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# Identifying Early Modern Human ecological niche expansions and associated cultural dynamics in the South African Middle Stone Age

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The archaeological record shows that typically human cultural traits emerged at different times, in different parts of the world, and among different hominin taxa. This suggests that their emergence is the outcome of complex and non-linear evolutionary trajectories—influenced by environmental, demographic and social factors—that need to be understood and traced at regional scales. The application of predictive algorithms using archaeological and paleoenvironmental data allows one to estimate the ecological niches occupied by past human populations and identify niche changes through time, thus providing the possibility of investigating relationships between cultural innovations and possible niche shifts. By using such methods to examine two key southern Africa archaeological cultures, the Still Bay (76–71 thousand years ago; ka) and the Howiesons Poort (66–59 ka), we identify a niche shift characterized by a significant expansion in the breadth of the Howiesons Poort ecological niche. This expansion is coincident with aridification occurring across Marine Isotope Stage 4 (ca. 72–60 ka) and especially pronounced at 60 ka. We argue that this niche shift was made possible by the development of a flexible technological system, reliant on composite tools and cultural transmission strategies based more on “product copying” rather than “process copying”. These results counter the one niche-one human taxon equation. They indicate that what makes our cultures, and probably those of other members of our lineage, unique is their flexibility and ability to produce innovations that allow a population to shift its ecological niche.

Middle Stone Age | Still Bay | Howiesons Poort | Ecological Niche Modeling | Paleoclimate

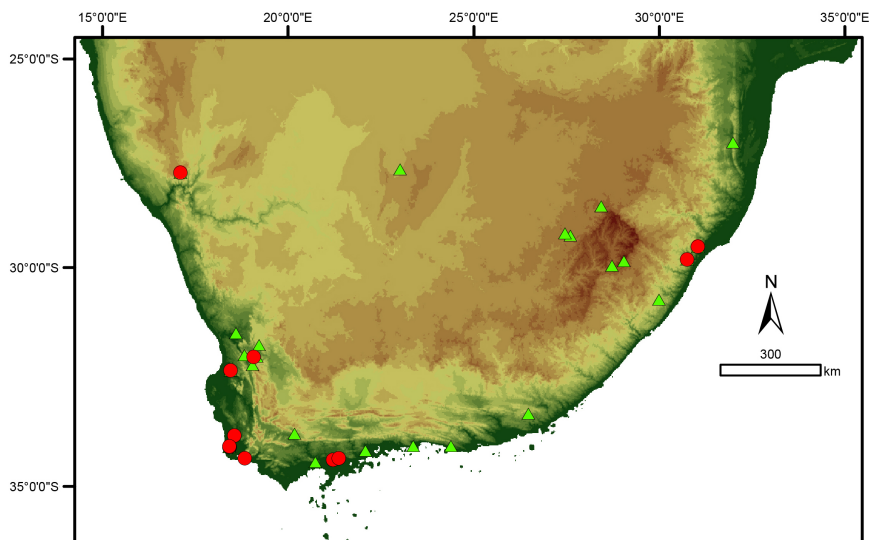
Research on animal behavior has made it clear that culture represents a second inheritance system that may have changed the dynamics of evolution on a broad scale (1–3). Understanding how this process has affected the evolution of our genus is a major challenge in Paleoanthropology. In what ways, and through what phases of evolutionary history, has human culture extended beyond that seen in other species? Were the cultural adaptations and associated cultural innovations that we observe in the archaeological record the direct consequence of our biological evolution or are they the outcome of mechanisms largely independent of it? In our lineage, if cultural innovations were directly linked to classic Darwinian evolutionary processes—such as isolation, random mutation, selection and speciation—one would expect a clear correspondence between the emergence of a new species and a related set of novel cultural behaviors. By shaping a new hominin species, natural selection would provide this species with a new cognitive setting resulting in the capacity for particular cultural innovations or behaviors. Such a mechanism would provide the possibility for cultural variability but would narrow its range of expression to the species’ biologically dictated potential. Although some would still argue that there is a direct link between cultural behavior and hominin taxonomy and, as a consequence, that the typically human secondary inheritance system only emerged with

our species, archaeological and paleogenetic research conducted over the last 20 years challenge such a view.

