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Title: Ecosystem Engineering in the Quaternary of the West Coast of South Africa.

Running Title: Ecosystem Engineering West Coast of South Africa

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Abstract

Despite advances in our understanding of the geographic and temporal scope of the Paleolithic record, we know remarkably little about the evolutionary and ecological consequences of changes in human behavior. Recent inquiries suggest that human evolution reflects a long history of interconnections between the behavior of humans and their surrounding ecosystems (e.g. niche construction). Developing expectations to identify such phenomena is remarkably difficult because it requires understanding the multi-generational impacts of changes in behavior. These long-term dynamics require insights into the emergent phenomena that alter selective pressures over longer time periods which are not possible to observe, and are also not intuitive based on observations derived from ethnographic time scales. Generative models show promise for probing these potentially unexpected consequences of human-environment interaction. Changes in the uses of landscapes may have long term implications for the environments that hominins occupied. We explore other potential proxies of behavior and examine how modelling may provide expectations for a variety of phenomena.

Keywords:

South Africa, niche construction, archaeology, evolution, generative modeling, paleoecology

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1. Introduction

Climate-driven ecosystem change has influenced human behavioral and biological evolution for the past 5 Ma^{1,2}, and there is now awareness that humans, in turn, have played a significant role in shaping Earth's ecosystems³⁻⁵. The complex and dynamic relationship between humans and the ecosystems in which they have lived provides a record of the human response to tremendous and sometimes rapid environmental change. Understanding this history has direct implications for our comprehension of and response to future climate change⁶. Identifying critical features of these relationships in the past has been challenging because (A) the consequences of human-ecosystem coupling are often displayed over long time frames (1000s-10,000s of years), (B) the resolution of local environmental proxies is often out of sync with highly-resolved regional-to-global-scale archives, and (C) we lack robust tools to disentangle the dynamics of natural and human systems, and their coupling, using archaeological and paleoecological datasets. We require new approaches to investigate human-environment interactions in deep time and gain a better understanding of signatures of anthropogenic impacts on past landscapes. Real strides in this work will require an integration of existing datasets to connect archaeological, paleoclimatic, paleontological, paleoecological, and geological archives that are extensively time-averaged. Here we hope to contribute our knowledge about the evolutionary consequences of human impacts on ancient ecosystems by exploring ways that the archaeological record can be leveraged to investigate triple inheritance theory in the context of time frames that extend across hundreds of thousands of years⁷.

The study of ancient behavior is often considered to be a study of adaptive changes in the past. Although we do not know the adaptive significance of many variation observed in the archaeological record, the assumption has often been that such changes benefited the fitness of hominins⁸. Investigations of the evolution of certain behaviors often look at variability in both the archaeological record and climate, under the assumption that the former must represent adaptations to the latter⁹. When explicit investigations are performed, the timing of behavioral and environmental changes is rarely synchronous^{10,11}. This may be related to differences in our ability to detect and/or measure variability in the behavioral record at the same resolution as in the climatic record¹². Currently, there are few recognizable differences in the more ancient records of hominin behavior (e.g., prior to the Late Pleistocene) which correspond with well-documented climatic fluctuations. This is likely also attributable to the fact that environmental changes have their own variability within and between hominin habitats in the past¹³. As such, there are a variety of environmental conditions to which hominins adapt, and the changes we see in the archaeological record may occur over millennia¹⁴.

The challenge is then to understand how the individual actions by hominins in the past result in the time-averaged archaeological record. Recently, many high-resolution attempts have investigated the exact parameters that can be modelled to explore the relationship between environmental variation (e.g. water availability, stone availability) and the human behavioral response to these effects (e.g. stone artifact frequency, type of artifacts found)¹⁵⁻¹⁷. In contexts with high temporal resolution, well-resolved behavioral changes may be linked to specific climatic events¹⁸, yet the vast majority of our understanding of the past relies on traces of behavior and records of past climates that are substantially time-averaged¹⁹. It is tempting to assume that the information preserved on time-averaged landscapes is not informative for understanding evolutionary patterns because of the inability to temporally link climate and behavior. However, as the identification of factors that shape and organize behavior depends on their persistence through time, time-averaged contexts may provide greater clarity on evolutionary patterns²⁰. While it is more difficult to conceptualize processes that generate these contexts relative to shorter

timescales, the integration of generative (agent based) modeling allows insights into ways that we can create expectations of the archaeological and paleoecological record over longer spans of time^{21,22}. In this manuscript we explore aspects of the coupling of human and natural systems in the Cape Floral Biome, specifically in the ecosystems of the western coastal plain of South Africa that share specific ecological parameters (winter rainfall, low nutrient soils, high endemism)²³.

2. The Fynbos Ecosystem in South Africa: An Anthrome?

In contrast to the large body of research exploring how the natural world has influenced human evolutionary history^{1,2}, there is less understanding of how humans influence the natural world over evolutionary time-scales (10^3 - 10^6 yrs.)²⁴. Empirical data from younger time periods indicate that humans are ecosystem engineers with wide-ranging impacts on past systems^{3,4,25}, yet there has been little investigation of these issues deeper in time (> 10 Ka). A major challenge is the perceived difficulty of integrating measures of environmental change from the geologic record, which typically occurs over thousands of years, with interpretations of human behavioral patterns that are understood at ethnographic timescales that are often shorter than a human lifespan (e.g., hunting activities, movement patterns). This has hindered a comprehensive understanding of human-environment interactions and the co-evolution of human and natural systems deeper in time (i.e., >10 Ka). We outline a framework for studying these relationships through examination of a system that is ideally suited to this purpose: the Quaternary archives of human and natural systems from the West Coast of South Africa.

The West Coast represents the core of the hyper-diverse Cape Floristic Region²⁶, an area encompassing approximately 90,760 km² along the southern and southwestern margin of Africa. The Cape Floristic Region is characterized by exceptional floral diversity, including ~9,000 plant species, of which over 68% are endemic²⁷. Fynbos is the dominant vegetation type and includes three main types: fynbos (fynbos heathland), renosterveld, and strandveld. Fynbos vegetation is dominant and characterized by sclerophyllous fire-dependent shrubland occurring on low-nutrient soils; renosterveld occurs on more nutrient-rich soils and consists of evergreen asteraceous shrubs with a rich herbaceous understory; and strandveld is a littoral thicket vegetation dominated by sclerophyllous broad-leaved shrubs and Restionaceae (restios), with succulents increasingly dominating on the western coastal plain of South Africa. The climate of the western coastal plain of South Africa is Mediterranean, characterized by hot, dry summers and cool, wet winters (i.e., winter rainfall zone). Fire plays a key role in structuring vegetation communities²⁸. In contrast to the diverse floras, the western coastal plain has historically supported a community of large mammalian herbivores dominated by small-bodied browsers which are relatively low in species diversity and biomass²⁹.

