionally targeted paleoclimate and paleoenvironmental sequences will add to our understanding of hominin origins. But the construction of such sequences will not, in and of itself, generate better understandings of hominin origins unless there is a robust connecting link between hominin resources and the environments in which those resources exist.

EXPLOITING THE COMBINED POWER OF BEHAVIORAL ECOLOGY AND AGENT-BASED MODELING

Hunter-gatherer economies, specifically those of our human ancestors, take all of their resources from the natural environment. The spatial and temporal distribution of resources therefore constrains population size and structure, mobility, social organization, territoriality, and technology; these, in turn, constrain most other social and reproductive patterns.[7–10] A productive integration of climate and environmental research with paleoanthropology requires formal understanding of how climates and environments, as reflected in proxies, shape the resource set crucial to hunter-gatherer ways of life. We need to build the causal chain from climate to environment all the way down to changes in the specific resources and fitness benefits of exploiting them. Using information about climates and environments and changes in them to explain hominin bio-behavioral evolution requires multi-step connective theory, from climate and geology to habitat to resource distribution patterns to behavior. Where does this connective theory reside, if it exists at all?

The most robust theory for connecting resource distribution patterns to economic behavior is foraging theory (FT), derived from behavioral ecology.[23–25] Models based on FT have been extensively employed by anthropologists.[26–29] The goal of these models is to make predictions about foraging decisions by assuming maximization of specified fitness-related currencies (for example, energy, nutrient utility, and reduction of starvation risk), given a specified option set, such as resource types available, patches, and times to forage, as well as constraints describing relationships between decisions and outcomes, such as density and distribution of resources, time required to obtain resources, and nutrient value of resources. FT divides resource choices into habitats, patches, and prey. Prey are generally single indivisible resource items that require an average

amount of time to acquire ("handle") and provide an average amount of nutrients when pursued (both of which are assumed to be known by the forager through prior experience). Foragers can either handle or ignore prey types when encountered. Because patches provide changing amounts of nutrients as a function of time invested in handling, foragers must decide whether and how long to handle each patch they encounter. Patches often contain multiple prey items. Habitats are regions containing known densities of prey and patches that do not change over specified foraging periods, so that gain rates in different

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habitats are fixed and constant over the time span of most foraging decisions. This conceptualization leads to hierarchical decision pathways, such as which habitat to choose for the next several foraging days, which patches to enter and for how long, and which prey items to exploit within those patches or when traveling between patches.[30] While optimal prey choice modeling is straightforward, combined prey choice and patch-handling time models that maximize energetic gain from mixed foraging require recursive calculation to solve.[25] This is because how long to stay in a patch depends on which prey will be taken, while which prey should be handled depends on how long foragers will stay in different patches.

FT and its underlying optimization modeling can also consider a variety of other decisions and constraints, such as trade-offs between different nutrient currencies (for example, protein or carbohydrate) or between nutrients and nonnutrient fitness goals, such as avoiding predation, mate searching, shelter, raw materials for tools, and child care. FT has been successful at explaining circumscribed sets of behaviors among a wide diversity of taxa, including humans: what prey sizes to choose, how long to exploit dispersed resource patches, and so on. It has been rather unsuccessful at providing compelling models of integrated sets of behaviors, or what we might think of as adaptive systems or organism lifeways. This is largely because the standard analytical models used in FT are ineffective at balancing the choices between widely different fitness enhancing resources. Mixed models including several of these component features may become too complex to solve with analytical techniques. We propose that integrating agent-based modeling with FT offers a powerful solution to the dilemma of applying FT to situations in which a forager has many, even a bewildering set, of fitness-enhancing resources of widely varying types, such as food, raw materials, and mates. Agent based models (ABMs) are computer simulation models that can be used to gain explanatory insight into collective outcomes when agents behave according to simple rules and interact with other agents, and with programmed ecological environments.