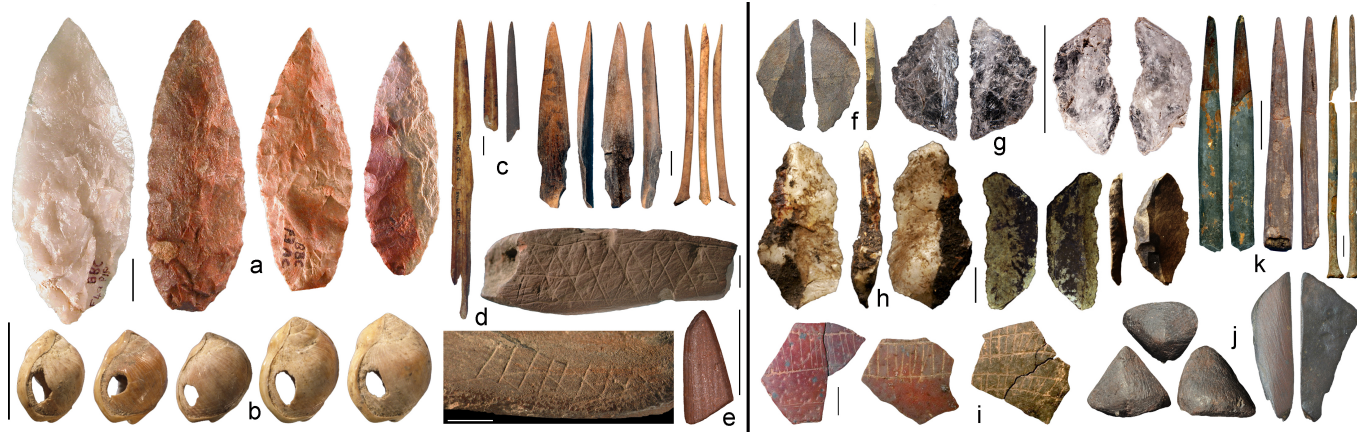
Firstly, for periods < 200 thousand years ago (ka), it is difficult to attribute a particular cognition and resulting cultural behavior to a particular fossil species since paleogenetic evidence shows that significant interbreeding occurred between Neanderthals, Denisovans, and anatomically modern humans (AMH) (4–6), thus blurring the concept of fossil species that many paleoanthropologists had in the past when interpreting morphological differences between human remains. Each new round of publications concerning paleogenetics shows that we are confronted with a complex network of genetic relationships rather than distinct and simple lines of evolutionary descent. There is no reason to assume that such a pattern did not characterize other phases of our lineage’s evolution.

Secondly, archaeological discoveries show that the cultural innovations generally seen as reflecting modern cognition and behavior did not emerge as a single package in conjunction with the appearance of our species in Africa. We know that AMH emerged in Africa between 200–160 ka (ky cal BP) (7–9), but some behaviors considered as ‘modern’ are present in Africa before this speciation event. Ochre use appears at around 300 ka (10), and laminar blade production is observed perhaps as early as 500 ka (11). Other modern cultural traits are only observed in the African archaeological record after ca. 100 ka. This is the case with heating of stone to facilitate knapping or retouching, pressure flaked bifacial projectile points, microlithic armatures, mastic-facilitated hafting of stone tools, formal bone tools, abstract engravings, the production of paint and pigment containers, personal ornaments, and primary burials (12–15). Furthermore, many key cultural innovations are present outside Africa well prior to AMH dispersal. In Europe, Neanderthals employed pigment at many sites by at least 250–200 ka. They also used complex lithic technologies, composite tools, and complex hafting techniques by at least 180 ka (16). At Bruniquel, France, Neanderthals broke and moved four tons of stalagmites in order to build a circular structure deep within a cave 176 ka (17). At a number of sites, starting at 130 ka they used raptor claws and feathers, probably for symbolic activities (18, 19). They made abstract designs on a variety of media (20, 21). Neanderthals in the Near East and Europe engaged very early in a variety of

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**Fig. 1.** Map of southern Africa indicating the locations of Still Bay (red circles) and Howiesons Poort (green triangles) archaeological sites, the geographical coordinates of which were used as occurrence inputs to estimate the two cultures' respective ecological niches. Sea level depicted at -70 m b.s.l.



**Fig. 2.** Left: Still Bay artifacts (a: bifacial points made of quartz and silcrete; b: perforated *Nassarius kraussianus* shell beads; c: bone points and an awl; d: engraved ochre fragments; e: ochre fragment shaped by grinding). Right: Howiesons Poort artifacts (f: segment made of hornfels; g: segments made of quartz; h: flake and segments bearing residues of mastic; i: engraved ostrich egg shells; j: ochre fragments shaped by grinding; k: bone point and awls; a-b: Blombos Cave; f, g, k: Sibudu Cave; h, i, j: Diepkloof Shelter). Scales = 1 cm. Sources: a (41); b (photos by FdE and CH); c (98); d (12); e (photo by CH); f (53); g (99); h (59); i (61); j (100); k (55).

