Once upon a time in the Pleistocene: integrating Paleoanthropology and evolutionary psychology

di Matteo Bedetti

This paper examines how evolutionary psychology integrates paleoanthropological evidence to reconstruct the evolution of the human mind. Using the savanna hypothesis as a case study, it introduces the concept of stylization bias and argues for a more historically grounded integration of paleoanthropological evidence into the discipline's methodology.

Keywords: evolutionary psychology, savanna hypothesis, paleoanthropology, philosophy of evolutionary biology, archaeology.

1. Introduction[1]

What role should evidence from deep human prehistory play outside the disciplines that produce it? In the philosophical debate surrounding the historical sciences, geology, paleontology and archaeology are frequently praised for their remarkable ability to draw upon and integrate methods and insights from other fields[2]. One well-known example is the adoption in archaeology of 14C dating, a method originally developed by physicists[3]. Another striking example is the more recent, and extraordinarily successful, incorporation of ancient DNA analysis into paleoanthropology[4]. While this phenomenon certainly deserves careful philosophical reflection, in this paper we will argue that attention should also be directed toward the opposite flow of information: from paleoanthropology and archaeology to other disciplines. Although paleoanthropology has traditionally borrowed more than it has lent in terms of technologies and methods, evidence concerning human evolution nonetheless plays a pivotal role in several neighboring fields. Indeed, research programs that seek to reconstruct our psychological and behavioral evolution depend (also) on data provided by paleoanthropologists and archaeologists. Human behavioral ecologists, evolutionary psychologists, cultural evolutionary theorists, and related scholars must rely on fossils, artifacts, ancient DNA, and the inferences drawn from these sources as the fundamental epistemic scaffolding for their hypotheses. For instance, human behavioral ecologists seeking to formulate adaptive hypotheses concerning the evolution of childhood cannot disregard the paleoanthropological record, which offers crucial evidence regarding when this life stage emerged, in which ecological and social contexts, and so on. To neglect such data would amount to speculation detached from historical reality[5].

In this paper, we will focus on one of the most renowned sciences concerned with the evolution of human behavior, evolutionary psychology. The aim is to discuss how evolutionary psychologists integrate (or should integrate) findings

1 - The content of this paper has been presented in condensed form in my book M. Bedetti, *La mente preistorica: analisi epistemologica della psicologia evoluzionistica,* Mimesis Edizioni, Milano 2025.

2 - See, for example, A. Currie, *Rock, bone, and ruin: An optimist's guide to the historical sciences* MIT Press, Cambridge 2024.

3 - R. Chapman - A. Wylie, *Evidential reasoning in archaeology,* Bloomsbury Publishing, London 2018, chapter 4.

4 - D. Reich, *Who we are and how we got here: Ancient DNA and the new science of the human past*, Oxford University Press, Oxford 2018. See also S. M. Downes, *The role of ancient DNA research in archaeology*, in «Topoi» 40 (2021), pp. 285-293.

5 - A. Meneganzin - A. Currie, *Not wasted on the young: Childhood, trait complexes & human behavioral ecology, in Studies in History and Philosophy of Science* 109 (2025), pp. 12-20.

from paleoanthropology and related disciplines in their methods. More specifically, the emphasis will be on paleoenvironmental reconstructions and their importance for formulating adequate hypotheses about our cognitive adaptations.

The structure of this paper is as follows. We begin with a brief overview of evolutionary psychology, outlining its core tenets. We then examine the methodological framework of the discipline, with particular attention to the so-called top-down and bottom-up approaches, both of which rely in essential ways on paleoanthropological evidence. Next, we examine a specific hypothesis in evolutionary psychology regarding the purportedly evolved human preference for certain habitats, a case that illustrates how claims about our evolutionary past are often advanced without sufficient engagement with the pertinent paleoanthropological and paleoecological record. We show how this hypothesis ought to be revised in light of such evidence and, finally, conclude with broader reflections on how the methodological foundations of evolutionary psychology might be reconfigured to better integrate paleoanthropological insights.

2. Evolutionary psychology: a primer

Evolutionary Psychology (EP) explains human cognition and behavior as products of evolution, arguing that the mind is composed of specialized adaptations evolved through natural and sexual selection to solve recurrent ancestral problems such as mate choice, kin recognition, social exchange or danger avoidance. The field emerged between the 1980s and the 1990s, especially through the work of Cosmides and Tooby integrating evolutionary biology with information-processing models of the mind borrowed from cognitive sciences[6]. Nowadays, it remains a vibrant research program, with a large community of scholars identifying with its framework and a notable degree of public visibility.

One of the main tenets of evolutionary psychology is that psychological mechanisms are designed by natural selection to process information in ways that (pre)historically increased fitness. These mechanisms are thought to be predominantly domain-specific, modular, universal, and largely invariant across cultures, and the core goal of the discipline is to uncover the structure and function of these evolved modules and to understand how they manifest in modern behavior, even when modern environments differ markedly from ancestral ones. Closely

6 - L. Cosmides - J. Tooby, *From Evolution to Behavior: Evolutionary Psychology as the Missing Link*, in *The Latest on the Best*, edited by J. Dupre, MIT Press, Cambridge 1987, pp. 277-306; J. Tooby L. Cosmides, *The psychological foundations of culture*, in *The Adapted Mind*, edited by J. Barkow L. Cosmides J. Tooby, Oxford University Press, Oxford 1992, pp. 19-136.

related to this aspect is the concept of the Environment of Evolutionary Adaptedness (EEA), the statistical composite of selection pressures that shaped human cognition. Although in principle each cognitive mechanism (adaptation) may have its own specific EEA, reflecting different selective contexts, many evolutionary psychologists usually associate our general EEA with the African savanna of the Pleistocene (from 2.58 million years ago to 11.700 years ago), where the members of our genus (Homo) evolved and lived as hunter-gatherers. What both conceptions have in common is the belief that our cognitive evolution stopped with the invention of agriculture, at the beginning of the Holocene[7]. According to evolutionary psychologists, evolutionary processes are slow, especially when they involve complex organs such as the brain, so it is a priori very unlikely that new psychological adaptations have evolved in such a short time. As a result, many of our evolved mechanisms are mismatched with modern environments, as illustrated by our preferences (e.g., for high-fat or sugary foods that were once adaptive but can be maladaptive today[8]).