By combining FT and ABMs, one can model a series of nested economic decisions of human foragers, including, for example, where and when to forage (such as spring versus neap tides in coastal settings); optimal group size for both search and pursuit of resource types, such as single hunter versus cooperative hunting[31]; which prey types to handle when they are encountered, such as shellfish versus small mammals; how long to exploit patches of resources, such as rocky versus sandy shores; and how to trade-off food gains with time spent in child care or avoiding
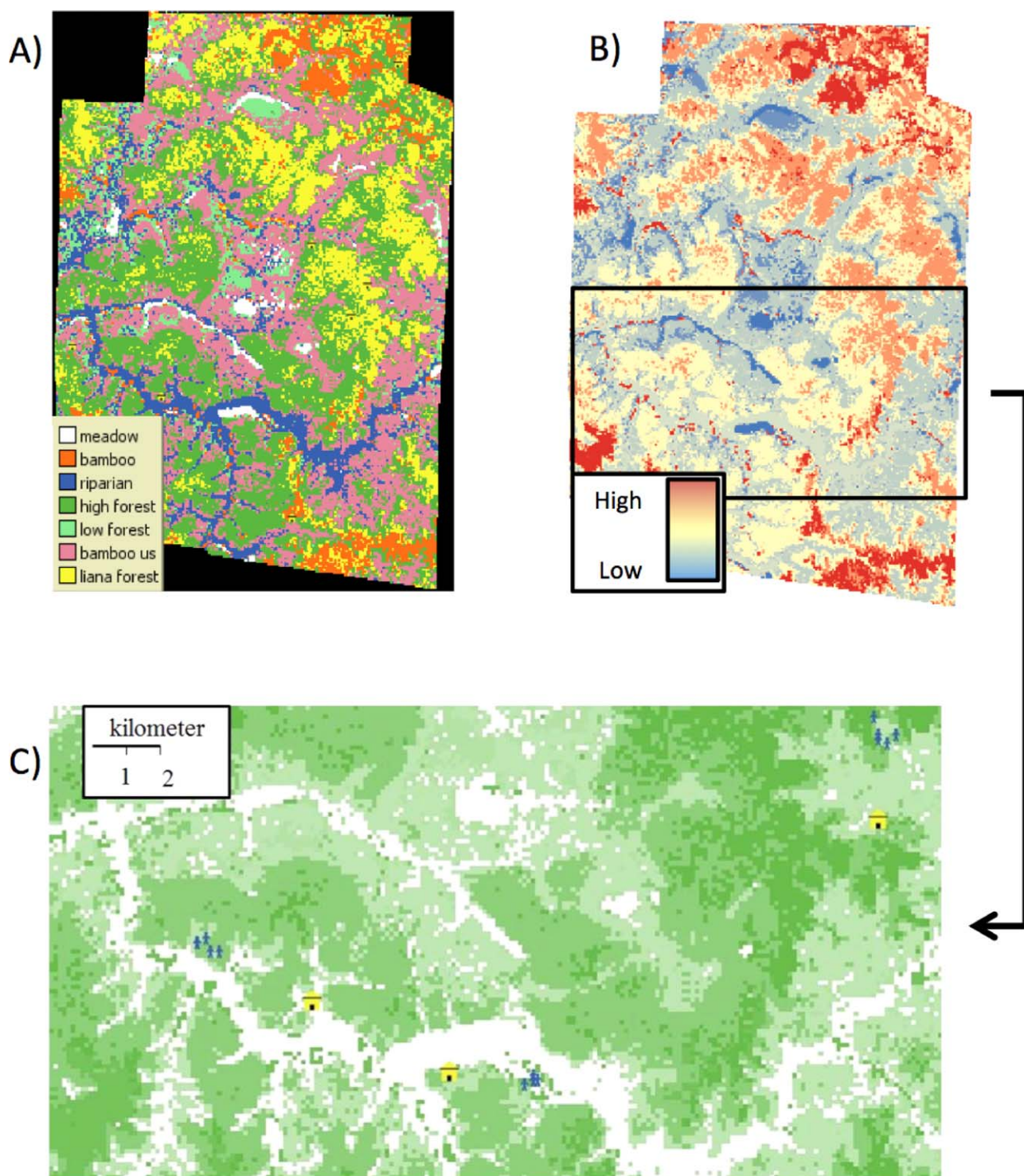
Figure 1. The transition from a vegetation map to an ABM map. A) The vegetation map of the Mbaracayu Reserve; B) a map of 100 m x 100 m grids estimating Capuchin encounter rates; C) the ABM map of resource distributions and encounter rates for agents to exploit. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

predators. Agents' behavior can be changed to study the effects of ranking different encountered options of food, spatial memory, exchange of information, and coordination. We can incorporate the value of nutrients other than energy because humans are omnivores.[32] They also consider goals such as risk and reduction of variability in addition to nutrient maximization,[33] whether prior knowledge of resource location and availability through time is likely and the value of foraging for information e.g.[25]), as well as the fitness value of
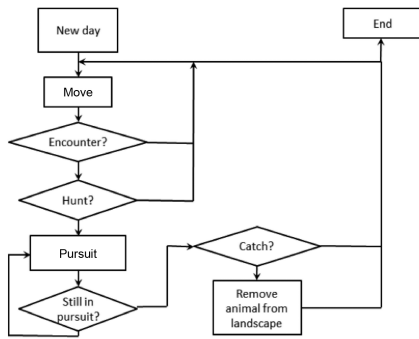
Figure 2. Flow chart of the model for one hunter during one day. The model is run in steps of 5 minutes for an average of 355 minutes of hunting a day.

