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RESEARCH ARTICLE

REVISED Use it or lose it: A model-based assessment of the hypothesis that European Neanderthals relied on wildfires to create their campfires

[version 2; peer review: 3 approved, 1 approved with reservations]

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Abstract

Background

There remains debate about the pyrotechnical capabilities of Neanderthals. Evidence of fire has been found at many Middle Palaeolithic sites, widely accepted to be associated with Neanderthals. However, multiple Neanderthal sites show a marked decrease in evidence for fire use during colder periods. This counterintuitive pattern was explained by the possibility that some Neanderthal groups were unable to create fire at will and relied on wildfire. Here, we evaluate the plausibility of this "wildfire hypothesis" through formal modeling.

Methods

We computed the probability of a group of Neanderthals losing campfire-making skills due to cultural loss. The EMBERS model codes four empirically motivated mechanisms of skill loss: variability in use, period in between uses, memory decay and number of experts.

Results

Our results indicate that losing the ability to use wildfire was more likely than retaining it for most of our parameter values within reasonable ranges. Significantly, demography, in the form of expert

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numbers, was the least significant mechanism of loss. The rate of memory loss at group level, and intervals between uses were markedly more important than demography. Variability in time between uses was by far the strongest driver of loss. These results, linked with the estimated climatic, mnemonic, and demographic conditions for the Neanderthals' occupation of Europe in cold periods, support the plausibility of the wildfire hypothesis. Our results also highlight the need to pay more attention to cultural loss as a factor in cultural evolution.

Teaser

Our modeling demonstrates the feasibility of the controversial hypothesis that some European Neanderthal groups were unable to create fire at will and instead relied on wildfire to start their campfires.

Keywords
fire use, cultural evolution, cultural loss, Neanderthals, climate, modeling, archaeology



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REVISED **Amendments from Version 1**

We updated the discussion addressing future work towards other cultural traits, such as lithics, being affected, or not, by the loss of fire.

We also addressed clarification on nomenclature and definitions of the wildfire cultural package as including both the forage of embers from wildfires and the maintenance of fire, and answer to the reviewers to clarify which assumptions we overestimate, or underestimate loss.

We also expand the discussion to add more citations on literature on knowledge keeping by oral societies, importance of child-play in knowledge acquisition and retention, as well as literature on group skill decay and retention. Following these points, we expanded the discussion to address the expected predictions that EMBERS has regarding impact of variable natural hazards in general, and how it can inform the retention or loss of difficult-to-transmit-knowledge dependent expertise on disaster management.

Any further responses from the reviewers can be found at the end of the article

Introduction

The development of the ability to control and create fire is generally accepted to have been a key event in human evolution[1,2]. Many benefits of these abilities have been recognized. In addition to the obvious ones of providing heat and light and enabling food to be cooked, fire would have allowed individuals to manufacture a range of entirely new artifacts, protect themselves against pests and predators, and increase hunting returns via landscape burning[3–5]. The advantages of fire are so great, according to some researchers, that its use influenced the evolution of our digestive and nervous systems[6,7]. It has even been suggested that we, modern humans, are obligate fire users (*i.e.*, we cannot survive without fire)[7]. By the same token, however, ethnographic studies illustrate how difficult fire is to control and curate[8,9]. It is clear from these studies that the ability to create fire has been lost by multiple human groups in the last few hundred years, despite them having elaborate cultural scaffolds for high-fidelity transmission of knowledge and skills across generations[8,9].

While there is consensus that the development of the ability to create and control fire was a milestone in human evolution, several issues concerning the history of pyrotechnology remain poorly understood. It is unclear, for example, how early hominins managed to occupy northern Europe without fire[10]. Another poorly understood issue — and the one on which we focus in this paper — is whether the Neanderthals (*Homo neanderthalensis*) were consistently able to create fire at will and maintain this ability via cultural transmission across the many millennia of their tenure. Evidence of fire has been found at many European Middle Palaeolithic sites, which means there is no question that Neanderthals sometimes used fire. Yet, opinions differ as to whether they were able to create fire from scratch. Many researchers have assumed that the Middle Palaeolithic fire evidence indicates that Neanderthals were readily capable of creating, controlling, and curating fire[11,12]. However, over the last 15 years the notion that all Neanderthals at all times were fully capable pyrotechnologists has been challenged and an alternative possibility proposed, which is that some, perhaps many, Neanderthal groups relied on wildfire to start their campfires and, as a consequence, were prone to losing the know-how required to manage fire during periods of climatic cooling, when wildfires were less frequent[13–16].