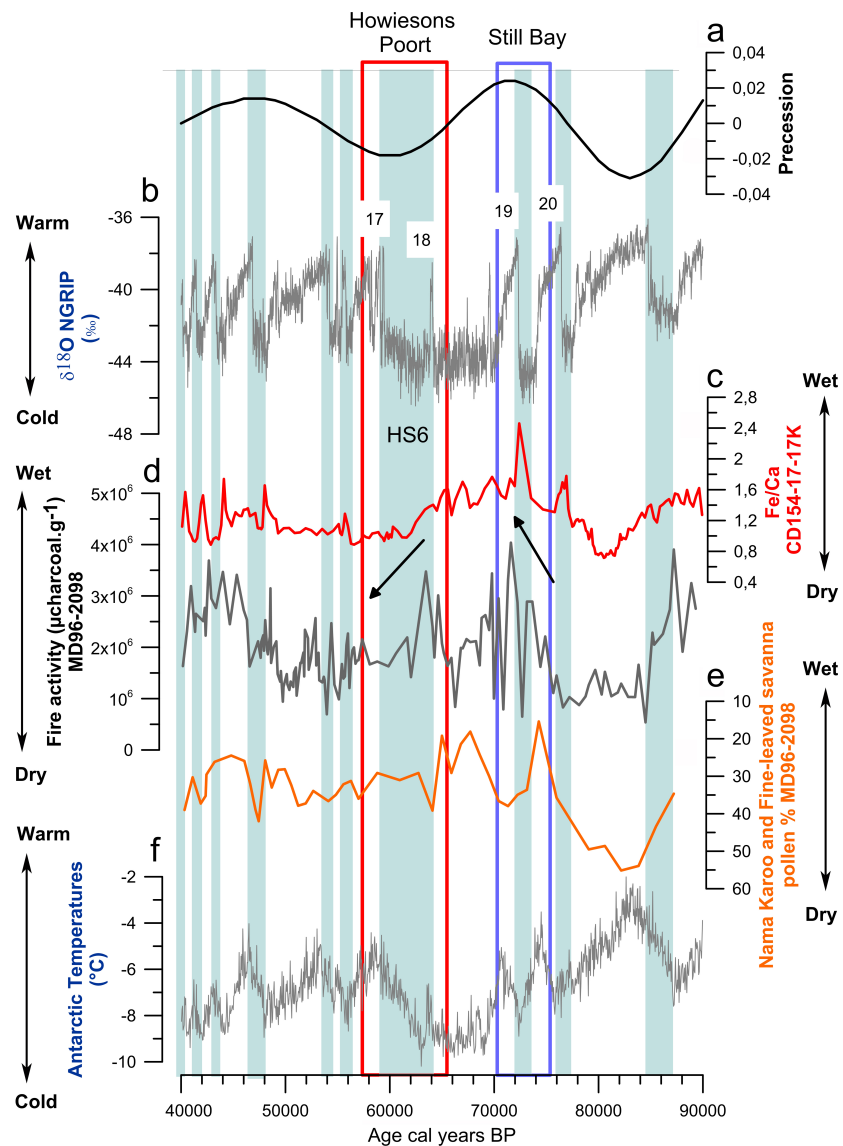
funerary practices including deliberate burials with simple grave goods. The last Neanderthals in Italy and France produced formal bone tools. They also produced a variety of personal ornaments consisting of animal teeth, fossils, and marine shells, some of which were colored with ochre (22, 23). Additionally, isolated occurrences of innovative cultural traits are recorded at much older sites in Europe and Asia (24), and well-established innovations (e.g., Middle Stone Age shell beads) disappear abruptly from the archaeological record and similar behaviors later reappear in different forms and sometimes on different media (14, 25).

This evidence demonstrates that typically modern human cultural traits emerged at different times, in different parts of the world, and among different hominin taxa. Such taxa appear more and more to be the phenotypic expression of a largely shared, plastic cognition (26, 27), and the emergence of typically human innovations the result of complex and non-linear evolutionary trajectories that need to be understood and traced at regional scales.

It is clear that cultural innovations were triggered by several interconnected and dynamic factors, likely biological, environmental and cultural. Since speciation does not appear to have played a role in the emergence of key innovations, we need

to explore the potential for relationships between biology and culture at the population level, and in particular within those past African populations that first developed behaviors that incorporated suites of these traits. Such an endeavor, though, is handicapped on the biological side by a sparse Upper Pleistocene hominin fossil record, the absence of pre-Holocene paleogenetic data, and a long history of human presence and intra-continental dispersals that complicate interpretations of modern genetic data. Understanding how AMH were biologically structured in the Middle Stone Age is also hampered by the fact that, as recently shown by genetic analyses (6, 28) highlighting the introgression of archaic genes into the African gene pool, they were certainly not ubiquitous across the continent. In order to overcome such limitations, research has focused on better defining the nature and chronology of the cultural entities that may reflect past population structure and distributions (29, 30), in addition to documenting the complexity of innovations recorded in the Middle Stone Age and exploring their social and cognitive implications (31–33). Others have attempted to identify a correspondence between environmental or climatic variability and the emergence of cultural innovations in the hope of identifying causal links (34–38). These attempts, though, have no designed means, apart

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**Fig. 3.** Climate variability during the time interval 90 ka and 40 ka encompassing the Middle Stone Age cultures Still Bay (76–71 ka: blue rectangle) and Howiesons Poort (66–59 ka: red rectangle). From top to bottom: a) Precession index (101); b) NGRIP  $\delta^{18}\text{O}$  curve on the GICC05 chronology (68); c) Fe/Ca curve from core CD154-17-17K collected from the Eastern Cape margin indicating changes in river discharge (38); d) Microcharcoal particle concentration curve from core MD96-2098 collected off the Orange River on the western South African margin indicating changes in fire regime and precipitation (65) (this study); e) Nama Karoo and Fine-leaved savanna pollen percentage record from core MD96-2098 indicating changes in precipitation (67); and f) Temperature curve for Antarctica from the EPICA ice core (102). Arrows situated between curves (c) and (d) indicate long-term trends in humidity during the Still Bay and Howiesons Poort intervals.