resource acquisition beyond provisioning (for example, costly signaling[34]). Because of these complications, no single model of foraging behavior can be asserted on theoretical grounds to be the "correct" model. Instead, we can simulate expected behavior under a variety of assumptions and then look for robust patterns that appear likely under a range of conditions and compare those to the empirical record.

How do we know that the decision rules and logic defined in an FT-guided ABM will produce biologically and ethnographically realistic outcomes? We propose that these can be tested on spatial and temporal data sets that exist for modern hunter-gatherers and nonhuman primates to create realistic models to apply across the time span of human origins. Our research program has already begun this process using data from the Ache foragers of Paraguay.[31] Detailed information on resource distribution patterns and foraging decision criteria drawn from FT[32,35–37] were used to develop an ABM of foraging behavior based on ecological parameters of the environment and prey characteristics measured in the Mbaracayu Reserve, Paraguay. We began with a vegetation map developed from systematic field observations and subsequent supervised classification of a Landsat 7 TM image with six optical bands and one thermal band.[35] We then superimposed a grid of 58,408 one-hectare cells. Each 100 x 100 meter cell in the model was assigned a vegetation type based on the overlap

with the vegetation map. These included seven major vegetation classes easily distinguished by anthropologists and the Ache: meadow or grassland, large bamboo forest, riparian forest, high forest, low forest, small bamboo understory, and liana forest. We elected to keep the vegetation types simple because when we extend this ABM approach to prehistoric hunter-gatherers our paleo-vegetation maps will, of necessity, be simple. Each cell was assigned prey encounter rates based on measured vegetation-specific encounter rates, growth, migration and harvest rates, and the recent passage of a hunter (inducing game to flee or "hide" for some time) (Fig. 1). Our simulated foragers then followed a simple one-day foraging routine (Fig. 2).

Comparison of the predicted foraging behavior from the model to the ethnographically observed behavior of Ache hunter-gatherers who inhabit the region showed a close match for daily harvest rates, time allocation, and species composition of prey. The model has also been used, under Ache-like ecological conditions, to explore the implications of social living, cooperative hunting, and variation in group size and mobility. However, in each of the alternative-agent-based foraging models developed for the Ache, the resource distributions are well-known, measured through extensive sampling with random transects. What do we do with the past?

CONSTRUCTING A PALEOSCAPE MODEL

In the research agenda we advocate, the behavior of our simulated foraging agent will be guided by FT-based rules of logic and behavior. However, that agent needs an environment or landscape within which it faces choices of known costs and benefits; this poses the greatest challenge to the paleoanthropologist projecting into the past. In the modern world, we can quantify these with direct and remote observation and modeling. But to understand how climate and environment affected hominins in the past, we need to

reconstruct or hindcast a model of the ancient paleoscape.[38,39]

The paleoscape model, which is a robust projection of the main resource sets valued by our ancient hominin, with costs and benefits attached to each, is used to make spatially explicit predictions for different climate states. How do we build a paleoscape model rooted in FT and suitable for an ABM? This must begin by defining and locating the mosaic of meaningful habitats and resource patches on the landscape. This mosaic is probably best represented by vegetation types and other spatially explicit units that have resources within them, such as rivers, lakes, coastline, inselbergs, and raw material sources. To illustrate this, we will make regular reference to our research effort on the south coast of the Cape of South Africa, where we are building a paleoscape model to help us better understand the lifeways of early modern humans.