Sandgathe and colleagues[13–16] developed this hypothesis to explain results of analyses of fire residues at two caves in southwest France that were occupied by Neanderthals, Pech de l'Azé IV and Roc de Marsal. Sandgathe and colleagues[13–16] showed that the Neanderthals who occupied these sites frequently used fire when the climate was temperate but greatly reduced their use of it, or perhaps even stopped using it, as conditions became increasingly cold. Sandgathe and colleagues[13,14] proposed that this counterintuitive pattern indicates that at least some groups of Neanderthals relied on naturally occurring fire to make their campfires. They argued that this hypothesis explains the significant decrease in the use of fire during cold climatic periods by Neanderthals at the two sites because lightning strikes are more common in temperate conditions than in cold ones and, therefore, so are wildfires.

The pattern of less evidence for fire use during colder periods than in warmer ones is not limited to Pech de l'Azé IV and Roc de Marsal. Sandgathe and colleagues have since documented it at a number of other sites. In 2018, they demonstrated that the pattern is also seen at a third Middle Palaeolithic site in southwest France, Combe Grenal. More recently, they showed that the pattern occurs at Middle Palaeolithic sites in other parts of Europe too[16]. In this study, they analyzed the percentage of burned lithics in layers deposited in more temperate conditions versus layers deposited in cooler conditions at seven Middle Palaeolithic sites and an Upper Palaeolithic site. Four of the Middle Palaeolithic sites — Abri du Maras, Abric Romani, Sesselfelsgrotte, and Kulna — are not in southwest France. Abri du Maras is in southeast France; Abric Romani is in Spain; Sesselfelsgrotte is in Germany; and Kulna is in the Czech Republic. Sandgathe and colleagues found that the percentage of burned lithics was higher in layers deposited in warmer conditions than in layers deposited in cooler conditions at all of the Middle Palaeolithic sites. This is consistent with their earlier results[13,14] and suggests that the pattern of greatly reduced evidence for fire use during colder periods than in more temperate ones is a relatively common one.

In the time since Sandgathe and colleagues[13–16] first outlined their hypothesis in print, a number of counterarguments have been put forward. The most challenging of these relates to the plausibility of the hypothesis. Sorensen[17] argued that it is likely that there would only have been "modest differences in fire ignition frequencies between climatic periods" (16, pg. 19). The corollary of this, according to Sorensen[17], is that Neanderthals would still have encountered wildfires in the landscape in cold and dry periods, and therefore an inability to create fire and reliance on harvesting wildfire cannot explain the decline. Sandgathe and colleagues[15]

rejected this criticism on the grounds that there is a near-universal consensus among climatologists, ecologists, and atmospheric scientists that lightning-caused wildfires are much more common in warm and humid conditions than in cold and dry ones. Although Sandgathe and colleagues[15] were correct about the consensus among specialists regarding the association between lightning-caused wildfires and climatic conditions, Sorensen's point about Neanderthals still encountering wildfires in cold periods is well taken. Lightning strikes would not have stopped entirely as climatic conditions deteriorated. Rather, they would have become less frequent and more irregular. Thus, a key question regarding the plausibility of Sandgathe and colleagues'[13–16] hypothesis is: Could multiple groups of European Neanderthals have lost the ability to use wildfire to create campfires as climatic conditions became colder and drier, even though they still encountered wildfires on occasion?

That hominins occupying the, at times, frigid mid-to-high latitudes of Europe could have lost so patently useful a skill as employing wildfire to light a campfire seems implausible. However, ethnographic evidence suggests that the loss of useful skills is actually a relatively common occurrence among humans, especially in groups that are small and isolated. For example, the loss of the ability to create two useful technologies in parts of Oceania prior to the arrival of Europeans was discussed by Rivers in the early part of the 20th century[18]. One of these technologies was the canoe. Rivers recounted that the people of the Torres Islands had previously made canoes but were no longer able to do so, and that the same held for the people of the island of Mangareva. The other technology was the clay pot. By comparing the distribution of archaeologically recovered pottery sherds with ethnographic accounts of pottery manufacture, Rivers demonstrated that the number of islands on which clay pots were produced had decreased over time. Rivers argued that the absence of suitable raw materials could not explain all of these losses. Among the alternative factors Rivers argued should be considered are religious beliefs, interaction with immigrants, and the loss of communities of specialist craft producers due to catastrophes. Boyd *et al.*[19] highlighted another pertinent case that illustrates that skills can be lost even if they are useful — the Polar Inuit of northwest Greenland. When European explorers visited this group in the mid-19th century, they found that they remembered kayaks, bows-and-arrows, leisters, and heat-saving igloo-entrances, but no longer knew how to make them. The Polar Inuit explained that the know-how required to produce these items had been lost due to an epidemic in the 1820s that killed the group's most knowledgeable members, its elders. These ethnographic examples suggest it is plausible that some Neanderthal groups could have lost the ability to use wildfire to light campfires even though it was a useful survival skill.