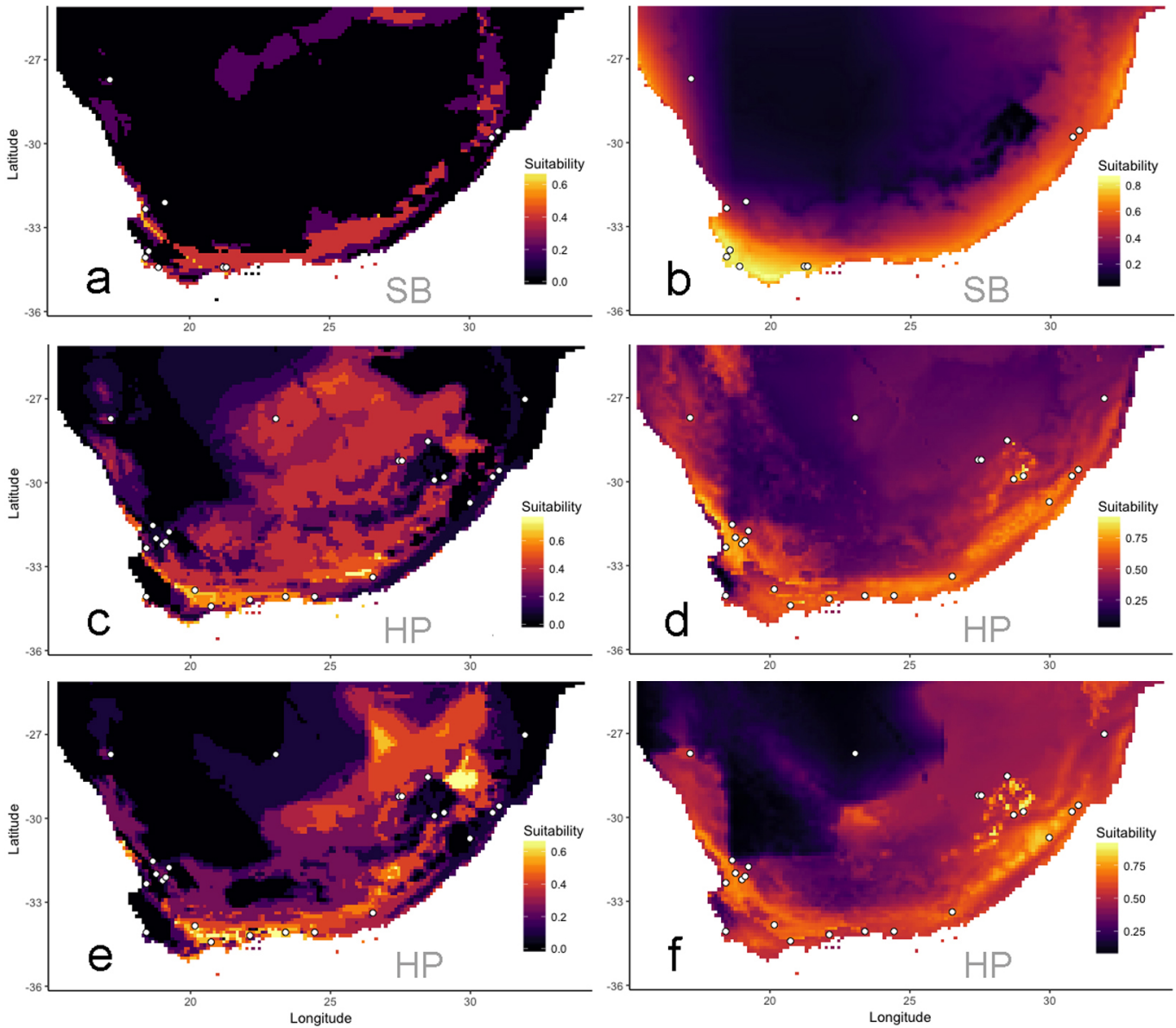
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from recurrence, with which to verify the hypothesis that climate may have influenced culture, to identify the suites of environmental parameters (i.e., the ecological niche) within which each archaeological culture operated, nor to evaluate how these relationships varied through space and time. The emergence of key cultural innovations in our lineage may reflect changes in the nature of such relationships. Identifying and disentangling such relationships is a key challenge for the involved disciplines. The failure to do so may result in oversimplified scenarios. For example, Ziegler et al. (38) conclude that cultural innovations during the Middle Stone Age in southern Africa were triggered by periods of humidity that produced higher levels of biomass and consequent increases in human population density. This scenario, however, only relies on the mean age of each culture and climatic conditions associated with those means, and it does not take into consideration the full age range of each recognized archaeological culture. Furthermore, their model insinuates hiatuses in the archaeological record following the post-Howiesons Poort that are not seen in most southern African archaeological sequences.

In a previous study, we stressed the need to consider the relationship between past human cultures and environment as a

dynamic process that occurred at a regional level (39). We argued that to do so, one needs to develop heuristic tools that enable the quantitative comparison and evaluation of individual cultural trajectories, their associated behavioural changes through time, and the mechanisms that operated behind such trends. This may allow for the identification of points in time during which human cultures substantially reorganized their second inheritance systems thus moving closer to the system characteristic of historically known and present-day populations.

A regional cultural trajectory can be conceived of as a succession of cultural packages, which we term cohesive adaptive systems. A cohesive adaptive system is a cultural entity characterized by shared and transmitted knowledge reflected by a recognizable suite of cultural traits that a population uses to operate within both cultural and environmental contexts (39). This concept differs from that of 'technocomplex' or 'archaeological culture', commonly employed in archaeology, in that exploited environmental conditions (i.e., the eco-cultural niche) contribute to the definition a past cultural adaptation. When faced with successive climate changes, a cohesive adaptive system can conserve, expand, or contract its ecological niche, with 'ecological niche' being defined



**Fig. 4.** Ecological niche predictions for the Still Bay (SB) archaeological culture at 72 ka (a, b), the Howiesons Poort (HP) archaeological culture at 66 ka (c, d), and the HP at 60 ka (e, f) produced with Bioclim and Maxent, respectively.

in the Grinnellian sense as the environmental and resources conditions suitable for a species or population (40). Associated cultural traits, and the way in which they were transmitted, may also evolve in such situations and highlight significant changes in the way in which culture influenced human populations. Research strategies have been developed to investigate such interactions.