It is important that habitats and patches have specific characteristics that allow us to project their placement on the paleoscape in the past. At the Cape, the first and most important habitat feature that can be spatially delimited is the coastline. The coast is low-hanging fruit to a modeler; its location and shape are easy to project into the past since they are products of sea level and topography,[38] and its location is crucial to a human forager that uses coastal foods.[39] Figure 3 shows the distance to the coast from site PP13B at 1.5 ka time steps during the time of occupation as projected by the coastline model. It also shows both the type of intertidal habitat exploited, as reconstructed from shellfish discarded on site, and the occupation intensity, as determined from archeological excavations. This very simple component of a paleoscape model shows that coastline distance has a clear impact on hunter-gatherer occupation of the site: when the coast is far away, the hunter-gatherers either abandon the site or leave it lightly occupied. The next step is to improve the detail of our model by subdividing the coastline into habitat types, such as sandy
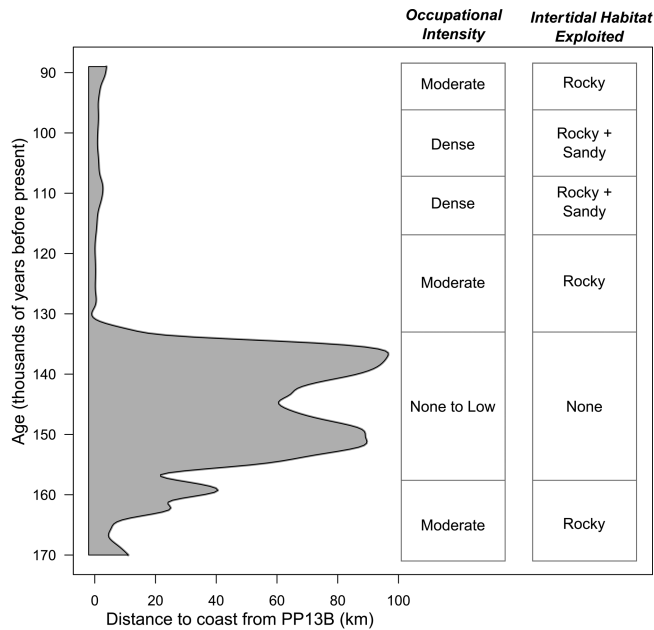
Figure 3. Application of a simple component of the paleoscape model. The figure shows the distance to the coast over time from site PP13B, the intertidal zone exploited by people as reconstructed from discarded mollusk remains and the intensity of human occupation as reconstructed from the archeology.

day basis, might be important to early humans. Research then needs to be done to generate encounter distributions and return rates for relevant resources.

Glynn Isaac[48] set in motion a research strategy in paleoanthropology to characterize potential hominin resources by organizing a coordinated study of plant distribution,[49,50] plant exploitation,[51] and animal carcass distribution and use[52] in ecosystems considered to be models of where hominins had lived. Isaac's foresight was in seeking knowledge of the foraging returns from resources in different habitats. Isaac eschewed the application of FT, which thrived in other research realms such as Great Basin archaeology.[53] The research program advocated by Isaac was largely abandoned after a first generation of effort. So, to this day, we still have very little knowledge of the foraging returns of the major resource types in East Africa and their occurrence in the different East African habitat types. We argue that such knowledge is essential for any interpretations or modeling of early hominin diet. For example, while new research has uncovered a fascinating pattern of changes in the dietary isotopes of early hominins,[54] there is no knowledge of how this relates to different food types, their return rates, and their potential encounter rates in the various habitats. We argue that a theoretically grounded interpretation of these changes in dietary isotopes and their relation to climate and environmental change will not be feasible until such knowledge exists.

The paleoscape model has both empirical and hypothetical dimensions. The empirical dimension is the construction of a model for present conditions; the hypothetical dimension then projects it into the past under differing climate states. In our study, we seek to generate four model states: strong interglacial (equivalent to the modern conditions), moderate interglacial, moderate glacial, and strong glacial. We choose these four states because they are tractable and cover most of the range of climate variation over the temporal boundary conditions of

beach versus rocky shore, and then assign prey encounter and harvest rates, as well as depletion rates to each habitat. We have now collected most of the relevant data using modern coastal people.[40] The experimental measurement of resource acquisition rates has become an increasingly common method in ethnoarcheology and hunter-gatherer studies.[41–45] Work of this type is needed wherever hominin foraging is of interest.

The location and productivity of terrestrial habitats and resource patches may be more difficult to define and model. In order to hindcast relevant resource distributions, the distribution and character of these patches must be predictably determined by basic climatic and edaphic characters, including the amount and season of rain, as well as geology, slope, and drainage. In our study, we chose the major vegetation types of the Cape Floristic Region,[46,47] most of which are unique to this region of high species endemism, with fynbos, renosterveld, strandveld, succulent karoo, afromontane forest, thicket, and riparian vegetation as habitats. In East Africa, the most appropriate units would

also likely be vegetation types such as edaphic grassland, acacia woodland, and so on. Each region would need a classification appropriate to that region. Vegetation communities are chosen to define habitats because broad vegetation types are generally associated with or defined by suites of plant and animal species (ecological communities), some of which provide key resources for hunter-gatherers. Vegetation types are expected to provide a first order approximation of the density and distribution of those resources.