3. The methods of evolutionary psychology

We briefly presented evolutionary psychology and some of its core tenets. Now we will introduce EP's two main heuristics for hypotheses generation: the top-down approach and the bottom-up approach. The top-down method, also called functional analysis[9], moves from general evolutionary principles to specific hypotheses about the structure and function of cognitive mechanisms. It is usually presented in six steps[10] (Tooby & Cosmides, 1989; Lieberman, Cosmides & Tooby, 2007). We will focus on the first two steps, since it is primarily at this stage that insufficiently constrained reconstructions of ancestral conditions risk generating serious epistemic distortions:

Step 1: Identification of a recurrent adaptive problem: a problem that repeatedly affected ancestral survival or reproduction and was relevant to fitness.

---

7 - J. Tooby L. Cosmides, *The Theoretical Foundations of Evolutionary Psychology*, in *The Handbook of Evolutionary Psychology*, edited by D.M. Buss, John Wiley & Sons Hoboken 20162, pp. 3-87.

8 - D. Buss, *Evolutionary Psychology: The New Science of the Mind*, Routledge London7 2024.

9 - D.J. Buller, *Adapting minds: Evolutionary psychology and the persistent quest for human nature*, MIT Press Cambridge 2005.

10 - J. Tooby - L. Cosmides, *Evolutionary psychology and the generation of culture, part I: Theoretical considerations*, in «Ethology and sociobiology», 10 (1989), pp. 2949; D. Lieberman J. Tooby L. Cosmides, *The architecture of human kin detection*, in «Nature», 445 (2007), pp. 727-731.

Step 2: Determining how that adaptive problem appeared in the evolutionary past: once the problem is defined abstractly, it must be reconstructed in its ancestral context.

The remaining stages involve developing a computational model of the adaptive challenge, inferring the minimal structure of the putative cognitive mechanism, empirically testing alternative hypotheses through a variety of methods, and finally assessing the degree of fit between the proposed model and observed human behavior. A classic example is Cosmides' hypothesis of a cheater-detection module[11], which starts from the adaptive problem of social exchange, reconstructs its Pleistocene context, proposes a domain-specific cognitive adaptation, and tests its predictions empirically, including through cognitive experiments and neuroscientific lesion studies[12].

The bottom-up method works in the opposite direction. It begins with an observed psychological trait, behavior, or preference in the present and tries to infer the adaptive function it may have had in the past. This is why it is often called *reverse engineering*[13]. For example, the widespread fear of snakes has been interpreted as evidence for a threat-detection mechanism shaped by recurrent danger in ancestral environments[14]. Bottom-up reasoning is especially vulnerable to producing "just-so stories"[15], narratives that explain the presence of a trait by appealing to a hypothetical adaptive history, without seeking independent evidence beyond the story's apparent plausibility. On the other hand, the top-down approach would not be subject to this kind of criticism. Indeed, while reverse engineering *assumes* that a trait is an adaptation and proposes an adaptive explanation for it, functional analysis is predictive, since it is possible to test hypotheses derived from it against the empirical evidence:

---

11 - L. Cosmides, *Deduction or Darwinian Algorithms?*, Doctoral dissertation, Harvard University, Cambridge 1985; L. Cosmides J. Tooby, *Evolutionary psychology and the generation of cultur*e, part II: Case study: A computational theory of social exchange, in «Ethology and sociobiology», 10 (1989), pp. 51-97; L. Cosmides - J. Tooby, *Cognitive adaptations for social exchange*, in *The Adapted Mind*, edited by J.H. Barkow - L. Cosmides - J. Tooby, Oxford University Press Oxford 1992, pp. 163-228;

12 - L. Cosmides - J. Tooby, *Neurocognitive adaptations designed for social exchange*, in *The handbook of evolutionary psychology*, edited by D.M. Buss, John Wiley & Sons, Hoboken 2016.

13 - D. Dennett, *Darwin's Dangerous Idea: Evolution and the Meanings of Life*, Simon and Shuster, New York 1995; S. Pinker, *How the Mind Works*, Penguin Books, London 1997.

14 - A. Öhman - S. Mineka*, Fear, phobias and preparedness: Toward an evolved module of fear and fear learning*, in «Psychological Review», 108 (2001), pp. 483-522.

15 - With reference to Rudyard Kipling's 1902 collection of stories for children, in which the English writer invents amusing and imaginative explanations for how animals acquired certain characteristics.

> Our hominid ancestors had to be able to solve a large number of complex adaptive problems, and do so with special efficiency. By combining data from paleontology and hunter-gatherer studies with principles drawn from evolutionary biology, one can develop a task analysis that defines the nature of the adaptive information-processing problem to be solved […]. Once one understands the nature of the problem, one can then generate very specific, empirically testable hypotheses about the structure of the information processing mechanisms that evolved to solve it […]. One virtue of this approach is that it is immune to the usual (but often vacuous) accusation of post hoc storytelling: The researcher has predicted in advance the properties of the mechanism[16].

As the quotation above shows, Cosmides, Tooby, and Barkow adopt strikingly strong language, suggesting that functional analysis is entirely immune to charges of storytelling. But as we will show shortly, this is not the case. Indeed, both top-down and bottom-up approaches often share a deeper methodological limitation: a tendency to operate with minimal integration of paleoanthropological and archaeological evidence. When the Environment of Evolutionary Adaptedness is invoked without careful attention to the actual ecological, technological, and social conditions of ancestral populations, as reconstructed through the historical sciences, evolutionary explanations risk becoming disconnected from plausible scenarios of human evolution and, consequently, being empirically inadequate. The next sections will address this specific issue.