Predictive algorithms, originally created in the field of ecology, are able to estimate the ecological niche occupied by a past cohesive adaptive system (i.e., the eco-cultural niche) by using the geographic locations of archaeological sites where the cohesive adaptive system has been recognized along with chronologically relevant paleoenvironmental data. Using these data, the predictive algorithms first identify the environmental parameters shared among the archaeological sites and define the relationships between these parameters. These relationships are then used to estimate a cohesive adaptive system's ecological niche. Another important capacity of these algorithms is that they can be used to examine niches between time periods thereby allowing one to determine whether or not successive populations

exploited different niches. By comparing the material cultures of two or more successive cohesive adaptive systems, and taking into account environmental frameworks within which they operated, one can evaluate whether or not cultural innovations were a response to environmental fluctuations. Equally as important, one can identify the degree of resilience of a cohesive adaptive system to environmental change.

The goal of this study is to apply this approach for the first time to two key Middle Stone Age archaeological cultures, the Still Bay (SB) and the Howiesons Poort (HP) of southern Africa. The SB represents the first known cultural adaptation in which technological and symbolic innovations of a comparable complexity to those seen in modern hunter-gatherers appears as a coherent and recognizable package. After a possible hiatus, we observe a new archaeological culture, termed the HP, characterized by dramatically different and simplified lithic technology, as well as markedly different symbolic material culture. The available archaeological and paleoenvironmental datasets of this period are of sufficient resolution to make this period of the Middle

Stone Age an ideal laboratory for exploring how typically human behavioral packages arose and evolved in one particular region and for identifying potential mechanisms at work.

### Cultural and Chronological Contexts

#### The Still Bay

This archaeological culture, observed at sites located in coastal areas of southern Africa and predominantly concentrated in southwestern regions (Fig. 1), is characterized by the production of bifacial foliate points, often made from fine-grained, non-local lithic materials (Fig. 2a). At the key site of Blombos Cave, the majority of these points have been heat-treated prior to flaking with hard and soft hammer percussion, and finished using a technique termed pressure flaking. The latter allows for more refined shaping of the object by giving the knapper better control over its final form. Modern-day experiments indicate that this knapping technology requires a long period of apprenticeship. SB bifaces were multifunctional and served as both projectiles and cutting tools. Examinations of SB lithic assemblages (41) show that these bifaces were often repeatedly resharpened and had long use-lives indicating that they formed a curated component of the SB lithic toolkit. The SB is also the first archaeological culture in which formal bone tools (i.e. artefacts made of animal osseous material shaped with techniques, such as scraping, grinding and incising, specifically conceived for these materials) are observed at multiple sites rather than as rare elements in single assemblages. Technological and functional studies show that the two different classes of tool—projectiles and awls (Fig. 2c)—were produced with different techniques and that special attention was paid to the finishing of the bone projectile points, suggesting that they were highly valued and possible status items. The SB is also the first archaeological culture in southern Africa associated with personal ornaments. These take the form of marine shells (*Nassarius kraussianus*) that were deliberately perforated, stained with ochre, and strung together in a variety of arrangements (33) (Fig. 2b). Use-wear analyses indicate that they were worn for extended periods of time (42). Other elements of SB symbolic material culture include elaborately engraved abstract patterns on ochre pieces (Fig. 2d), as well as more simple engravings on bone items. Also present in assemblages are ochre pieces bearing traces indicating that they were processed in order to produce red powder (Fig. 2e), which likely was used for both functional and symbolic purposes.

With respect to chronology, a majority of SB sites have yielded optically stimulated luminescence (OSL) ages that range between 76 ka and 71 ka (34, 43–45). Debate exists as to accuracy of this range due to older OSL and thermoluminescence (TL) dates from Diepkloof rockshelter (45–48). Since the inexplicably older set of dates from Diepkloof remains a unicum, we will use the currently accepted chronology (45, 49, 50). Debate also exists as to whether this culture is technologically homogeneous or rather characterized by regional and temporal variability (41). This, however, remains an open issue due to a lack of chronological resolution and the small number of contextually reliable archaeological assemblages.

#### The Howiesons Poort

This archaeological culture, observed in both coastal and inland regions of southwestern and northeastern South Africa (Fig. 1), is principally characterized by the presence of backed blades and bladelets (i.e., lithic blades steeply retouched on one side to form crescent-shaped segments) (Fig. 2f, g) that were predominantly used as components in composite hunting weapons. These tools, while not highly standardized dimensionally or morphologically, were made with a lithic reduction system that was geared towards the production of thin, straight blades, some of which were retouched to make this culture's *fossil directeur* along with denticulated tools (29, 41, 51). Raw materials used for the lithic technology were predominantly local or near-local

in origin, in clear contrast to what is seen for SB bifaces. Similar to the SB, though, HP groups also sometimes heated lithic raw materials before they were reduced to produce blades (52) and occasionally used pressure flaking (53). Bifacial points are absent in the HP, with the exception of a single site where specimens that are smaller and of lower quality have been recovered (54). Bone tools recovered from HP sites consist of awls, pressure flakers, shaped splintered pieces (*pièces esquillées*), and small projectile points (55) (Fig. 2k). It has been argued that HP backed segments and bone points were used as bow-delivered arrow points based on use-wear, fracture patterns, and morphometrics (56–58). The interpretation that these tools were hafted is supported by the presence of mastic remnants observed on some backed pieces (31, 59) (Fig. 2h). At present, with the exception of a perforated conus shell found within an infant burial at Border Cave (60), personal ornaments are lacking in HP assemblages, and undisputed symbolic behavior is limited to the decoration of ostrich egg shell water containers with a variety of abstract designs made up of linear engravings (51, 61) (Fig. 2i). Red ochre (Fig. 2j), also sometimes incorporated into mastic mixtures, was widely used by HP groups.