There are also a number of archaeological examples of the loss of useful skills. In view of the space constraints, we will highlight just two. The details of the first example were elucidated by Riede[20]. Riede showed that towards the end of the Pleistocene some hunter-gatherer groups in Northern Europe stopped using bow-and-arrow technology in the aftermath of the massive Laacher See Eruption, which occurred around 13,000 BP. Riede attributed the disappearance of bow-and-arrow technology to the groups becoming isolated due to the ash fallout. The second example concerns concrete. Scholars have long been puzzled by the abandonment of the use of concrete in many parts of Europe after the collapse of the Roman Empire, given concrete's clear advantages for construction[21,22]. These archaeological examples also suggest it is plausible that some Neanderthal groups could have lost the ability to use wildfire to light campfires, despite its evident utility.

Further support for the plausibility of Sandgathe and colleagues'[14] hypothesis is provided by studies reported by McCauley *et al.*[9] and Sugiyama[23]. McCauley *et al.*[9] consulted ethnographic texts for a sample of 93 hunter-gatherer groups and collected data pertaining to fire use in settlements. McCauley *et al.*[9] found that several groups did not know how to make fire at the time the ethnographic data were collected. The groups in question were the Onges, Yuquí, Warlpiri, Sirionó, and northern Aché. The Onges and Yuquí collected natural fire and then conserved it for as long as possible. If an individual's fire went out, they borrowed a firebrand from a neighbor. The Warlpiri were entirely reliant on industrially produced matches to make fire. The Sirionó explained to ethnographers that they used to know how to create fire with a friction method but no longer possessed this knowledge. If all their fires were extinguished, the Sirionó raided nearby settlements for fire. Not all Aché groups were able to make fire with traditional methods at the time of contact in the 1970s. The Southern Aché were able to do so but the Northern Aché were no longer able to create fire with traditional methods, and they were only able to remember some of the details of the methods. Importantly, McCauley *et al.*[9] only recorded a practice as absent when the relevant ethnographic reports specifically stated that the group did not engage in the practice, so the absence of the ability to make fire in these cases is reliable. In her study, Sugiyama[23] analyzed a large sample of hunter-gatherer oral narratives pertaining to the acquisition of fire. Her results show that pyrotechnical knowledge was highly variable among ethnographically documented hunter-gatherers. They also underscore that creating fire from scratch was not a trivial matter. This is indicated by the fact that fire was obtained by raiding neighboring groups in a number of the oral narratives, despite the obvious risks of raiding. Together, McCauley *et al.*'s[9] and Sugiyama's[23] findings indicate that, prior to the development of friction matches in the 19th century CE, the know-how required to manage fire would have been much more fragile and easily lost than is usually assumed.

Here, we report a study that was designed to shed further light on the plausibility of Sandgathe and colleagues'[13–16] hypothesis. In the study, we modeled a scenario in which a Neanderthal group solely used lightning-caused wildfire to create its campfires, passed on the relevant techniques via social learning, and was isolated from other Neanderthal groups for long periods

of time, which is consistent with the results of recent analyses of ancient DNA derived from Neanderthal remains from the site of Grotte Mandrin in southern France[24]. We call the model we developed "EMBERS". EMBERS was designed to enable us to estimate the probability of a Neanderthal group retaining the ability to use wildfire to create campfires in the face of variation in the interval between occurrences of wildfire (e.g., once every two years *vs* once every five years) and the level of unpredictability associated with these intervals (e.g., once every two years with a 10% variability on the interval *vs* once every five years with a 50% variability on the interval).

Before proceeding further, it is important to clarify that neither Sandgathe and colleagues'[13–16] hypothesis nor our study assumes the existence of cognitive differences between Neanderthals and modern humans. Critics often argue that Sandgathe and colleagues'[13–16] hypothesis requires Neanderthals to have been cognitively inferior to modern humans. This is not the case, however. The putative inability of European Neanderthals to create fire from scratch could have been due to the nature of their cognition, but equally it could have been due to non-cognitive factors, in the same way that the failure of some modern human groups to invent certain technologies (e.g., the wheel, the bow-and-arrow) or—as noted above—to lose fire-making skills had nothing to do with their cognitive abilities and was instead a consequence of factors like environmental conditions, demography, and chance. In other words, Sandgathe and colleagues'[13–16] hypothesis is agnostic about why Neanderthals did not develop the ability to create fire at will. The criticism also does not hold for our study. We only included one cognition-related variable in our model—the time it takes to forget the skills required to use wildfire to create a campfire and then maintain it—and the values we used for this variable were derived from previously published work involving living people. Thus, we also did not assume the existence of cognitive differences between Neanderthals and *Homo sapiens*. On the contrary, we assumed that Neanderthals were identical to modern humans with respect to the one aspect of cognition included in the study.

Key assumptions of the model

Modeling past hominin behavior always involves making multiple assumptions[25]. Some of these assumptions have substantial impacts on the results; others have only minor effects. In this section, we outline the assumptions of EMBERS that fall into the former category.