Human impacts on ecosystems of the West Coast of South Africa in historic times are well-documented, and include landscape transformation and fragmentation, introduction of invasive species, altered fire regimes, and eradication of large mammals²⁹⁻³¹. At the same time, the archaeological record attests to a human presence on the western coastal plain that extends for at least the last million years³². Archaeological and paleoenvironmental archives provide clues suggesting considerable prehistoric human impacts on the hyper-diverse fynbos biome well before European colonization of South Africa (17th century). Pastoralists brought livestock to the region ~2,000 years ago, and historic accounts indicate that they used fire to promote grass growth for their herds, some of which were massive in size^{29,33}. The combination of fire and overgrazing and its effects on historic vegetation change is suggested by pollen records of the West Coast of South Africa³⁴. This signature provides a clear basis for inferring similar effects in longer-term sedimentary archives. Further back in time, archaeological evidence attests to increasing human impacts (e.g., greater harvesting pressure) on marine and terrestrial faunas through the Holocene, likely due to increasing human population^{35,36}.

This demographic shift has also been invoked to explain (in part) the extinction of several large-bodied grazers in the Cape Floristic Region near the Pleistocene-Holocene transition³⁷. Changes in the diversity of mammalian species in the Cape Floristic Region are evident in the Late Pleistocene. Faunal diversity (richness) is highest in the earliest parts of the fossil record on the West Coast of South Africa^{32,38}. Temporal declines in species richness is evident, with the lowest diversity recorded in the late Pleistocene and Holocene record. Many of these changes may be related to the different temporal contexts of these records (i.e. greater time averaging earlier in the Pleistocene record). However, there are precipitous drops in species richness in the fossil record at the end of the Middle Pleistocene (Hoedjiespunt, Duinefontein)^{39,40} compared to earlier time horizons.

Other aspects of the paleoecology of the Cape Floristic Region on the West Coast of South Africa are less well known. In particular, the prehistory of how humans used fire in the landscape of the Cape Floristic Region remains poorly understood. Hominins had acquired sophisticated knowledge of fire by at least 164,000 years ago⁴¹. Investigations on the origin of pyrotechnology identified evidence for the possible use of fire by the Early Pleistocene elsewhere in southern Africa⁴². Anthropogenic fire regimes may have aided foraging activities in the low nutrient parts of the ancient landscape⁴³. Similar patterns have been identified in Australia where burning of the landscape increases landscape heterogeneity and amplifies biodiversity⁴³.

There is intriguing evidence suggesting that the human footprint in the hyper-diverse fynbos biome is both ancient and considerable. However, the long-term human impact on this landscape, and its compound influence on trajectories of human-ecosystem coupling, have yet to be fully explored. In depth investigation of the impact of humans on ancient landscapes in South Africa needs to answer several key questions: To what extent is the current composition of the fynbos biome on the West Coast of South Africa an anthropogenic biome?²⁴ Has the long history of humans in this environment resulted in an ecosystem that requires some degree of human impact to maintain a stable state? Is the present ecosystem the product of passing certain thresholds in the interaction between environmental and human influences?

The answers to these questions will have profound impacts on our understanding of ecological inheritance, in the sense that even Pleistocene hominins may have inherited an ecosystem that was perturbed by previous generations of hominins⁴⁴. An exploration of human impacts on these ecosystems will provide the rare instance where archaeological data can provide input on the interplay between humans and their environments on a spatio-temporal scale that is relevant to evolutionary mechanisms⁴⁵. To explore these patterns at these scales, it is necessary to investigate the archaeological record in novel ways. Hypotheses need to be framed in a way that takes account of the vastly different scales that different pieces of information provide. Integration of broad-scale climatic records (e.g. offshore sediment cores) need to contend with the fact that these records represent highly-resolved time frames, yet spatially amalgamated information. On the opposite end of this spectrum are local environmental records that provide information with relatively small spatial averaging. The integration of these datasets will provide the chance to understand how local environmental contexts differ from, or responded to, broader climatic influences. The differences between these two records may provide insights into how humans modified local ecosystems.

The habitats of the West Coast of South Africa represent an ideal location to investigate the possible influence of human behaviors on ancient ecosystems because of several key factors. First, long-term records of environmental change are available in both terrestrial and marine contexts. These long-term records allow us to model the relationship between global climate changes and local ecosystem structure. This provides the chance to explore how ecosystem change is reflected in archaeological and geological records in which long time-spans are recorded as a cumulative record of individual interactions (i.e., time-averaging). Second, the presence of multiple aeolian-dominated sedimentary exposures allows for landscape-scale investigations of human and natural systems spanning the past one million years of human occupation in the Cape Floral Biome (Fig. 1). Third, multiple generations of archaeologists and geologists working on Quaternary research in the region have generated numerous large and well-curated archaeological, geological, and paleoecological collections^{23,39,46-48}.

3. Evolutionary Patterns in Archaeological Data

Investigations into the evolutionary significance of hominin behavior have often focused on large-scale trends in hominin behavior⁴⁹. As previously noted, broad-scale behavioral changes are often assumed to represent advances in some fitness benefit⁵⁰. There is evidence that tool use does reflect changes in access to certain resources (e.g. cutmarks that reflect changes in access to mammalian food sources), however current evidence is paltry and often contested⁵¹. Investigations into long-term trends in form of artifacts⁵² or landscape-scale behaviors⁵³ assume that some kind of fitness benefit is accrued in association with these changes in behavior. The empirical archaeological record provides a basis for measuring changes in behaviors, but these are most likely context dependent⁵⁴. Recent reviews of long-term trends in the archaeological record show that even when certain linear trends exist (e.g. changes in artifact dimensions over time), more complex interactions exist between contextual variables and the behavioral record. In other words, no single behavioral variable can capture the full spectrum of the intersection between hominin behavior and ecology⁵⁴. Many of the models of the evolutionary significance of human behavior are rooted in human behavioral ecology⁵⁰. These approaches often explore differences between modeled behaviors and those identified in the archaeological record⁵⁵. The power of these models is that they require archaeologists to be explicit about the assumptions of behavior inherent in evolutionary explanations and generate theoretically-informed predictions of behavioral change. Behavioral ecological approaches are ideal for explaining archaeological patterns because they focus on direct relationships between empirical data and hominin responses to environmental patterns. Theoretically, both can be modelled and investigated.