The HP has predominantly been dated with OSL and TL techniques and appears to have lasted for a slightly longer period of time than the SB. HP dates range between roughly 66 ka and 59 ka (34, 51, 62). As with the SB, some OSL dates of the HP at Diepkloof are significantly older (47, 48) than the corpus of dates available from other South African sites, as well as from other OSL dates obtained at the same site (63). Based on the fact that the newly re-calculated dates for the Diepkloof HP (63) cluster with the HP dates from other dated contexts (50), we will use the 66–59 ka range as the chronological interval for the HP in this study. Shortly after ca. 59 ka, we observe the appearance of the post-Howiesons Poort archaeological culture.

#### Paleoenvironmental Context

These two archaeological cultures occurred during two very different climatic phases (Fig. 3). At the orbital scale, the SB occurs in a phase of precession maximum during which one observes higher seasonality and an increase in precipitation in the Southern Hemisphere (64–67). To the contrary, the HP is contemporaneous with a decrease in precession with the minimum reached towards its end (ca. 60–59 ka). This resulted in lower seasonality and drier conditions (SI Appendix, Fig. S1). In addition to orbital climatic variability, SB and HP cultures were also subjected to suborbital climatic fluctuations, the so-called Dansgaard-Oeschger (D-O) cycles expressed over Greenland by alternating cold stadials and temperate interstadials, as well as intermittent and extreme cooling episodes recorded in the North Atlantic, termed Heinrich Stadials. These millennial-scale events are also recorded in Antarctic paleoclimatic records.

The SB occurs during a period comprised by Greenland Interstadial (GI) 20, Greenland Stadial (GS) 20, and GI 19 (Fig. 3) (68). This culture disappears from the archaeological record during the initial phase of GS 19 (GS 19.2). The HP appears towards the end of GS 19 and is present across GI 18 and GS 18 (ca. 64.4–59.4 ka, which corresponds to Heinrich Stadial (HS) 6) (69). The suite of diagnostic elements characteristic of this archaeological culture are no longer present by ca. 59–58 ka, a period marked by rapid climatic oscillations (i.e., GI 17.1, GS 17.1, GI 16.2, GS 16.2). It is following this interval that the Post-Howiesons Poort adaptation appears.

The impact of the D-O millennial scale climatic variability and HSs on the Southern Hemisphere regional climates has been recently investigated. Model experiments and climate reconstructions suggest that GS and HS events resulted in increased sea surface temperatures and humidity in the South Atlantic and Southwestern Indian Ocean (70–74). For southern Africa, Ziegler et al. (38) examined the elemental composition of marine

681 sediments from an Indian Ocean core and proposed that GS  
682 and HS events are characterized by increased erosion reflecting  
683 higher precipitation that triggered increases in vegetation cover  
684 and biomass. Recent research has provided direct data concern-  
685 ing vegetation cover and biomass for this region. Pollen and  
686 microcharcoal records from marine core MD96-2098, retrieved  
687 off southwestern Africa (65, 67) (this study), show repeated  
688 millennial-scale changes in humidity during the last glacial period  
689 that also indicate, within the uncertainties of the independent ice  
690 and marine chronologies, that GS and HS events were associated  
691 with increases in humidity. Such increases are inferred from  
692 peaks in microcharcoal concentration due to grass-fueled fires  
693 and decreases in pollen from vegetation characteristic of open  
694 environments, such as Nama Karoo and fine-leaved savanna (Fig.  
695 3d, e). However, when the entire chronological interval for both  
696 the SB and HP is taken into account, a more complex climatic  
697 pattern is observed, characterized by an alternation of wet and  
698 dry events. Despite this variability, the general pattern revealed  
699 by all available continental proxies across the entire range of  
700 each archaeological culture shows an overall trend towards higher  
701 humidity during the SB and generally dryer conditions during the  
702 HP. The contradictory pattern proposed by Ziegler et al. (38) is  
703 probably due to the fact that they do not consider the entire range  
704 of these two cultures, but rather only look at the humidity trends  
705 coincident with each culture's mean age.

## 706 Materials and Methods

### 707 Paleoclimate modeling

708 To estimate ecological niches exploited by the SB and HP, we used  
709 paleoclimatic and vegetation simulations produced by Woillez and collaborators  
710 (66) (SI Appendix, Paleoclimatic simulations) for the periods of 72  
711 ka and 60 ka. Since the two simulations are primarily constrained by orbital  
712 parameters and do not estimate sub-orbital variability, we used the 72 ka  
713 simulation to represent climatic and environmental conditions for the SB and  
714 the initial HP (ca. 66–63 ka), and the 60 ka simulation to represent conditions  
715 for the terminal HP (ca. 63–59 ka). The use of the 72 ka simulation as a  
716 proxy for climatic conditions of the initial HP is justified by the relatively  
717 high humidity observed at the onset of H56, as evidenced by vegetation,  
718 fire activity, and erosion proxies (Fig. 3e, d, c, respectively). To estimate the  
719 SB and HP eco-cultural niches, we used temperature of the coldest month,  
720 maximum precipitation, minimum precipitation, mean annual precipitation,  
721 mean annual temperature, and a measure of biomass from the relevant  
722 paleoclimatic simulations.