Then we need to define and measure the typical distribution of patches and prey types that would have been important to hominins within each habitat type. Critical resources used in technology or manufacture can also be treated as patches or "prey" with optimal requirements for acquisition over defined time periods. To a hunter-gatherer in the Cape and, indeed, in most other environments, the suite of important resource types might include things like resins for glues, wood for fires, animals to hunt, carbohydrate-rich food plants, stone for tools, ochre sources, fresh water, and other things that, on a day-to-

modern human origins.[55–57] Our first attempt will be with strong glacial conditions. The goal is to project the distribution of habitats into the past under these conditions. While this is reasonably straightforward for some structural characteristics, like the coastline, it is more difficult for others, like submerged riverine floodplains and aeolianite reefs. Delimiting habitats that are defined by vegetation types is an even greater challenge. However, there have been significant advances in techniques to project vegetation and plant species using correlative distribution models[58,59] and mechanistic dynamic global vegetation models.[60–62] Such models have been used with paleoclimatic reconstructions to address questions in biogeography and evolution, including those related to Pleistocene glacial refugia, megafaunal extinctions, Holocene paleoecology, and human paleo-biogeography.[59] Franklin and colleagues[63] lay out a paleodistribution modeling approach that is a core feature of our research strategy.

Paleodistribution modeling studies typically use the same suite of modern statistical and machine learning models[64] that are well established in vegetation distribution modeling,[65] to associate observations of vegetation type (or species) with environmental predictors (climate, geology, soil, topography) derived from geographic information system (GIS) maps. We acknowledge that the Pleistocene may have held vegetation types that have no modern analog; one is possibly on the Paleo-Agulhas Plain, currently under water off the south coast of South Africa. In contrast, dynamic global vegetation models are simulation models based on first principles understanding of plant ecophysiology, competition, and demography, even extending into aspects of shade and fire tolerance, that predict the distribution of functional communities (for example, forest or grassland) in given environments. These models, built or tested on contemporary distributions, can be applied to predictively map distributions under past[61,66] or future climates[60,62,67] by substituting the climate maps and assuming that

other environmental factors are static (or that their distributions, such as distance to coast, can be also be reconstructed). For example, paleodistribution models of subtropical thicket, a species-rich vegetation type that supports a large browser fauna and is currently found in the eastern and southern Cape region of South Africa, are consistent with the hypothesis that the extent of this vegetation was greatly reduced during a strong glacial such as the Last Glacial Maximum, and contracted into basin valleys.[66,68] These paleodistribution predictions can also then be tested using independent evidence; in the case of the subtropical thicket, model results are supported by phylogeographic[69] and ecophysiological[70] evidence.

A key element of the paleoscape model is therefore a spatially explicit reconstruction of those aspects of climate that control or limit vegetation or other resource distributions at a relevant scale. These include, for example, bioclimatic variables such as mean precipitation during the warm season or minimum temperature of the cold season[71,72] under the climatic boundary conditions of strong/moderate interglacial to moderate/strong glacial states, including shifted wind systems and weather patterns. The development of global circulation models to predict future climate change is an extremely active and growing research field, and has largely driven the concomitant application of such models to past climate states (for example, the Paleoclimate Model Intercomparison Project stages 1, 2, and 3). However, these models are simulated at coarse environmental scales, whereas paleodistribution models for biological components require far greater resolution.[59] Topography modifies synoptic weather and climate so that temperature and moisture regimes experienced by organisms vary with elevation, hillslope position, slope, and exposure.[73] Thus, global circulation model simulations need to be downscaled for biological applications. This downscaling is not trivial and has received much attention.[74] Downscaling can be divided into two primary approaches, statistical and

dynamical.[75] Whichever approach is used, the climates or distribution models will need to be tested against independent lines of evidence, such as paleoarchival or phylogeographic evidence.[76] Thus, coarse-scale climate simulation data that are downscaled to reconstructed topographic surfaces (for example, accounting for changes in sea level and coastline position[77]) and validated against independent evidence are crucial for modeling paleoscapes at a scale relevant to human foragers.

In our case, we benefit from the fact that the Climate Studies, Modelling and Environmental Health research group of the Council for Scientific and Industrial Research has in recent years developed an extensive regional climate modeling capacity in South Africa through the application of a high resolution, dynamic climate model.[78] The variable-resolution global climate model, known as the conformal-cubic atmospheric model of the Commonwealth Scientific and Industrial and Research Organisation is normally implemented on computer clusters of the South African Centre for High Performance Computing. We run this model on USA Extreme Science and Engineering Discovery Environment supercomputers to hindcast paleoclimate. We downscale global simulations of paleoclimate over the south coast of South Africa at about 8 km resolution. Similar collaborations between paleoanthropological projects and climate modelers can provide the paleoclimates to create our paleoscape maps.