Behavioral ecological approaches are useful for explaining the day-to-day activities of individuals in the past, providing insights into interactions between individuals and their local selective environment⁸. Large-scale processes may be more relevant to evolutionary selection, yet they might not be sufficient to explain variability in individual behaviors³. Selection is evident as emergent patterns that occur not only through the realization of short-term goals but also through interactions that are not obvious from individual-level behaviors⁴⁵. The difficulty with these broader processes is that they operate at spatial and temporal scales that do not easily translate to our ethnographic understanding of behaviors⁵⁶. Although there are some examples of humans implementing changes in behavioral patterns that are directly focused on ecosystem engineering⁵⁷, it is also likely that many of the long term modifications to ecosystems are unconscious⁵⁸. The overall evolutionary consequences of individual behaviors are best observed over time scales that may have been impossible to predict at the time of behavioral change. Emergent patterns in the archaeological record require us to investigate contextual variables at spatial and temporal scales more relevant to human evolutionary processes (e.g., thousands of years and square kilometers).

These types of emergent patterns of behavior and their ecological correlates operate at scales that are more relevant to the growing body of theory on niche construction⁷. Although niche construction is difficult to identify in modern contexts⁵⁸, it has gained significant traction in archaeological literature³. This is particularly interesting because of the possibility that niche construction, for example, can contribute to our understanding of triple inheritance⁵⁸. In other words, do ancient hominins inherit an ecosystem that is modified in such a way that subsequent generations are adapted to this modified environment? This provides a conundrum for archaeologists and paleontologists because we often look at hominin behavior as a response to environmental change. If, in fact, ancient hominins were responsible for constructing local habitats, then identifying their responses to global climatic changes may not be the best line of inquiry⁷. The real question is whether or not we can correctly identify components of human impacts on local ecosystems. Attempts to identify Pleistocene hominin impacts have suggested that our predecessors have little influence on ancient ecosystems^{48,59}. However, humans currently influence almost every ecosystem on the planet⁶⁰, so it seems unlikely that human activity had no influence in the remote past.

A further difficulty in identifying niche construction relates to timing. Although niche construction can be manifested in numerous ways, two major features of niche construction are usually changes in behavioral patterning and consequent changes in the environment⁷. Examples of niche construction often relate to local perturbations of environments (although it can also involve relocation). Inceptive niche construction is the result of events in which human behavior changes, and the ecosystem structure responds to those behaviors. Counteractive niche construction relates to attempts by hominins to modify local ecosystems such that they can ameliorate the impact of broader-scale environmental changes. Each of these examples requires an understanding of the timing of events. In highly-resolved archaeological and paleontological sequences, the timing of these events may be relatively easy to assess²⁵. However, a majority of the archaeological record represents palimpsests of behaviors that occurred over long periods of time²⁰, making the identification of the timing of perturbations difficult to assess. The timing of these events is important, as it may be difficult to assess the difference between groups of hominins moving into a location because of a more favorable environment, as opposed to humans moving into a habitat, and by their actions, creating a more favorable habitat. It may only be through the power of generative modeling that we are able to identify these features⁶¹. Generative models employ agents in simulated ecosystems to create hypothetical archaeological records. This simulates the process of time-averaging by allowing agents to create records that overlap depending upon changing environmental conditions.

4. Modeling the Past

Investigations of long-term trends and ecological inheritance require an understanding of time-averaged records of behaviors. The challenges of teasing apart human-driven versus natural ecosystem changes, and the interactions between them, can be addressed through generative modeling⁶¹. Generative models, in which micro-scale interactions produce macro-scale patterning, are particularly powerful in their ability to develop testable predictions concerning expected empirical patterns in archaeological and geological archives under different configurations²². The development of models requires well-founded assumptions of uniformity between observations of systems operating in the present and analogous processes operating in the past as reflected in archaeological and geological archives. These observations may be derived from contemporary human activity and ecological processes. However, while the formation of such archives is the outcome of short-term actions, patterning in these records relevant to human evolution and paleoecological processes occurs at temporal scales that exceed human lifespans. Such records not only accumulate evidence of individual human behaviors or ecological processes, but are also organized in time and space, resulting in emergent qualities that are not captured by a study of proximal causal mechanics alone⁶². Paradoxically, the long duration of geological and archaeological data which allows us to view time-transgressive patterns is exactly the feature that makes understanding their dynamics so difficult.

Computer simulations can circumvent this difficulty by representing the “verbal logic”⁶³ of a process or system presumed to have operated in the past, functioning as a laboratory where that logic can be tested and outcomes compared. Generative models such as agent-based and individual based models are well-suited to the task of understanding long-term accumulations by simulating how patterning emerges through the interactions of individual system components over time⁶¹. Parameter spaces, or combinations of variables defining the totality of possible outcomes⁶⁴, are explored incrementally to evaluate their influence on the behavior of the model²¹. When grounded in an experimental framework, generative models can be used to evaluate the ways in which a set of proposed mechanisms might be expected to produce patterning in an observed archaeological or paleoecological proxy, and suggest empirical tests for evaluating their differences. The objective is to understand how the patterns form in a proximal sense; that is, in the absence of wider organizing forces, how the mechanics might be expected to behave. In particular, we focus these models on proxies that are abundant in the archaeological and

paleoecological record, which increases the likelihood of having large enough datasets to compare these patterns across more than one parameter configuration.

An example application explores the record of ungulate dental remains as ecological proxies of ancient ecosystems. Stable carbon isotopes ($\delta^{13}\text{C}$) are widely used to track the relative contribution of C_3 (dicots and temperate grasses) and C_4 (tropical grasses and sedges) plants in the diets of fossil herbivores^{65,66}. Unlike other African settings, the West Coast is dominated by C_3 grasses, reflecting the dominance of winter rainfall and a cool growing season⁶⁷, though there is evidence for some C_4 grasses during the Pleistocene⁴⁰. This poses a challenge for interpreting the $\delta^{13}\text{C}$ signature of fossil teeth, because it is uncertain whether a C_3 signature reflects consumption of C_3 grasses or dicots. This issue can be rectified through application of dental microwear texture analysis (DMTA), which discriminates between consumption of grasses and dicots based on patterns of microscopic wear (e.g. scratches and pits) on tooth enamel⁶⁸. Both proxies in tandem can inform on whether fossil herbivores were consuming dicots versus grasses, and whether those grasses were C_3 or C_4 .