4. The stylization bias

Evolutionary psychology has produced many results but faces key criticisms: adaptationist bias[17], challenges to massive modularity and universality from evidence of plasticity and cross-cultural variation[18] and pressures from niche

16 - L. Cosmides - J. Tooby - J.H. Barkow, *Introduction: Evolutionary psychology and conceptual integration*, in *The Adapted Mind*, Oxford University Press, Oxford 1992, p. 11.

17 - S.J. Gould - R.C. Lewontin, *The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme*, in «Proc. R. Soc. Lond. B.», 205 (1979), pp. 581-598; E. Lloyd, *Adaptation*, Cambridge, University Press Cambridge 2021.

18 - F. d'Errico - I. Colagè, *Cultural exaptation and cultural neural reuse: A mechanism for the emergence of modern culture and behavior*, in «Biological Theory», 13 (2018), pp. 213-227; D.J. Buller - V. Hardcastle, *Evolutionary psychology, meet developmental neurobiology: Against promiscuous modularity*, in «Brain and Mind», 1 (2000), pp. 307-325.

construction and gene–culture coevolution, which undermine a strictly Pleistocene-fixed view and point to continued evolution into the Holocene[19] and many more.

In this section, we address a final critical point that has received relatively little attention in existing literature. As we will argue, the reification of the Environment of Evolutionary Adaptedness, combined with the limited use of paleoanthropological evidence in top-down and bottom-up approaches, has led to the formulation of empirically inadequate hypotheses. This discussion aims to contribute to a more historically grounded approach within evolutionary psychology.

We have already noted that there are two distinct ways of conceptualizing the Environment of Evolutionary Adaptedness (EEA) of the human mind. The first tends to equate it with the Pleistocene African savanna, whereas the second defines it as the set of selection pressures that shaped a given adaptation. Tooby and Cosmides claim that they only ever advocated the latter conception, and only appealed to the former in the early stages of their thinking, to make their ideas more understandable even to those without prior knowledge of evolutionary biology or those who considered all human behavior adaptive in the modern world[20]. Despite this, a stereotypical image of the EEA – as a Pleistocene savanna inhabited by small bands of hunter-gatherers – appears to have crystallized within certain research traditions of EP. Combined with the tendency to rely on superficial descriptions of the EEA while largely disregarding recent findings from paleoanthropology and prehistoric archaeology, this has the effect of diverting their heuristic strategies and fostering the development of inadequate hypotheses. We can call this phenomenon "*stylization bias*", because it involves replacing complex and up-to-date reconstructions of our evolutionary history with a crystallized and stereotypical view of human evolution. This bias does not stem from a lack of evidence about our deep past. Also, stylization bias should not be understood as a criticism of abstraction or idealization per se. Some degree of abstraction is unavoidable in any scientific attempt to reconstruct long-term evolutionary processes, and idealized models often play an important heuristic role in scientific explanation and theory construction[21]. Rather, the problem arises when idealized representations of the EEA become reified and disconnected from the

19 - K.N. Laland - J. Odling-Smee - S. Myles, *How culture shaped the human genome: bringing genetics and the human sciences together*, in «Nature Reviews Genetics», 11 (2010), pp. 137-148; R. Powell, *The Future of Human Evolution*, in «The British Journal for the Philosophy of Science», 63 (2012), pp. 145-175.

20 - K.N. Laland - G.R. Brown, *Sense and nonsense: Evolutionary perspectives on human behaviour*, Oxford University Press, Oxford 2011, p. 124.

21 - *E.g.* Michael Weisberg, *Simulation and Similarity: Using Models to Understand the World,* Oxford University Press, Oxford 2013; Angela Potochnik, *Idealization and the Aims of Science,* University of Chicago Press, Chicago 2017.

increasingly fine-grained evidence provided by paleoanthropology and archaeology. In this sense, stylization bias can be interpreted as a form of epistemically problematic idealization: a simplification that ceases to function as a useful heuristic and instead distorts the historical complexity of human evolution.

As we will see when examining the environments inhabited by our ancestors, human evolution has been (and continues to be) a complex phenomenon that resists simplistic generalizations. Over time, both our ancestors and the contexts where they lived underwent profound transformations: their habitats, diets, social practices, and much else changed dramatically. For this reason, attempts to reduce such complexity to a single statement– for instance, that "our ancestors lived in the African savanna"– are inevitably inadequate. In the next section we provide an example of this bias.

5. The savanna hypothesis

Deciding where to move, live and camp is an extremely important adaptive problem for every mobile living organism. Selecting a suitable location – one that offers a reasonable balance between shelter and camping opportunities, access to essential resources (water, food, tool-making materials, and so on), and minimal exposure to predators or other dangers – could mean the difference between life and death. This line of reasoning (step 1 of the top-down approach) led evolutionary psychologists to hypothesize, on the basis that much of our evolution took place in the African savanna (step 2), that modern humans possess a predilection for environments reminiscent of the latter. In other words, a cognitive adaptation expresses an aesthetic preference for savanna-like landscapes where our species evolved. This inclination was then tested through psychological experiments. We are thus faced with a paradigmatic case of functional analysis, where evidence about our evolutionary past serves to provide constraints during the phase of hypothesis generation. Aptly named the *savanna hypothesis*[22], this idea was famously proposed by Gordon Howard Orians in a series of articles and book chapters[23]. For Orians, the African savanna was an optimal ancestral environment

22 - This should not be confused with the other "savanna hypothesis", widely debated in paleoanthropology, which argues that the African savanna played a crucial role in shaping the evolution of bipedality in our ancestors (see, for example, M. Domínguez-Rodrigo, *Is the "savanna hypothesis" a dead concept for explaining the emergence of the earliest hominins?*, in «Current Anthropology», 55 (2014), pp. 59-81, and comments therein). Both versions of the hypothesis, however, have been challenged by recent evidence concerning the paleoecologies of our hominin ancestors.