Paleoscape modeling at fine grain allows us to synthesize mosaic maps of habitat types based on vegetation, coastal proximity, rivers, and other features. Human foragers, however, do not search for, pursue, and redistribute habitat types. Instead, they exploit (and are exploited by) individual resources and organisms that are found in habitats. Hence, the next step in the causal chain to behavior is to convert a suite of habitat types into probabilistic maps of resource distributions through time and space. This can be accomplished primarily by two methods, field-based census and literature reviews

Comparison to Paleoanthropological Record

Compare to archaeological data, isotopic results on diet, anatomical data, etc.

Develop Agent Based Simulation

Agent rule-set built from Behavioral Ecology and Ethnographic Observation

Experiments – Agent Released into Paleoscape

Generate explicit expectations to be tested in the paleoanthropological record

Explore impacts of changing parameters e.g. hunting type (cooperative versus solitary), communication between hunters, territorial or not, etc.

Paleoscape Model for a Specified Climate State

Projected habitat types and paleotopography

Gridded 100m × 100m overlay

Each grid includes resources and their return rates

Paleovegetation

Vegetation distribution models

Dynamic global vegetation models

Proxy archives

+

Resource Return Rates

Studies of modern people (hunter-gatherers

Experimentally-derived resource return rates

Literature –derived resource return rates

Paleoclimate

Proxy archives (lake cores, speleothems, diatomite isotopes, etc.) build details and test model predictions

Downscaled global climate models generate expectations

Go to another Climate State

+

Paleogeography

Geology and soils (onshore/offshore mapping)

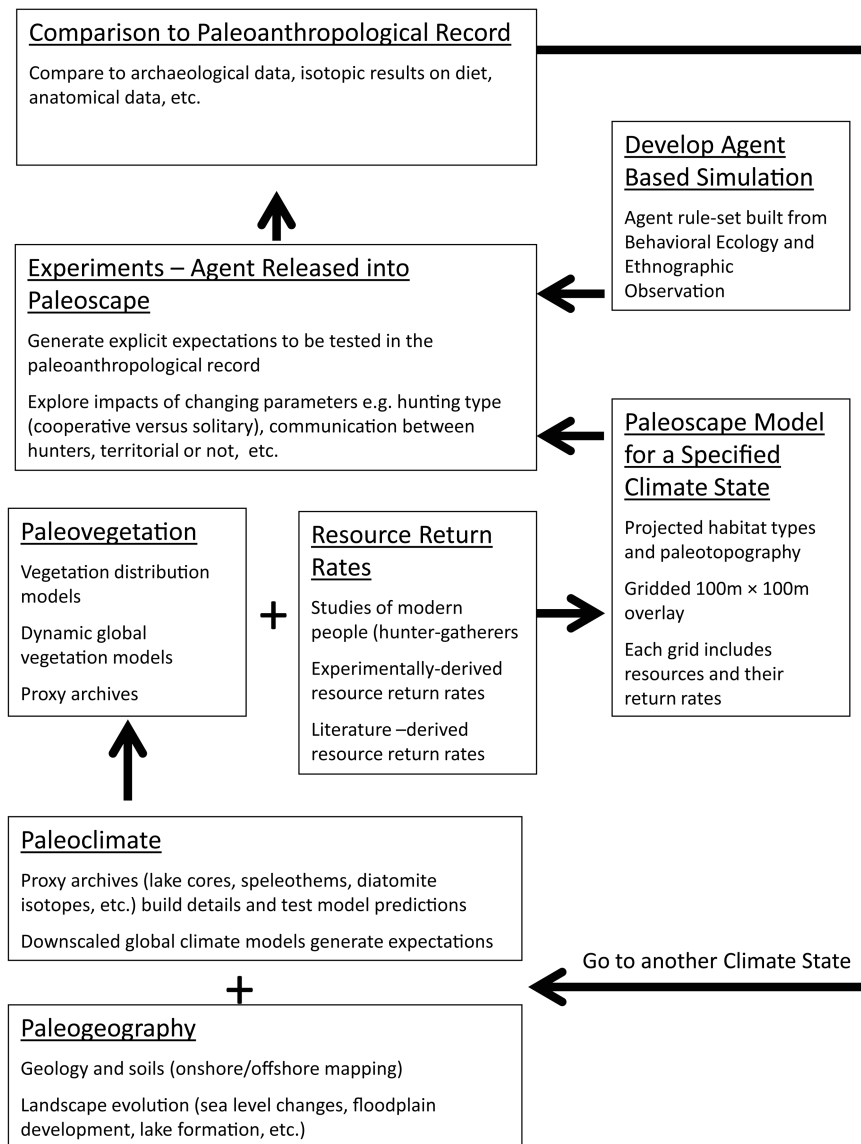Landscape evolution (sea level changes, floodplain development, lake formation, etc.)