To capture important elements of this process, we model habitats with different levels of fragmentation (reduction of continuous tracts of a single vegetation type), different amounts of woody and graminoid vegetation, and different proportions of ungulates adapted to grazing versus browsing (as well as mixed feeding). The underlying maps that detail the distribution of vegetation are necessarily amalgamations based on potential frequencies of vegetation as determined from our knowledge of the ecosystem of the Pleistocene⁶⁹. Although models, like this one, are heavily influenced by the underlying maps of ecosystems, we choose to keep the basic parameters of these modelled ecosystems vague so that they have broader applicability across a range of possible locales. By modifying the parameters of the underlying vegetation maps, we can then assess the influence of various components of the vegetation structure. This provides the chance to explore the proxies of ancient vegetation in more detailed ways (e.g. spatial distribution, seasonal variation).

We develop these models to predict the variation in proxies of ancient vegetation using multiple simulated proxies of ungulates. These simulated ungulates move and feed, thereby recording simulated proxies of the habitat they occupy both in and on their teeth (i.e. isotopic signature and dental wear). These simulated proxies are then “discarded” into an accumulated and time-averaged record. After a simulated animal dies, these teeth are deposited in a virtual sedimentary record. Once this virtual sedimentary record of dental specimens has been created, it can then be sampled across space. This sampling simulates the vagaries of the fossil record, whereby not all ancient habitats can be sampled at equivalent levels. It is then possible to use combined isotopic and microwear signatures to explore the extent to which paleodietary signatures faithfully represent different vegetation regimes (Fig. 2).

This example (M1) exhibits the key traits of the experimental approach of generative modeling we use to address time-averaged records. The parameter space is defined by variables that can be explored within clearly delineated limits (e.g. highly fragmented to highly homogenous habitats). The individual activities of ungulates, played out over time, produces aggregate patterning in the attributes of the simulated dental assemblage. Additional models, used to explore different processes and proxies, follow similar form. For example, another model (M2) explores how the distribution of fuel load (vegetation that can be burned), the return rates of different plants, and ignition frequency⁷⁰ contributes to evidence of different burning regimes on ancient landscapes (e.g. polycyclic aromatic hydrocarbons, burned phytoliths, microcharcoals)^{71,72}. A third (M3) examines how lithic reduction and selection, as well as patterns of forager movement (e.g. tortuosity) and raw material availability, contribute to geometric attributes in stone artifact assemblages^{22,73}. These generative models, discussed in more detail below, can be used to derive expectations from different configurations of human behavior (e.g. firing, movement) and environmental conditions (e.g. fuel loads, raw material distributions) on time-averaged records (e.g. microcharcoals, artifact assemblages).

The findings from this experimental stage are then used to suggest mechanisms that might lead to the emergence of known patterns, providing provisional explanations and opportunities to seek links between multiple

models. For example, a parameter configuration in M3 might be shown to produce patterning in stone artifact assemblages consistent with those recorded in the field, while a configuration in M1 might be consistent with recorded distributions of isotope and wear patterning. Through the theoretical link of humans seeking desirable habitats for hunting and foraging, for example, we aim to determine whether both patterns (stone artifacts and dental patterning) might emerge from a common socioeconomic process (foraging) as expressed in the model. If they do, then the theoretical link is provisionally secure. If not, then the theoretical link requires reconsideration, leading to insights into the processes in question based on the mechanics of the models themselves.

These coupled models are placed into a spatially-explicit context where resource availability is driven using the long-term paleoclimate proxy data (e.g. marine cores), with knock-on effects for human populations. At the same time, human agents within the models are given the capacity to change their behaviors, such as rates of burning or species targeting, in response to changes in the environment. In the outcomes of these interactions, constrained by the empirical patterning discussed above, we examine how human groups, given certain capacities for adaptation, may influence the local environmental conditions analogous to those found through time. The variation in (modeled) forager response to different levels of habitat variation and comparisons with the empirical archaeological data help us develop hypothetical narratives about how the human response to environmental change varied through time, identified using regularities in model time-series outcomes²¹. We then compare this with measures of human impact on environments to determine which aspects (if any) of ecosystems on the West Coast of South Africa may be the product of—and potentially dependent on—human behavior.

5. Preliminary Results: Landscape Use

Models of the ecosystems of the West Coast of South Africa are still ongoing and require further data to provide a fuller explanation of the interaction between hominin behavior and ecosystem variance. However, some understanding of changes in hominin movement patterns allows for a preliminary investigation into how humans may have used landscapes differently in the past⁷⁴. Here we focus on the archaeological records of two well studied ancient landscapes at different temporal scales. The Geelbek Dunes have been the subject of intensive landscape scale archaeological investigation for over a decade^{75–77}. Deflation of Quaternary deposits in the Geelbek dunefield has exposed several land surfaces (e.g. paleosols) that have been dated and provide insights into the use of these ancient ecosystems from the Middle Stone Age (~150 ka) through to recent times (~200 years BP)^{76,77}. Although most archaeological materials were recovered from surface contexts, the ability to identify underlying paleosols that are associated with specific time horizons allows for an understanding of changes in landscape use at different times in the past^{76,77}. The extensive mapping that has been conducted throughout this dunefield provides a rare opportunity to investigate these patterns over relatively large spatial scales⁷⁷. High densities of stone artifacts recovered from these landscapes allow for an investigation of the types of movement proxies that are described in our models.

The ecosystems of the mid-Pleistocene of the Cape Floristic Region are recorded in another nearby dunefield locality known as Elandsfontien. Over 100 years of investigation into the prehistory of Elandsfontien have produced one of the largest faunal assemblages available from the African mid-Pleistocene^{39,78,79}. Excavations at Elandsfontien have recorded the presence of hominins that produced Acheulean tools^{32,78,80} and indicate that hominins had some behavioral association with the fauna found at the locality⁸¹. Explorations of the isotopic ecology of the region suggest that hominins occupied this environment at a time when the region hosted an abundant large mammalian fauna in association with an ecosystem that differs dramatically from the contemporary low-nutrient strandveld that exists in the region today^{32,82–84}. Hominins may have transported stone artifacts to the dunefield to gain access to large mammal resources. These ancient landscapes likely date from the mid-Pleistocene and may even predate the Brunhes-Matuyama boundary³².