23 - G. Orians, *Habitat selection: General theory and applications to human behavior*, in *The evolution of human social behavior*, edited by J.S. Lockard, Elsevier, Chicago 1980, pp. 49-66; G. Orians, *An ecological*

because its scattered acacia trees offered food, shelter, and vantage points, while the open landscape promoted grazing herbivores and wide visibility, aiding both resource acquisition and danger detection. Most importantly, under the "classical" conception of the EEA, the African savanna is portrayed as the environment in which "99 percent of our evolution" took place. According to this view, our lineage evolved and remained in this setting for most of its history until, between roughly 100,000 and 70,000 years ago, *Homo sapiens* left Africa and began to disperse across much of the world. Because our ancestors are thought to have lived in the savanna for the majority of their evolutionary past, it is assumed that humans developed an enduring preference for this type of environment.

Orians' hypothesis was initially supported by studies showing cross-cultural preferences for savanna-like features, such as specific acacia tree forms[24], and for savanna landscapes overall, especially among younger individuals, suggesting a possible innate bias[25]. However, subsequent research produced mixed and contradictory results with participants not consistently preferring savannas and sometimes favoring other environments like rainforests, even without direct experience, a result that cannot be fully explained by cultural learning[26]. Despite these issues, the savanna hypothesis remains influential in evolutionary psychology and is still cited as an explanation for landscape preferences in textbooks and evolutionary scholarly works[27]. At this point, it is legitimate to ask why this case

and evolutionary approach to landscape aesthetics, in *Landscape meaning and values*, edited by E.C. Penning-Rowsell - D. Lowenthal, Allen & Unwin, London 1986, pp. 3-25; G. Orians - J.H. Heerwagen, *Evolved responses to landscapes*, in *The adapted mind: Evolutionary psychology and the generation of culture*, edited by J.H. Barkow - L. Cosmides - J. Tooby, University Press, New York 1992. The latter contribution contained in *The Adapted Mind*, the manifesto of evolutionary psychology.

24 - *Ibidem.*

25 - J.D. Balling - J.H. Falk, *Development of visual preference for natural environments*, in «Environment and behavior», 14 (1982), pp. 5-28.

26 - R. Sommer, *Further cross-national studies of tree form preference*, in «Ecological Psychology», 9 (1997), pp. 153-160; D. Dutton, *Aesthetics and evolutionary psychology*, in *The Oxford handbook for aesthetics*, edited by J. Levison, Oxford University Press, New York 2003; J.H. Falk - J.D. Balling, *Evolutionary influence on human landscape preference*, in «Environment and behavior», 42 (2010), pp. 479-493; K.T. Han, *Responses to six major terrestrial biomes in terms of scenic beauty, preference, and restorativeness*, in «Environment and Behavior», 39 (2007), pp. 529-556; P. Hartmann - V. Apaolaza-Ibáñez, *Beyond savanna: An evolutionary and environmental psychology approach to behavioral effects of nature scenery in green advertising*, in «Journal of Environmental Psychology», 30 (2010), pp. 119-128; J.M. Moura - W.S. Ferreira Júnior - T.C. Silva - U.P. Albuquerque, *The influence of the evolutionary past on the mind: An analysis of the preference for landscapes in the human species*, in «Frontiers in Psychology», 9 (2018), p. 2485.

27 - I. Silverman - J. Choi, *Spatial Navigation and Landscape Preferences*, in *The Handbook of Evolutionary Psychology*, edited by D.M. Buss, John Wiley & Sons, Hoboken 2015; D. Buss, *Evolutionary Psychology: The New Science of the Mind*, cit.

study has been chosen for closer examination. After all, isn't it generally accepted that our species evolved primarily on the African savanna? Most depictions of early humans, whether in museum displays, textbooks, or documentaries, tend to situate them within environments evocative of that biome. The following section examines what paleoanthropological and paleoecological research reveal about this.

6. The paleoecology of our ancestors

Human evolution is sometimes portrayed in popular representations as an "escape" from closed wooded or forested environments, where the common ancestor between humans and chimpanzees probably lived (and where the latter still live), to the more open ones of African savannas. More open environments are thought to have favored the adoption of an upright posture, which was crucial for freeing the hands to manipulate and make tools. In turn, these tools enabled access to higher-energy resources, thereby supporting the evolution of our brain, a metabolically expensive organ. This process likely created a self-reinforcing, virtuous cycle in which technological, ecological, and cognitive changes mutually amplified one another[28].

While not entirely mistaken, some aspects of this narrative have been increasingly challenged over the past decades. In particular, the savanna does not appear to have consistently played a decisive role in human evolution. Evidence suggests that some of the earliest hominins lived in closed, wooded, or at least "mosaic" environments, where more closed and more open habitats coexisted, rather than in open savannas. The paleoecology of *Orrorin tugenensis* (~6 Mya), one of the earliest putative hominins, points in this direction[29]. The case is even clearer with *Ardipithecus ramidus*, whose fossils were discovered in Ethiopia and date to about 4.4 million years ago. Paleoenvironmental reconstructions based on its morphology, carbon isotope analyses of dental enamel, associated fauna and flora, and soil isotopic composition all point to a predominantly wooded habitat[30].

---

28 - Richard Potts dubbed these reconstructions of human evolution "intrinsic explanations", see for example R. Potts, *Environmental hypotheses of hominin evolution*, in «American Journal of Physical Anthropology», 107 (1998), pp. 93-136, for references to several of these reconstructions.