Figure 4. A schematic diagram of the research model outlined in this paper.

that provide information based on detailed biological and ecological studies. This step will result in temporally patterned probabilistic locations and densities of specific resource patches, such as fruit groves, mollusk-bearing reefs, and patches of geophytes (plants with underground storage organs), and individual prey types, such as rock hyrax, eland, octopi, *Turbo* snails, and *Cyphia* tubers, within each habitat or patch that can be verified by surveying a random sample of mapped habitats. Currently, for example, we estimate that the biomass density of underground storage organs shows about a five-fold range across the major habitat types along the coastal region of the Agulhas plain in South Africa. The density of each species in each habitat type is being determined through experimental field work. Future monitoring of not-yet sampled locales within identified habitats can determine if these estimates are robust. This type of conversion is a critical missing step in prior paleoanthropological studies and is the primary reason why climate and vegetation data in these studies cannot confidently be converted into specific behavioral and evolutionary predictions.

After resource encounter rates have been established at an appropriate scale, we need detailed information about each resource type that is relevant to the theorized decision criteria of the forager. Minimally, this will include estimates of mean "handling time" required to harvest a prey or patch, then process the resource for consumption; the probability that an attempted "pursuit" of the resource will be successful; and the mean expected food value from a harvested item. When the resource target is distributed in patches, the cumulative gain rate with exploitation time ("gain function") must be established. The measures of handling time, success rate, and mean prey weight can all be obtained through either ethnographic observation or field experiments. Observation should be of foragers using similar technology (or some appropriate adjustment for technology based on experimentation) and attempting to harvest a similar prey type to those being modeled. When this is not possible, ethnographically informed experimentation can also produce useful estimates of the required parameters.[42–44,79,80] Finally, food types must be analyzed in the laboratory for nutrients relevant to the decision criteria developed in the next step of the process. Minimally, this will include both energy and protein content for the edible portion of each resource type.[32]

The last step is to predict forager behavior under conditions of known resource density and distribution, using theoretically based assumptions about forager goals and evolved decision- making algorithms. As a starting point, many behavioral ecologists assume that foragers are designed to maximize nutrient gain rates through time because, according to some monotonically increasing function, these can be converted into higher genetic contribution through time.[25] When foragers are assumed to maximize energy gain rates, specific models that test the outcomes associated with different dietary choices, movement patterns, group sizes, and investment in territorial defense can be examined.

Decisions that maximize the gain rate can be detected when compared against other possible behavioral strategies. Alternatively, we can assume other foraging goals, such as meeting a specified nutrient threshold each day (variance sensitive foraging) or maximizing the probability of obtaining large and widely shared food items (costly signaling). Once the environment is specified and the forager goals are programmed, we can simulate harvest patterns under those conditions and derive predictions about archeological assemblages that would be produced under those assumptions. The ultimate goal is to produce a series of models that make different assumptions about forager behavior in the recreated environment and result in archeologically testable predictions.

The Ache model[31] provides a concrete example of how this can be accomplished. Resource censuses based on over 11,000 km of random diurnal transects within this region allowed us to estimate the encounter rates of 26 potential prey species within the seven major habitat types discussed earlier. For detailed foraging analyses, we focused on two dozen of these species, including those that comprise over 95% of the meat in the Ache diet.[37] This allowed us to assign each 100m x 100m square within the Ache model landscape to a habitat type based on Landsat imagery and GIS mapping (Fig. 1A), then convert habitat type to a list of mean resource encounter rate probabilities for a forager searching in each one-hectare area (Fig. 1B). Because encounter rates were based on reports by the hunters themselves and recorded only when a pursuit of the prey item was possible, these represent true foraging encounter rates (by time or distance), not just census observations of prey. (A herd of impala on a distant hillside is not a foraging encounter because no pursuit is possible for the hunter.) We developed a computer simulation in which agents behave according to the prey choice algorithm of FT[25] and hunt the same number of hours per day as Ache foragers. Hunters also camp together, search randomly, and join

each other in cooperative pursuits. Game is spooked when hunters search an area recently searched or depleted when harvested. Game also migrate and reproduce according to known biological parameters. The model is realistic and empirically based, yet simple enough to capture basic outcomes. The model also suggested that both the observed Ache mobility pattern and observed band size are close to optimal, given the search interference and pursuit cooperation that is possible with multiple hunters. This exercise shows that if we can accurately produce estimates of the foraging potential of a landscape, here directly