The Quaternary archaeological record indicates a temporal increase in the movement pattern of stone-tools through space⁸⁵. This is likely associated with changes in movement patterns that relate to shifts in the biology and sociality of more recent hominin populations⁸⁶. We expect broad differences in the use of space to reflect the evolution of behavior and sociality through time. The needs and capabilities of mid-Pleistocene hominins, which predate the dramatic behavioral changes seen with the appearance of modern humans⁸⁷, will likely be reflected in more tortuous movement with fewer instances of longer-distance linear transport. These patterns are expressed in the archaeological record as the result of cumulative behaviors which translate to emergent patterns when repeated over millennia⁷³. Ethnographically, patterns of landscape use are largely dictated by the availability and distribution of resources. An increase in aridity during interglacial periods⁸⁸ may favor human mobility patterns that integrate large, more structured movement through space (i.e. greater connectivity between a network of targeted locations over large territories) and a greater reliance on logistical forays⁸⁹. This is further enhanced by longer-distance social networks allowing a greater use of space in later time horizons⁹⁰.

More tortuous paths are easily identified with behavioral indicators recorded in whole assemblages⁸⁶ (Fig. 3). In archaeological contexts where assemblages are dispersed across large areas, it is possible to assess the overall landscape usage. Both Geelbek and Elandsfontein have multiple archaeological sites spread across laterally exposed landscapes for several kilometers^{32,77}. Analysis of stone artifact assemblages indicates that mid-Pleistocene (1.0-0.7 Ma) archaeological sites at Elandsfontein produce a pattern indicative of more circuitous paths and lower velocity of movement through the landscape (Fig. 4). This stands in contrast to patterns exhibited in the “bays” (deflation surfaces where Quaternary sediments are exposed at the surface) of the Geelbek dunefield. Based on geological context and results of radiometric studies, specific archaeological collections from the individual “bays” (deflation surfaces where exposed Quaternary sediments are exposed can be seen at the surface) can be definitively assigned to specific time frames. Thus, it is clear that the behavioral record from all localities at Geelbek reflect patterns of landscape use by hunter-gatherers who inhabited this region during parts of the Late Pleistocene and late Holocene (~5-0.2 ka). This patterning suggests that these hunter-gatherers utilized specific locations on the landscape as hubs of activity. These loci represent areas where occupation occurred repeatedly, while other locations on the landscape seem to show only sporadic use. It should be noted that a variety of different strategies of landscape use certainly existed in the past. However, its underlying structure may have shifted from the Early Pleistocene into the Late Pleistocene, such that hunter-gatherers used facets of the landscape in fundamentally different ways⁹¹. This type of patterning would be expected when people use certain parts of the landscape for logistical forays and others as central places⁹² and stands in contrast to the patterns exhibited at Elandsfontein, where hominins appear to use many parts of the landscape in similar ways (Fig. 4).

It should be noted that the toolkits found at these two sites differ in terms of their technological patterns. In general, Elandsfontein contains large bifacially flaked cores in many localities, although there is significant variation across the dunefield. The archaeological record at Geelbek includes prepared core technology of the Middle Stone Age and small laminar technologies of the Later Stone Age. Furthermore, the collection strategies and temporal depth of these two sites differ greatly. The materials from Elandsfontein stem from systematic excavations of discrete stratigraphic units and derive from a horizon that is relatively contemporaneous across this ancient dunefield (although thousands of years of time averaging are still likely)³². The collections of artifacts from Geelbek stem from surface contexts associated with specific geomorphological features. Although the Geelbek collections come from deflated surfaces, the amount of time averaging there is likely less than that seen in the excavated samples from Elandsfontein⁷⁶. Despite the differences in the types of stone artifacts and the formation processes of these assemblages, these indicators of assemblage-level movement allow useful comparisons because the time averaged nature of these assemblages is still reflective of past behavior^{22,86}. The analysis of behavior we describe here utilizes assemblage-level metrics which have been shown to display real patterns despite time averaging⁸⁸. The volume ratio provides an opportunity to study landscape use patterns over very different spatial and temporal scales. These underlying patterns of mobility and landscape use represent fundamentally different ways of using

ancient landscapes. They may similarly influence the perturbations that humans had on different landscapes through time. The presence of hunter-gatherers in certain regions has been shown to increase the frequency and distribution of ignitions⁷⁰. As such, variability in mobility patterns may structure the patterns of fire regime changes on landscapes in the past.

6. Initial Models: Landscape Scale Combustion Patterns

The differences in mobility patterns documented at Elandsfontein and Geelbek may translate to variable anthropogenic perturbations of these ancient ecosystems. Highly concentrated behavior in instances of high space redundancy may result in conspicuous concentrations of combustion. Fires may happen in concentrated areas (as opposed to being distributed widely across ancient landscapes)⁷², impacting the available fuel load in certain parts of the landscape (i.e. lower fuel loads in places that have more recently burned)⁹³. We developed a generative model that uses forager movement patterns to dictate the frequency and spatial distribution ignitions. These models suggest that differences in landscape-scale patterns of hominin movement can result in altered vegetation communities. Biochemical proxies of wildfires in the past may provide a mechanism for understanding the distribution of larger landscape fires.

Local fire histories that deviate from patterns expected by local climatic variables and regional patterns of fire recorded in long-term records (e.g. microcharcoal records in offshore cores) are likely driven by local fuel conditions and potentially anthropogenic ignition. Identifying unprecedented increases in charcoal accumulation and the abundance of possible burned phytoliths as well as abrupt shifts in fire frequency may help identify anthropogenic fire regimes⁹⁴. In addition, further indicators of anthropogenic fire will take advantage of advances in archaeological science and micromorphological investigations to identify anthropogenically altered sediments⁷². Our models are aimed at identifying anthropogenic combustion in general terms rather than individual instances (i.e. hearths).

Altered fire regimes can dramatically modify the vegetation structure of Cape Floristic Region plant communities⁹⁵. We therefore expect that anthropogenic fire regimes will influence vegetation, leading to a disconnect between vegetation structure and climate. The frequency of ignitions may be influenced by anthropogenic impact, with the resultant size and duration of fires influenced by fuel load⁹⁶. We use generative models to identify the influence of fire on ancient landscapes given different climatic factors. Generative models incorporate details of plant regeneration depending upon vegetation type. Our initial models indicate that dispersed ignitions (in high movement tortuosity scenarios) under high fuel load scenarios (e.g. glacial periods with increased rainfall) may cause fluctuation in species composition and extinction, which creates opportunity for diversification and speciation in different vegetation schemes⁹⁷; see Fig. 5). This suggests that in the context of different patterns of forager movement, humans created different vegetation structures merely by modifying the way they used ancient landscapes.