29 - M. Pickford - B. Senut, *The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya*, in «Comptes Rendus de l'Académie des Sciences-Series IIA-Earth and Planetary Science», 332 (2001), pp. 145-152.

30 - T.D. White - B. Asfaw - Y. Beyene - Y. Haile-Selassie - C.O. Lovejoy - G. Suwa - G. WoldeGabriel, *Ardipithecus ramidus and the paleobiology of early hominids*, in «Science», 326 (2009), pp. 64-86; T.D. White - C.O. Lovejoy - B. Asfaw - J.P. Carlson - G. Suwa, *Neither chimpanzee nor human, Ardipithecus reveals the surprising ancestry of both*, in «Proceedings of the National Academy of Sciences», 112 (2015), pp. 4877-

Moreover, although *A. ramidus* retained many adaptations for arboreal life, it also displayed traits specialized for bipedal locomotion, such as a shortened upper pelvis. This is particularly significant because it shows that around 4 million years ago our ancestors lived in wooded environments and were at least partly arboreal, yet were already exhibiting adaptations for bipedal walking.

Subsequently, a series of climatic changes that promoted the spread of open grasslands across Africa, particularly in East Africa, a region central to several major developments in human evolution[31]. Accordingly, members of the genus *Australopithecus* appeared to be better adapted to arid environments than *Ardipithecus*. But even during this period, evidence indicates that hominins inhabited mosaic environments combining features of both forests and savannas. Moreover, these long-term aridification trends were punctuated by alternating wet and dry phases, which caused significant fluctuations in vegetation patterns[32].

However, this seemingly privileged link with the African savanna is disrupted by *Homo ergaster/Homo erectus*, the first hominin to leave Africa and colonize parts of Asia[33]. The reasons behind these migrations are still not entirely clear, but during its dispersals *H. ergaster* encountered a wide range of environments beyond the savanna, from tropical forests[34] to highly arid deserts[35]. This demonstrates that *H. erectus* already possessed considerable ecological flexibility that, until recently, was thought to characterize only later members of our genus, such as the *Neanderthals* and *Homo sapiens*. Subsequently, *Homo heidelbergensis*, which emerged during the Middle Pleistocene[36] is thought to have been the main actor in a second major dispersal out of Africa, spreading into Europe and Asia.

4884; but see T.E. Cerling - J.G. Wynn - S.A. Andanje - M.I. Bird - D.K. Korir - N.E. Levin - C.H. Remien, *Woody cover and hominin environments in the past 6 million years*, in «Nature», 476 (2011), pp. 51-56.

31 - T.E. Cerling, *Development of grasslands and savannas in East Africa during the Neogene*, in «Palaeogeography, Palaeoclimatology, Palaeoecology», 97 (1992), pp. 241-247; T.E. Cerling - J.M. Harris - B.J. MacFadden - M.G. Leakey - J. Quade - V. Eisenmann - J.R. Ehleringer, *Global vegetation change through the Miocene/Pliocene boundary*, in «Nature», 389 (1997), pp. 153-158.

32 - N.E. Levin, *Environment and climate of early human evolution*, in «Annual Review of Earth and Planetary Sciences», 43 (2015), pp. 405-429.

33 - G.P. Rightmire, *Patterns of hominid evolution and dispersal in the Middle Pleistocene*, in «Quaternary International», 75 (2001), pp. 77-84.

34 - P. Roberts - N. Boivin - J. Lee-Thorp - M. Petraglia - J. Stock, *Tropical forests and the genus Homo*, in «Evolutionary Anthropology: Issues, News, and Reviews», 25 (2016), pp. 306-317.

35 - J. Mercader - P. Akuku - N. Boivin - A. Camacho - T. Carter - S. Clarke - P. Durkin, *Homo erectus adapted to steppe-desert climate extremes one million years ago*, in «Communications Earth & Environment», 6 (2025), p. 1.

36 - A. Profico - F. Di Vincenzo - G. Lorenza - P. Marcello - G. Manzi, *Filling the gap. Human cranial remains from Gombore II (Melka Kunture, Ethiopia; ca. 850 ka) and the origin of Homo heidelbergensis*, in

But it was primarily our species that inhabited and exploited a wide range of biomes – from open savannas and temperate woodlands to coastal areas and high-altitude environments – including tropical forests, which were also widespread in Africa, and remain poorly studied[37]. During the Pleistocene and the Holocene, African forests went through periods of expansion and contraction driven by climatic fluctuations. In many regions, this resulted in mosaic landscapes where forests alternated with savannas and grasslands. These mixed environments offered unique opportunities for hominins, allowing them to exploit the resources of both ecosystems. Far from being hostile places to avoid, as sometimes still assumed, these environments instead represented resource-rich contexts[38]. For example, the site of Panga ya Saidi (Kenya) shows that humans produced symbolic tools, practiced burials and exploited mixed forest environments 78 ka[39]. With the outflow of sapiens from Africa, we witness within not even 100,000 years the colonization of almost every biome on Earth, confirming our incredible adaptive abilities[40].

Finally, the great climatic variability of the Pleistocene should also be considered. Indeed, throughout the Pleistocene there was an alternation of cold and dry phases and warm and wet phases, which caused a series of profound environmental changes[41]. Climatic fluctuations probably favored the selection of some behavioral flexibility, rather than adaptation to a specific biome. Adaptability to different

«Journal of Anthropological Sciences», 94 (2016), pp. 41-63.

37 - E.M. Scerri - P. Roberts - S. Yoshi Maezumi - Y. Malhi, *Tropical forests in the deep human past*, in «Philosophical Transactions of the Royal Society B», 377 (2022), 20200500. There are several reasons for this. First, fossils are less likely to be preserved in tropical environments, where heat, humidity, and acidic soils accelerate decomposition. Second, Western researchers and colonizers have long regarded tropical forests as hostile, untouched wilderness, which has contributed to a lasting bias against studying them (Patrick Roberts, personal communication).