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measured by field work, then an agent that follows the prey choice algorithm of FT predicts Ache behavior very well. It then follows that if we can accurately produce these foraging potential estimates for paleoscapes, we can use an ABM grounded in the prey choice algorithm to make high quality predictions of hominin behavior in the past. This pilot work appears to confirm our proposition for paleoscape modeling: The placement of individual resources on a virtual landscape is the critical step that allows modeling and specific behavioral predictions based on foraging theory and climate-driven habitat change.

To summarize, climate, geological, and topographical projections are used to create a spatial mosaic of likely habitat types, which, in turn, deterministically predict resource densities and

distributions (Fig. 4). These, in conjunction with measured parameters of costs and benefits of each resource type, become the set of constraints relevant to behavioral patterns, the outcomes of which can be tested through ABM. This results in explicit predictions about behavioral patterns that should have been common in past periods and environments. The final behavioral predictions, such as composition of exploited foods or group size and movement patterns, can then be tested against archeological assemblages from relevant time periods. In this way, modeling, driven by both empirical measures of environment and simulated behavioral outcomes, generates the test implications driving subsequent paleoanthropological research. The chain of causality is complex, but highly explicit at every step. The testing of hypotheses derived from predicted behavior ensures that the process is transparent and repeatable.

CONCLUSIONS

This paper highlights strategies to test dynamical connections between hominin resources and the environment as a means of progressing to a fuller understanding of hominin origins. Some stages of this research model in paleoanthropology are already well advanced. For example, the development of high resolution sequences of proxies for climate and environmental change and understandings of the relation of these proxies to real climate and environmental variables is a vigorous and productive science. As we move up the inferential chain in Figure 4, we enter increasingly weak theoretical territory. Research that links climates and environments to resource distribution patterns and their return rates is moribund, leaving the top of the chain powerless to make strong inferences. Both FT and ABM have independently made great strides. However, we argue that only by joining the two can we productively apply FT to questions of broad adaptive systems and organism lifeways and thus construct the "shifting adaptive landscapes" called for by Kingston.[14]

We understand that we map out an ambitious research program. Some may say that we cannot possibly create models of any validity for the extraordinary time spans confronted by paleoanthropologists. In our opinion, this is clearly incorrect with regard to the latter parts of the human origins record, where our environmental and climate information is undergoing a revolution in temporal resolution and specificity. Applying our research strategy to the far reaches of the Pleistocene and Pliocene is admittedly difficult. Nevertheless, even simple models have the potential to make important predictions and reveal unanticipated insights that can guide our research agenda in a much more productive manner than can the correlative endeavor that currently dominates the discipline. The multidisciplinary approach pioneered in paleoanthropology in the 1960s laid the foundation for a research agenda that would allow us to understand if and how climate and environment helped shape the evolution of our species. But to attain that goal we need to advance to the next level of strong inference, grounded in a robust and theoretically sophisticated research strategy that builds bridges between our proxies for climate and environment and those things that drive the decisions of an organism on a day-to-day basis. Finally, we need to understand the evolutionary implications of climate change acting on behavior, morphology, physiology, and cognition. This theoretical frontier will require us to model, for example, the conditions under which life history changes will evolve, cooperative behavior will be favored, increased social learning will be spread, theory of mind will become adaptive, increased social network size will be common, and complex communication will emerge.

The NRC report called for significant injections of funding to develop the high resolution climate and environmental sequences that, we agree, are key parts of a program of research to develop causative explanations for hominin evolution. But without construction of the changing paleoscapes that define the resource distributions that drive an organism's behavior, these new sequences will tell us little about hominin evolution. Research into understanding the details of the resource landscape of hominins has somehow been lost in paleoanthropology. Along with the efforts at sequence development, we need the combined studies of resource distributions and returns and paleoscape modeling to make those new climate and environment sequences useful. Advanced climate and habitat modeling, behavioral ecology and agent-based computer simulation of behaviors and outcomes can provide the toolset for developing causative explanations of hominin origins.

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