These models can create expectations about the heterogeneity of landscape vegetation in the past. Generative models can establish scenarios whereby these patterns can be repeated over thousands of years to produce expectations for a time averaged paleoecological record under different fire regimes. This is one mechanism whereby anthropogenic impacts may, in fact, increase the diversity of certain ecosystems. It is possible that the specific movement patterns of foragers and associated climatic variables related to past habitats (e.g. higher rainfall under glacial conditions) may have been the key to higher ecosystem diversity in the past. The generative models that we have developed create expectations that we can investigate in the archaeological and geological record. At present these models are based on assumptions about the Cape Floristic Region ecosystems rather than empirical data. Our model of ancient landscape behavior and its impact on fire regimes still needs far more refinement. However, we believe this may provide insight into some components of niche construction on a broader scale. In Australian contexts anthropogenic perturbation actually increases the return rate of some

ecosystems⁴³. These scenarios will test whether different movement patterns on ancient landscapes had an impact on the ecosystems of the West Coast of South Africa while demonstrating the intersection of long-term behaviors and ecosystem change.

7. Conclusion

Understanding the evolutionary significance of aspects of hominin behavior in deep time is difficult⁴⁵. Archaeologists have long relied on the tenets of human behavioral ecology to examine the evolutionary pressures on past human behaviors. Almost certainly foragers adapted to changing habitats throughout the Pleistocene to tailor their behavior to the variability in environmental contexts. These adaptive behaviors were implemented to increase the fitness of individuals and their immediate offspring in ways that align with concepts of inclusive fitness⁸. These types of behavioral ecological approaches provide a powerful mechanism for generating expectations of past behaviors on an individual level¹⁵, the long-term consequences of which may result in patterns that are not initially evident from individual actions. Emergent patterns that require thousands of years to develop are rarely conspicuous results of the behaviors that can be described on ethnographic time scales⁵⁶. The time-averaged nature of the archaeological record (especially in the Middle and Early Pleistocene) requires archaeologists and paleoecologists to investigate patterning at this scale. Aspects of niche construction theory and the concepts of ecosystem engineering also require examinations at temporal and geographic scales that are beyond the bounds of many standard archaeological studies (e.g. single sites and relatively constrained chronostratigraphy). We have outlined an approach to the study of ancient human and environmental dynamics in the unique ecosystem of the Cape Floristic Region. It is plausible that the ecology of Pleistocene habitats in the winter rainfall region of southwest South Africa was entangled with components of human behavior. Generative modeling provides the means to create expectations for the archaeological record that may provide insights into possible niche construction in the past. In particular, we focus on patterns of movement that can be identified through basic measures in the archaeological record. These relatively simple differences may have long-term consequences in terms of the ways in which hominins perturbed habitats in the past. Human movement patterns may represent a distinct component of inceptive niche construction⁶ that is easily identifiable in long-term records of behavior. Exploring these evolutionary mechanisms in the past requires novel ways of looking at the archaeological record.

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Conflict of Interest Statement

All authors are not aware of any conflict of interest associated with the results of this study.

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Figure Legends

Figure 1. Location of examples of West Coast archaeological landscapes that can be investigated. Inset: The approximate chronology of archaeological localities relative to the $\delta^{18}\text{O}$ record from Barnola et al. 1987⁹⁸.

Figure 2. The spatial distributions of different vegetation types (e.g., C3/C4 monocots, C3 dicots) on simulated landscapes are informed by paleoenvironmental proxies (in this example pollen from GeoB1711-4). Agents move through those spaces, consuming vegetation according to given dietary rules. They accumulate isotopic signatures (1st 30% of time steps) and dental microwear (short term: last 10% of time steps). Their teeth become the local fossil assemblage. These assemblages are then sampled. Resulting patterns are used to develop hypotheses about the empirical data from the paleontological record. The two landscapes can be distinguished by variation in microwear (y-axis) and hypothesized carbon isotope signatures (x-axis) in mixed feeders (black dots), grazers (red dots), and browsers (green dots).

Figure 3. Stone-tool assemblage proxies (e.g., cortex ratio) have been developed to identify different patterns of landscape use in palimpsest contexts. The Y-axis represents the frequency of values of a given cortex ratio for a specific locale. The distribution of values represents multiple instances of these behaviors. In these two modeled scenarios, the distribution of values distinguishes between different levels of movement tortuosity on landscape scales.

Figure 4: Preliminary archaeological data from Elandsfontein (1.0-0.7 Ma) and Geelbek (3-3 ka) dunefields. Archaeological indicators of movement (volume ratio) indicate higher degrees of tortuosity at Elandsfontein than that at Geelbek.

Figure 5. Preliminary conceptual model results showing outcomes of vegetation burning simulation within a two-dimensional parameter space defined by movement tortuosity and percentage of fire-prone vegetation cover. Outcomes, such as phytolith concentrations (red), vegetation age structure (green/yellow), and microcharcoal abundance (orange) are recorded as spatial grids.



June 24th 2020

John Murray
Guest Editor
Evolutionary Anthropology

John

I am writing this letter as a cover letter and explanation of the revisions made to our manuscript entitled “Ecosystem engineering in the Quaternary of the West Coast of South Africa.” We have incorporated all of the reviewer’s astute revisions and we believe that the current manuscript is greatly improved from the original submission.

Here I will outline the detailed reviews that the reviewers provided and describe the changes we have made to respond to their concerns.

The first reviewer noted that even though our manuscript described details of the niche construction in various contexts we had not engaged with some components of the literature on this topic. In particular the work of Zeder (2012) and the assertion of deliberate efforts to engineer ecosystems. The reviewer asked that we address how these approaches deviate from more traditional behavioral ecological approaches. We have added some details about the Zeder’s work and the differences between behavioral ecological approaches and niche construction approaches. We have not directly laid out how this could be applied to the example of the West Coast of South Africa but rather reviewed the general differences between these two approaches. These details are described on lines 330-340.

The first reviewer also noted that in some of the interpretations of niche construction, the movement of foragers to new habitats is considered a kind of niche construction in that it might modify these new habitats. The reviewer poses a difficult dilemma when dealing with time averaged contexts as to whether or not the changes were the result of niche construction or if hominins moved to these habitats because they were more favorable. We have responded to this comment by describing how these different scenarios (i.e. 1-moving to a new habitat and subsequently changing it OR 2-simultaneous changes to the habitat that then draw hominins to the area because the conditions are more favorable) can be modeled with agent-based modeling. Understanding the temporal differences between movement to a location and subsequent movement after a habitat changes is a bit of a “chicken and egg” equifinality. We have mentioned this concern and discussed how these different phenomena may create different long-term patterns which can be modeled using agent-based / generative modeling. The details of this are described on lines 366-375.