38 - P. Roberts - M. Petraglia, *Pleistocene rainforests: barriers or attractive environments for early human foragers?*, in «World Archaeology», 47 (2015), pp. 718-739.

39 - C. Shipton - C. Clarkson - R. Cobden, *Were Acheulean bifaces deliberately made symmetrical? Archaeological and experimental evidence*, in «Cambridge Archaeological Journal», 29 (2018), pp. 65-79. M. Martinón-Torres - F. d'Errico - E. Santos - A. Álvaro Gallo - N. Amano - W. Archer - M.D. Petraglia, *Earliest known human burial in Africa*, in «Nature», 593 (2021), pp. 95-100.

40 - K.E. Westaway - J. Louys - R.D. Awe - M.J. Morwood - G.J. Price - J.X. Zhao - B. Sulistyanto, *An early modern human presence in Sumatra 73,000-63,000 years ago*, in «Nature», 548 (2017), pp. 322-325; reports one of the oldest non-African sites where *sapiens* are attested in a tropical forest, while we refer to the article by Scerri et al. 2022 for an overview of the most recent findings on the occupation of tropical African and non-tropical forests during prehistoric times).

41 - L.E. Lisiecki - M.E. Raymo, *A Pliocene Pleistocene stack of 57 globally distributed benthic δ18O records*, in «Paleoceanography», 20 (2005); T.D. Herbert, *The mid-Pleistocene climate transition*, in «Annual Review of Earth and Planetary Sciences», 51 (2023), pp. 389-418.

environmental conditions is also highlighted by the various waves of migrations that our ancestors underwent. Building on this, several theoretical models try to explain the relationship between the evolution of our ancestors and the environment. In recent years, the "*variability selection hypothesis*", proposed by Richard Potts, has had particular resonance[42]. According to Potts, fundamental changes in human evolution occurred concurrently with these phases of increased instability and phase reversal and have increased the ecological flexibility and adaptability of our ancestors to a range of different environments[43].

In summary, human evolution did not unfold exclusively in open environments such as the savanna; rather, our ancestors were capable of dispersing into and colonizing a wide range of habitats. Therefore, while the savanna undoubtedly played an important role in our evolutionary history, there is no compelling reason to regard it as our preferred biome or as the one in which we felt safest. At the present state of knowledge, it does not appear that most human adaptations have evolved to respond to the demands of a particular environment, so much as to respond flexibly and adaptively to a very variable ecological context[44].

In light of the evidence presented, the savanna hypothesis, as intended by evolutionary psychologists, is clearly inadequate. The heuristic process (the functional analysis) that generated it is based on a stereotypical view of human evolution that equates our evolutionary past with life in African savannas, and remains largely uninformed by paleoecological data. Recall that functional analysis starts by identifying an adaptive problem – in this case, determining the ideal habitat for human survival (step 1) – and then reconstructing how that problem manifested in our evolutionary past (step 2). It is precisely at this stage that the main difficulties arise when it comes to integrating paleoanthropological and paleoenvironmental evidence. As we have seen, most evolutionary psychologists argue that the African savanna provided the primary stage for human evolution.

42 - R. Potts, *Environmental hypotheses of hominin evolution*, cit; R. Potts, *Evolution and environmental change in early human prehistory*, in «Annual Review of Anthropology», 41 (2012), pp. 151-167, see E.S. Vrba, *Role of environmental stimuli in hominid origins*, in *Handbook of paleoanthropology*, edited by W. Henke - I. Tattersall, Springer, Berlin, Heidelberg 2015, pp. 1837-1886, for a complementary account of the relationships between human evolution and the unstable climatic and ecological conditions.

43 - For an overview of the role of ecological patterns in human evolution see also A. Parravicini - T. Pievani, *Multi-level human evolution: ecological patterns in hominin phylogeny*, in «Journal of Anthropological Sciences», 94 (2016), pp. 167-182.

44 - To further explore the wide range of environments in which our ancestors lived, see T.I. Foister - I. Žliobait - O.E. Wilson - M. Fortelius - M. Tallavaara, *Homo heterogenus: Variability in early Pleistocene Homo environments*, in «Evolutionary Anthropology: Issues, News, and Reviews», 32 (2023), pp. 373-385; E. Zeller - A. Timmermann - K.S. Yun - P. Raia - K. Stein - J. Ruan, *Human adaptation to diverse biomes over the past 3 million years*, in «Science», 380 (2023), pp. 604-608.

From this assumption, they infer that we should have developed an enduring preference for such environments, a preference that should still be observable in humans today. While this reconstruction may have seemed plausible in the '80s when the hypothesis was first proposed, it is no longer tenable in light of paleoanthropological evidence, which now points to a far more complex evolutionary scenario. Unfortunately, the tendency of evolutionary psychologists to underutilize paleoanthropological evidence and to rely on overly simplified reconstructions of our past, what we deemed the stylization bias, has allowed the savanna hypothesis to persist, albeit with mixed results. The inconsistent results of landscape-preference experiments can be better understood by recognizing that human evolution occurred in diverse habitats, shaped by adaptability and ecological versatility rather than specialization in a single biome.

But how should we revise the functional analysis underlying the savanna hypothesis in light of these remarks? Step 1 is not controversial in itself; choosing the right place to live is crucial for survival. The problem arises with step 2, which should draw on all the relevant evidence provided by paleoanthropology and, in this case, paleoenvironmental reconstructions. Rather than relying on a stereotyped account of human evolution, we should acknowledge its complexity and the environmental diversity in which our ancestors lived. If we were to preserve the same inferential structure as the original model, we might instead expect humans to show a preference for mosaic environments, a conclusion also reached by Rathmann and colleagues[45] or, more generally, for natural settings over heavily anthropized ones such as large cities. Alternatively, this preference could reflect a broader adaptive strategy for identifying suitable habitats without privileging any specific environment.