### 723 Ecological Niche Modeling and Hypothesis Testing

724 In order to reconstruct the potential ecological (eco-cultural) niches ex-  
725 ploited by the SB and HP and evaluate whether cultural changes between the  
726 two are associated with an ecological niche shift, we constructed a georefer-  
727 enced list of archaeological sites with levels that can be securely attributed to  
728 one of these cultures (Fig. 1; Table S1). We then used these occurrence data to  
729 conduct tests using both Bioclim (75) and Maxent (76) predictive algorithms  
730 within the 'dismo' R package (77, 78) (see SI Appendix, Ecological Niche  
731 Modeling). We use these two algorithms in order to explore the differences  
732 seen when models are allowed to extrapolate freely into combinations of  
733 environments that were unavailable during model training (Maxent) versus  
734 models that are constrained so that they do not extrapolate beyond the  
735 minima and maxima of the marginal environmental distributions of the  
736 examined population (Bioclim). Due to Maxent's ability to extrapolate, we  
737 anticipate that similarity between different target populations will generally  
738 be seen to be higher when environmental niches are modeled using Maxent  
739 as opposed to Bioclim. With these two algorithms we reconstructed both SB  
740 and HP niches using relevant climatic outputs and simulated biomass from  
741 the 72 ka simulation and compared these results. We also reconstructed the  
742 HP niche using simulation outputs for 60 ka and compared these estimations  
743 to those of the SB at 72 ka. A series of Monte Carlo randomization tests were  
744 conducted to assess the differences in the set of environments occupied by  
745 each culture. This approach is based on widely used methods in evolutionary  
746 ecology (the "background" or "similarity" test) (79, 80) that are used to  
747 assess whether two populations exhibit statistically significant differences  
748 in their environmental tolerances or associations (SI Appendix, Ecological  
749 Niche Modeling). We also conducted tests using measures of niche breadth  
750 (81, 82) to determine whether any observed differences between the two  
751 cultures' environmental niches represent a statistically significant expansion  
752 of the niche. Because some of these evaluations were conducted using  
753 different climate layers for the SB and HP (72 ka and 60 ka, respectively),  
754 modifications that employ Latin hypercube sampling were made to the  
755 background similarity tests (SI Appendix, Ecological Niche Modeling; Fig. S2).

## 756 Results

### 757 Niche estimations and similarity evaluations

758 Niche estimations for the SB at 72 ka produced with Bio-  
759 clim and Maxent both indicate a high probability of presence  
760 primarily restricted to the extreme southern and eastern portions  
761 of present-day South Africa (Fig. 4a, b). The most noticeable  
762 differences are that the Maxent prediction includes areas in  
763 the southwestern Cape as well as immediately coastal regions  
764 along the southeastern and eastern coasts. This broader Maxent  
765 prediction is due to this algorithm's propensity to extrapolate into  
766 environments not directly associated with the input occurrence  
767 data (i.e., archaeological sites). The predicted niches for the  
768 HP at 66 ka, produced with the proxy 72 ka outputs, include  
769 those regions predicted for the SB, as well as more inland areas  
770 including the Great Escarpment, the Highveld and Kaap Plateau,  
771 and broader areas within the southwestern Cape and western  
772 coastal regions (Fig. 4c, d). The niche estimations for the HP at 60  
773 ka remain geographically broader than those for the SB and still  
774 include major inland plateaus but are visibly shifted towards the  
775 east and northeast (Fig. 4e, f), which represent areas that were less  
776 affected by the eastward expansion of desert areas during Marine  
777 Isotope Stage (MIS) 4 (66).

778 Background similarity tests of overlap between the SB and  
779 HP niches both modeled with Maxent using the 72 ka climatic  
780 data produced no statistically significant result (SI Appendix,  
781 Fig. S3a; Table S2) meaning that their respective niches are not  
782 statistically different from one another. As pointed out above,  
783 this lack of significant difference between predictions is likely the  
784 result (see Materials and Methods) of the employed algorithm.  
785 To the contrary, these same tests using Bioclim found instead  
786 that SB and HP niche estimations using 72 ka climate outputs  
787 were less similar than expected by chance ( $I$ -statistic:  $p \sim .022$ ; SI  
788 Appendix, Fig. S3c; Table S2). Although HP niche estimates are  
789 slightly broader than those of the SB at 72 ka with both Maxent  
790 and Bioclim, these differences are not statistically significant (SI  
791 Appendix, Fig. S3b, d; Table S2). Niche overlap between Maxent  
792 models for the SB at 72 ka and the HP at 60 ka was neither  
793 greater nor less than expected by chance (SI Appendix, Fig.  
794 S3e; Table S2). However, overlap of Bioclim predictions for the  
795 SB at 72 ka and the HP at 60 ka was significantly lower than  
796 would be expected by chance ( $I$ -statistic:  $p \sim .013$ ; SI Appendix,  
797 Fig. S3g; Table S2), indicating that the two cultures occupied  
798 different ecological niches. Change in niche breadth between  
799 Maxent predictions for the SB at 72 ka and the HP at 60 ka is  
800 not statistically different from random expectations, although the  
801 approximate  $p$  value is fairly low ( $p \sim 0.11$ ) (SI Appendix, Fig. S3f;  
802 Table S2), suggesting that a greater sample size might establish  
803 the HP niche at 60 ka as significantly broader than the SB at 72  
804 ka. The difference in niche breadth for Bioclim models is greater  
805 than expected by chance ( $p \sim .027$ ) (SI Appendix, Fig. S3h; Table  
806 S2), indicating that the HP 60 ka niche is broader than that of the  
807 SB at 72 ka and points to an ecological niche expansion.