Reviewer 1 also asked how we were building the models of ancient ecosystems. The reviewer mentions that most models require some understanding of baseline conditions. We agree with the reviewer that we need to begin with some basic parameters of ancient landscapes. We have outlined how our models begin with very basic parameters so that they can be more generally applicable to broad scale patterns that are not influenced by smaller scale vegetation changes. This does not negate the importance of local conditions in understanding general patterns of behavior, however, we feel as though our models strike a balance to generalized enough that they can be applied to many systems on the west coast of South Africa during the last million years. The details of our response to this concern is on lines 415-430.

Reviewer 1 also mentioned that our suggestion that there is a “landscape of Late Pleistocene hunter-gatherers” is too vague and makes gross overgeneralizations about the past. It is true that there is likely far more than one landscape use type during the Late Pleistocene. We have corrected this language to acknowledge the diversity of landscape uses that occurred in the past. In addition, we have modified this text to indicate that our current models and patterns we subsequently identified are focused on identifying broad underlying patterns that are indicative of major structural changes in the way hominins use landscapes. These are patterns that are not evident on seasonal or even decadal time scales, but rather over hundreds of thousands of years. These changes are outlined on lines 509-518.

Reviewer 1 mentioned that we characterized the Elandsfontein site as having large bifacially flaked tools across a landscape. The reviewer correctly notes that there is substantial variability in the presence of bifacially flaked tools across this landscape. We have rewritten this sentence to note this generalization and now describe the Elandsfontein landscape as “frequently” reflecting bifacially flaked technology. This modification can be seen on lines 520-524.

Reviewer 1 also noted that the following sentence is redundant. “The costs and benefits of decisions made by individuals in the past most likely had substantial impacts on individual behaviors.” We agree with this assertion and we have removed this sentence.

Reviewer 1 also noted that our sentence on lines 581-584 uses the term adaptive design which could be interpreted as distinct from tactics that based on social and ecological contexts. We have removed this sentence because do not believe that it adds anything substantial to this paragraph.

Reviewer 2 noted that the figures were too small and could not easily be seen. We have now uploaded larger versions of these figures.

Reviewer 2 noted that our discussion of landscape usage among Acheulean hominins was lacking some key citations (De la Torre et al. 2014; Presnyakova et al. 2018). We have added these citations.

Reviewer 2 was also confused by certain sentences in our manuscript that describe the details of the generative models. We have modified the sentences on lines 420-430 to make this clearer. We believe the new version allows for greater clarity when describing these patterns.

Reviewer 2 notes that the context of the excavations at Elandsfontein and Geelbek differ greatly (Elandsfontein represents excavated assemblages and Geelbek is largely surface collections). Although we agree with the reviewer that these are substantive differences (and we have modified the text to highlight these differences) we also note that the measures we are using to compare between these assemblages (e.g. cortex ratios) are specifically designed to investigate patterns that are evident regardless of the site formation processes. This is precisely why we are using these methodologies. I agree with the reviewer that these contextual issues must not be ignored but we are hoping that the patterns we are investigating transcend various different site formation contexts. These changes can be seen on lines 530-540.

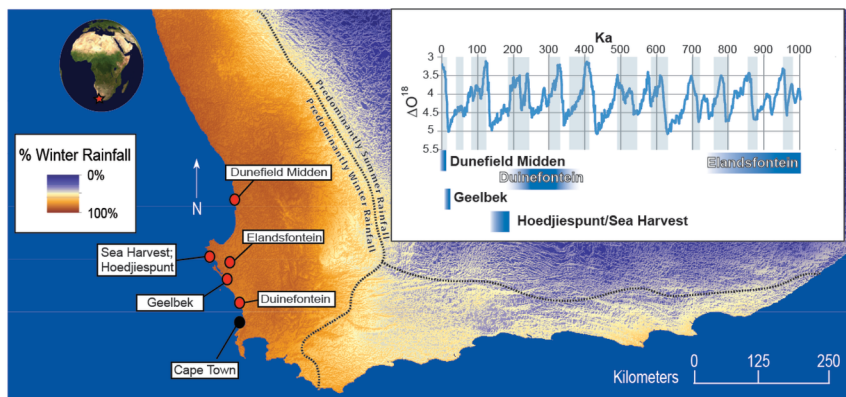
Boht of the reviewers also provided smaller comments on specific wording details and in particular Reviewer 2 noted that much of the text described potential patterns in a way that seemed to much like a proposal than a manuscript. We agree with the reviewer and we have tried to modify the text to reflect a more declarative tone. We believe these changes have made the manuscript better and more concise. We believe that all of the reviewer's concerns have been addressed in this modified manuscript.

Please do not hesitate to contact me if you have further questions about these revisions or the manuscript revisions.