7. How to revise the methods of evolutionary psychology

In section 3, when presenting the different heuristics of hypothesis generation, we showed that the founders of evolutionary psychology regard the top-down method as immune to accusations of producing just-so stories. This supposed immunity stems from the method's predictive nature: it begins with the formulation of a hypothesis about a cognitive adaptation, which is then tested against empirical evidence, thereby avoiding the construction of *ad hoc* explanations. In the last sections, we have shown that this immunity is far from guaranteed: if evidence from our past is not properly integrated into the process of hypothesis generation,

45 - J. Rathmann - K.M. Korpela - P. Stojakowits, *Pleistocene hypothesis-moving savanna perceptual preference hypothesis beyond savanna*, in «Frontiers in Psychology», 13 (2022), 901799.

there is a risk of producing empirically inadequate hypotheses. One might object that, in functional analysis, hypotheses are in any case tested against empirical evidence, and therefore can be refined or corrected through this process. This objection would be valid if evolutionary psychologists were willing to revise their hypotheses in light of empirical testing. But this is not what happened with the savanna hypothesis. Despite mixed results, the hypothesis continues to thrive in evolutionary psychologists' works.

Because of the stylization bias, EP hypotheses, compared to those of paleoanthropology, have typically a low *spatial*, *temporal* and *evolutionary* "resolution": they often treat the entire evolutionary history of humankind as a single, homogeneous block, overlooking the numerous transformations our lineage has undergone across space, time and phylogeny – from the succession of different species, to shifting environmental and ecological conditions, to the growing diversity and complexity of human lifeways. Paleoanthropology and archaeology, on the other hand, operate at a much finer resolution. Although EP must to some extent abstract from certain details to keep the generation process viable (it would not be feasible to consider all the evidence about our past), the level of abstraction caused by stylization bias leads to a hypothesis generation process that is inadequate.

But how should evolutionary psychologists revise functional analysis? We have seen that Tooby and Cosmides propose a process with six steps. In this partition of functional analysis, historical evidence is relevant to the second step: identification of a recurrent adaptive problem and characterize how the adaptive problem manifested itself in our evolutionary past. For these steps to be successfully completed, it is necessary to adequately reconstruct the EEA of an adaptation, that is, the set of selective pressures that shaped it. To do so, we should ideally do two things:

> Outline the period of interest. As already mentioned, not all adaptations will have the same EEA. To identify the relevant period, an initial review of paleoanthropological literature is already necessary. For example, meat consumption plays a fundamental role in hypotheses about the evolution of disgust: the evolution of this primordial emotion would be linked to proximity to carcasses, as scavengers and/or predators[46]. But when did the systematic consumption of meat begin? In other words, what is the EEA of disgust?

46 - D.R. Kelly, *Yuck! The nature and moral significance of disgust*, MIT Press, Cambridge (MA) 2011.

> Evolutionary psychology alone cannot answer this question; it needs paleoanthropological evidence[47].

Select all available relevant evidence. This step clearly depends on the adaptive problem we are investigating. If, for example, we are investigating the assumed differences in partner choice strategies between men and women, any data about the possible social structure of our ancestors and their evolution over time is pertinent. Number of individuals per group, sexual dimorphism, ratio between males and females, the presence of different roles, group mobility and intra-group migration. But also patterns of development and other data that can give us clues as to how the burden of childcare was distributed, and many more. In the case of the savanna hypothesis, paleoecological evidence was pertinent. (Historical evidence is then relevant for the following steps as well, as they require details of what informational resources were available to our ancestors, to infer what specifics of the cognitive mechanism evolved).

Of course, this process is not straightforward. Our knowledge of the past is extremely fragmentary, but it is rapidly increasing and being revised, which makes it difficult to stay up to date when conducting research in another discipline. At the same time, understanding what is relevant for reconstructing the EEA of a particular adaptation is not an easy task. In this regard, greater interdisciplinarity and collaboration with paleoanthropologists and archaeologists could be beneficial. Evolutionary psychologists often claim that the overarching aim of their discipline is the unification of all the human evolutionary sciences. Regardless of whether this undertaking is ultimately feasible, incorporating evidence from these disciplines appears to be one of the minimum requirements for pursuing this goal.

Historical evidence plays a similar role in reverse engineering. In this case, we start with the observation of a behavioral or psychological pattern in modern humans, but knowledge of the past is still required to work out the adaptive function of that particular trait. What is the function of jealousy (if any)? We cannot know unless we reason in terms of the specifics of the context in which it would have evolved. Moreover, paleoanthropological evidence is relevant for another reason. We mentioned that, according to Gould and Lewontin, adaptationist bias improperly leads researchers to divide organisms into independent traits. This issue also arises in evolutionary psychology, where the choice of a particular character as a trait with a separate evolutionary history is rarely justified. Considering the archaeological and fossil record can help evolutionary psychologists

47 - If the EEA of a particular adaptation for example calls into question primate evolution more generally (think of the attachment relationship between mother and child) then evidence from primate paleontology and primatology also become relevant.

reconstruct the history of certain characters and determine which are genuine individual traits and which are not. For example, Hauser and colleagues proposed that the language faculty should not be regarded as a single character but as a mosaic of different traits with distinct evolutionary histories[48] – a view consistent with the fossil and archaeological record[49]. For this reason, an evolutionary psychologist applying reverse engineering to the language faculty may actually be analyzing a composite of different characters, and thus working at the wrong level of analysis.