### 808 Discussion and Conclusions

809 To what extent does this study allow us to understand how  
810 human culture extended beyond behavioral adaptations observed  
811 in other species? Most species exhibit niche conservatism, con-  
812 traction or, more rarely, extinction when faced with climate  
813 change (83–85). Human populations, however, are unique in their  
814 capacity of cumulative culture and associated complex cultural  
815 transmission strategies that allow them to potentially adapt to  
816 climate change and environmental reorganization via cultural  
817 means. We observe such a pattern between the Still Bay and the  
818 Howiesons Poort of Southern Africa. The Still Bay was a coastal  
819 adaptation that exploited a relatively narrow niche during mild  
820 climatic conditions across a large region. To exploit that niche,  
821 Still Bay populations developed a variety of complex technologies  
822 and symbolic practices, some of which certainly entailed costly

modes of cultural transmission. A number of Still Bay cultural features, such as bifacial points and complex beadworking, could only be transmitted by communication and learning strategies that emphasize imitation (high fidelity copying) over emulation (low fidelity) (86, 87). Howiesons Poort populations significantly increased the breadth of their niche compared to the Still Bay. This expansion incorporated more arid and high altitude inland environments and demonstrates their ability to successfully cope with the more arid climatic conditions and higher ecological risk associated with MIS 4, and in particular its latter phase. This was made possible by developing a cohesive adaptive system reliant on more flexible technologies. The variety of employed lithic raw materials, blank production techniques, methods to retouch and shape those blanks to produce segments, which vary in form and size, are indicative of a flexible toolkit, and in this case one reliant on composite tools. With effective hafting techniques, such a toolkit would have been easily repaired and maintained. Due to its modular nature, the Howiesons Poort toolkit could be effectively employed in diverse environments. More importantly, the communicative strategies needed to transmit the knowledge necessary to perpetuate this technology can be based more on “product copying” (emulation) rather than “process copying” (imitation). In the latter, morphological similarity is associated with the same, or very similar, manufacturing techniques and sequences. For the former, one would expect to see artifacts that are morphologically similar despite being made from a variety of raw materials and techniques, as is observed in the Howiesons Poort. Such patterns could have been the result of a collapse of previously existing long distance cultural networks leading to the formation of more local “traditions”, again, which is exactly what we observe in Howiesons Poort bone and lithic technologies (53, 55, 88). The mechanism or mechanisms that operated behind such a process remain unclear (e.g., demographic changes, population replacement, cultural drift, etc.). While the Still Bay and Howiesons Poort certainly had adaptive strategies in common, it is probable that their cultural transmission strategies differed. Considering the niche and technological changes observed between the two cultures, along with the expertise implicit in some Still Bay technological innovations, we propose that training to create specialists, or “selective oblique transmission” (89), was used during the Still Bay to effectively convey these complex technologies and that this strategy was not, or to a greatly lesser degree, employed during the Howiesons Poort.

Numerous studies support the hypothesis that hunter-gatherer toolkit structure is driven, in part, by the risk of resource failure, i.e. more diverse and complex toolkits are associated with riskier environments (90–92). Data do not always support this prediction, though, and it has been proposed that the impact of risk on toolkits is dependent on the scale of risk differences among the studied populations (93). The degree of reliance on

copying (94), population size (95), and mobility (96) are other factors that may condition toolkit structure. None of these studies, however, are able to routinely predict what factors were implicated in shifts in toolkit structure among early AMH, nor address the issue of how past human niches may have changed when shifts in technology were concomitant with major climatic changes. The approach that we have applied here is an effective means with which to explore relationships between climate variability and cohesive adaptive systems at key moments in our evolutionary history. Its application to other regions and periods should allow us to follow, at regional scales, the complex interplay between cultural innovation, changes in modes of cultural transmission, and environmental variability. The results of the present study may be improved in the future by producing paleoclimatic simulations that capture millennial-scale environmental variability and by developing and employing methods (e.g., date estimations, Bayesian age modeling) that would allow one to attribute more precisely archaeological site levels to millennial-scale climatic phases. While the former is technically possible, employing such models will not be productive as long as the latter remains beyond our grasp, at least at present. By capturing the main climatic trends characteristic of the end of MIS 5 and MIS 4, our paleoclimatic simulations appear appropriate for examining culture-environment relationships when one considers the degree of chronological uncertainty associated with the two targeted cultures.

Our results demonstrate that in some early AMH regional cultural trajectories niche expansion was not always associated with cultural complexification (for an opposite case, see (97)). In this study’s case, complex cultural behaviors and inferred transmission strategies were replaced during a period of pronounced aridification with more flexible adaptations that were used to exploit a broader ecological niche. Increased cultural complexity and elaborated social learning strategies apparently were not always necessary for a culture to expand its ecological niche. Our findings support the view that the path followed by past human populations to produce adaptations and cultural traits, which most researchers would qualify as typically human, is not the outcome of classic Darwinian evolutionary processes in which the appearance of a new niche is often associated with a new species. Rather, the innovations characteristic of the Howiesons Poort represent cultural exaptation—innovations that use existing skills, techniques and ideas in new ways. The consolidation of these innovations depends on a population’s ability to develop, when necessary, new modes of cultural transmission that allow such innovations to be maintained through time.

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