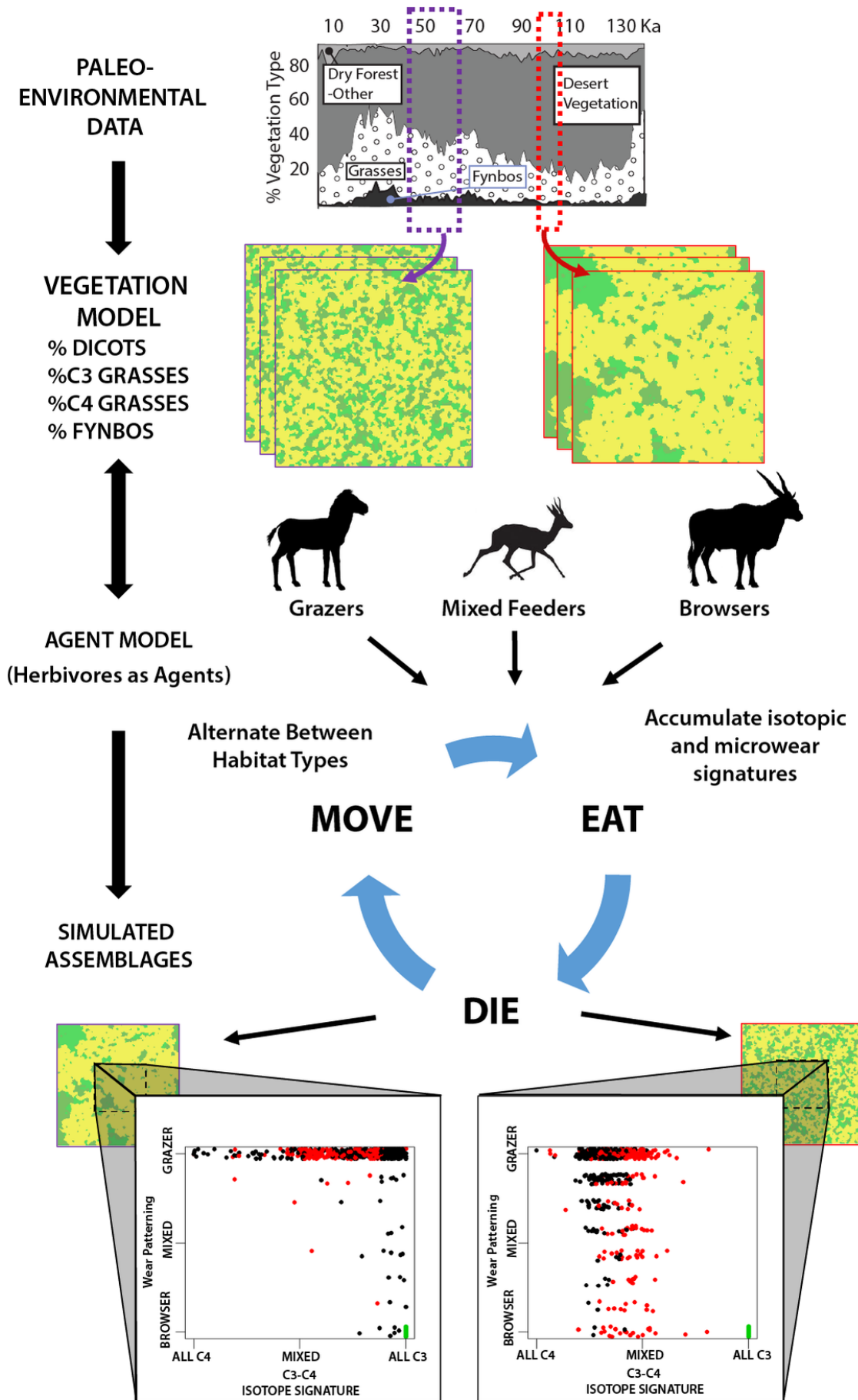
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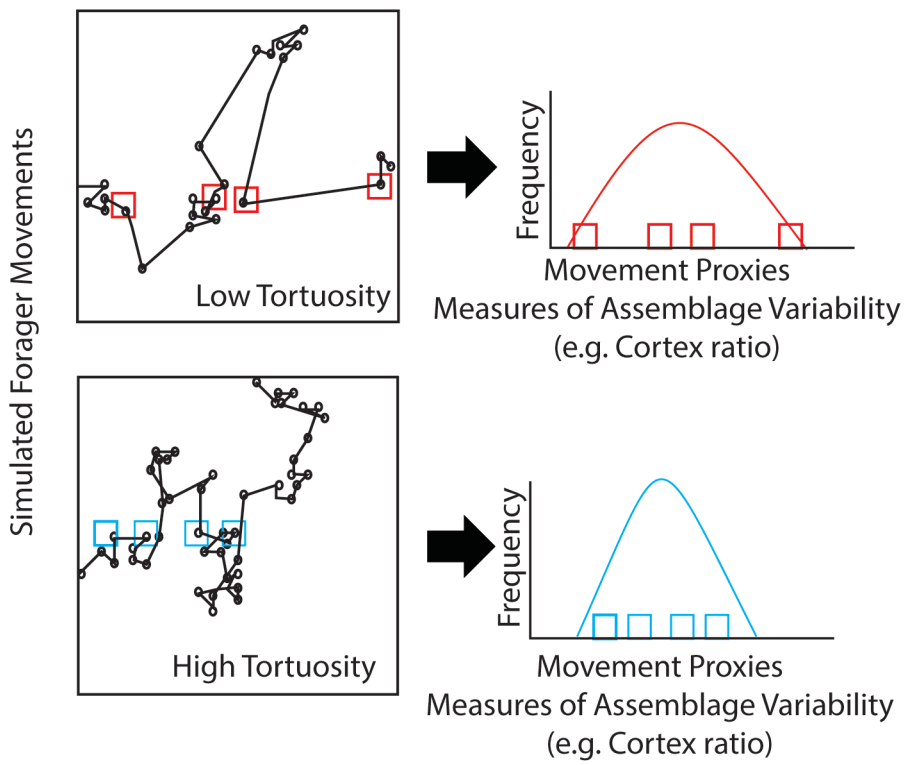
David R. Braun
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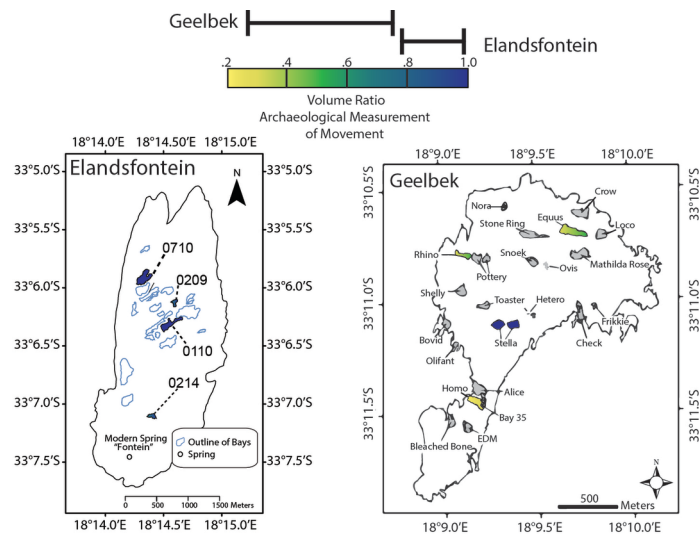
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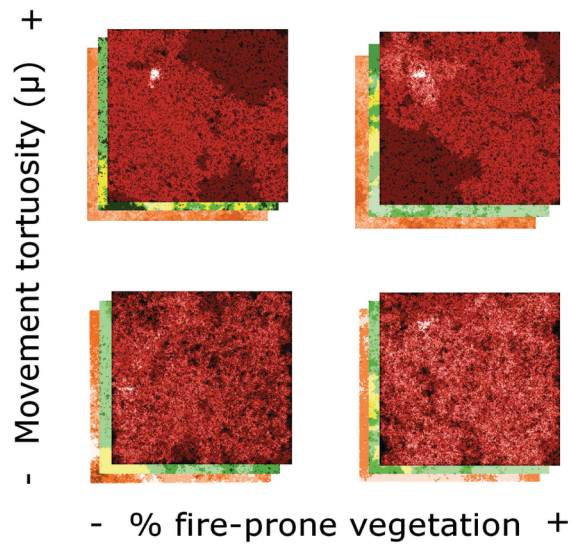
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