One final consideration is in order: fully integrating the evidence about our past risks being deeply disruptive to the methods of evolutionary psychology. The increasing complexity of reconstructions of our evolution seems to indicate a certain instability in the selective pressures to which we have been subjected, especially with regard to certain aspects of group life and adaptation to the environment. Identifying a cheater, collaborating with one's companions, finding the best place to set up camp, recognizing environmental dangers, etc. are problems that have changed continuously throughout our evolution. If selective environments changed repeatedly throughout the Pleistocene, then selection may have favored behavioral flexibility, ecological versatility, and broad learning capacities. On the other hand, evolutionary psychologists traditionally assumes that many human cognitive mechanisms evolved as domain-specific solutions to recurrent and relatively stable adaptive problems[50]. The inclusion of paleoanthropological evidence, therefore, risks being incompatible with evolutionary psychology, at least in its more traditional formulations. However, this need not necessarily be the case. In recent years, some evolutionary psychologists have become increasingly open to the possibility that cognitive modules may be more flexible and context-sensitive than originally assumed[51]. Should evolutionary psychology move in this

48 - M.D. Hauser - N. Chomsky - W.T. Fitch, *The faculty of language: what is it, who has it, and how did it evolve?*, in «Science», 298 (2002), pp. 1569-1579.

49 - A. Parravicini - T. Pievani, *Continuity and discontinuity in human language evolution: putting an old-fashioned debate in its historical perspective*, in «Topoi», 37 (2018), pp. 279-287; A. Parravicini - T. Pievani, *Mosaic evolution in hominin phylogeny: meanings, implications, and explanations*, in «Journal of Anthropological Sciences», 97 (2019), pp. 45-68.

50 - A perspective shared by several critics, see for example K. Sterelny - P.E. Griffiths, *Sex and death: An introduction to philosophy of biology*, University of Chicago Press, Chicago 1999.

51 - Consider, for example, how recent research in evolutionary psychology on mate-choice mechanisms has placed far greater emphasis on variability and sensitivity to a wide range of contextual factors. David Buss, *The Sexual Selection of Human Mating Strategies: Mate Preferences and Competition Tactics*, in *The Oxford Handbook of Evolutionary Psychology and Romantic Relationships*, a cura di Justin Mogilski e Todd Shackelford, Oxford University Press, Oxford 2023.

direction, its hypotheses may ultimately prove more compatible than previously thought with the growing body of evidence concerning human evolutionary history.

8. Conclusions

We have seen that, despite its relevance, evidence from paleoanthropology and archaeology is not always integrated into disciplines studying human cognitive and behavioral evolution. Focusing on evolutionary psychology and the savanna hypothesis, we have shown that its formulation overlooks paleoenvironmental evidence about the contexts of human evolution. Consequently, evolutionary psychologists may be testing empirically inadequate hypotheses[52]. Although there appear to be tentative signs of renewal within EP[53], this remains an issue that evolutionary psychologists must address. Indeed, some evolutionary psychologists seem to have recently taken a self-critical stance, admitting that the discipline should take archaeological and paleoanthropological evidence more seriously[54]. And ultimately, evolutionary psychologists cannot get away from doing this if they really want to achieve that unification of multiple fields of knowledge that they so yearn for.

The same concerns also apply to other related disciplines. As already mentioned, Meneganzin and Currie recently emphasized that human behavioral ecology needs to integrate evidence from paleoanthropology in order for its hypotheses to be historically sound[55]. Others have expressed the importance that models of cultural evolutionary theory be grounded in and tested against the archaeological record[56].

---

52 - To be clear, we are not claiming that every hypothesis in evolutionary psychology suffers from this problem; but rather that if historical evidence is not taken into account during hypothesis generation, then we risk formulating inadequate hypotheses.

53 - H.C. Barrett, *The Shape of Thought: How mental adaptations evolve*, Oxford University Press, Oxford 2015; see also G.R. Brown - K.N. Laland, *Sense and nonsense: Evolutionary perspectives on human behaviour*, Oxford University Press, Oxford3 2024.

54 - D.M.T. Fessler - J.A. Clark - E.K. Clint, *Evolutionary psychology and evolutionary anthropology*, in *The handbook of evolutionary psychology: Integrations*, 2nd edition, edited by D.M. Buss, John Wiley & Sons, Inc., Hoboken 2016, pp. 1029-1046; M.A. Abramiuk, *Evolutionary Psychology and Archaeology*, in *The SAGE Handbook of Evolutionary Psychology. Integration of Evolutionary Psychology with other Disciplines*, edited by T.K. Shackelford, SAGE Publications, London 2021, pp. 257-282.

55 - A. Meneganzin, Andra - A. Currie, *Not wasted on the young: Childhood, trait complexes & human behavioral ecology*, cit.

56 - See for example R. Garvey, *Current and potential roles of archaeology in the development of cultural evolutionary theory*, in «Philosophical Transactions of the Royal Society B: Biological Sciences», 373 (2018), 20170057; G. Tostevin, *Content Matters: the materiality of cultural transmission and the intersection of Paleolithic archaeology with cultural evolutionary theory*, in *Beyond the Meme: Articulating*

In any case, disciplines concerned with the evolution of the human mind cannot afford to treat paleoanthropology and archaeology as mere background sources of illustrative examples. If hypotheses about human cognition are meant to be genuinely evolutionary and historically grounded, they must be constrained by the best available evidence about the environments, ecologies, and lifeways of past hominins. Otherwise, the risk is that stylized narratives of human evolution will continue to replace the far more complex history revealed by the historical sciences. These fields have long drawn on insights and methods from other sciences, yet they also have much to contribute in return.

MATTEO BEDETTI
PhD in Research Methods in Science and Technology from the University of Urbino Carlo Bo. His research interests include the methods of historical sciences, and in particular, how paleoanthropology and archaeology deal with epistemically unfavorable situations.
m.bedetti1@campus.uniurb.it

Dynamic Structures in Evolution, edited by A.C. Love - W.C. Wimsatt, University of Minnesota Press, Minneapolis 2019, pp. 311-364.