One of the main assumptions of EMBERS is that the package of knowledge, skills, and equipment that would have enabled the Neanderthal group to use wildfire to create campfires is sufficiently complex that it cannot be reinvented from start to finish via individual learning and therefore must be the result of cumulative cultural evolution. The assumption can be justified, we believe, by considering the actions necessary to use wildfire to start a campfire in a temperate zone. These actions include (*a*) locating a wildfire in the landscape; (*b*) identifying a suitable ember to collect; (*c*) transporting the ember; (*d*) identifying, collecting, drying, and storing kindling and firewood[26]; (*e*) deciding on a suitable location for a fire in the camp (*i.e.*, a location that is sheltered from the wind and does not lead to heat and smoke affecting other communal activities)[26–28]; (*f*) arranging the kindling and firewood into one of the several possible fire lays (e.g., teepee lay, lean-to lay)[27]; (*g*) adding firewood to the growing fire in such a manner that air can still circulate and prevent the build-up of carbon monoxide[28,29]. Each of these actions involves knowledge, skills, and in some cases, special equipment. For example, starting fire from an ember requires detailed knowledge about the properties of tinder and wood[27], while the transportation of an ember has to be carried out in such a way that the ember does not harm the person carrying it. It also has to be carried out in such a way that the ember is not extinguished before arrival at camp. And these are not the only relevant actions. A group using wildfire to create a campfire likely will also try to maintain the fire for an extended period of time, and, if the group is like ethnographically documented hunter-gatherers[9], they will also try to transport fire between camps. Again, these actions involve knowledge, skills, and in the case of transporting fire between camps, special equipment[26,27,30,31]. Given the number and complexity of the actions involved, and the fact that some of them have to be carried out in a particular order, it is, we contend, highly unlikely that the WCP can be learned in its entirety through individual learning. It almost certainly has to develop through repeated experimentation, evaluation, and the transmission of knowledge and skills between generations. That is, it almost certainly has to be the product of cumulative cultural evolution. In line with this, we will from now on refer to the package of knowledge, skills, and equipment as the "Wildfire Cultural Package" or the WCP for short.

Crucially for present purposes, knowledge, skills, and technology assembled by cumulative cultural evolution can deteriorate and even disappear[19,32–34]. This can occur as a result of the loss of the relevant knowledge and skills (e.g., due to forgetting, destruction of books) and/or the loss of group members with the relevant knowledge and skills (*e.g.*, due to death, migration, burning of manuscripts)[35–37]. When creating EMBERS, we opted to model cultural loss as the reduction in the number of experts. We defined an expert as an individual with the knowledge and skills necessary to use wildfire to create and curate campfires (i.e., someone capable of using the WCP). We assumed that the number of experts undergoes exponential decay when the WCP is not utilized and immediately returns to a fixed maximum level each time the WCP is employed, providing that the number of experts does not drop below one during the interval of non-use.

Few longitudinal studies of the loss of knowledge and skills have been published, but those that have suggest it typically follows an exponential function. McKenna *et al.*[38] and Glendon[39] assessed individuals' ability to perform cardiopulmonary resuscitation (CPR) after different intervals without practice, and both studies found that the data fitted an exponential decay curve. Recently, Candia *et al.*[40] examined data on papers, patents, songs, movies, and biographies and found that

collective memory and attention decays biexponentially. In our study, we opted to assume that the loss of the knowledge and skills required to use wildfire to create a campfire followed an exponential decay curve, because CPR is more similar to the use of wildfire than are the activities that give rise to the types of data analyzed by Candia *et al.*[40]. Importantly, there is no difference between the two curves at the tail of the decay, which is the crucial part for our model of cultural loss.

Ethnographically-documented hunter-gatherers use a variety of social learning and transmission strategies[41]. We deliberately did not consider the impact of different social learning mechanisms (e.g., vertical transmission *vs* horizontal transmission) on the process by which the hypothetical Neanderthal group may lose the ability to use the WCP. We focused on the total number of experts regardless of how they obtained their knowledge and skills. This made the model simpler. It also—like the return to the maximum number of experts each time the WCP was used—reduced the probability of the WCP being lost, which in turn reduced the probability that EMBERS would support Sandgathe and colleagues' hypothesis[14–16]. This made our study conservative.

The last major assumption we made is that our hypothetical Neanderthal group could only utilize the WCP when they had direct access to wildfire and could not obtain embers in any other way if their campfire went out (e.g., by raiding neighboring groups as the Sirionó are known to have done[9]). This assumption, which links the frequency of use of the WCP to the frequency of occurrence of wildfire (as opposed to, say, volcanic eruptions), is at the heart of Sandgathe and colleagues'[13–16] hypothesis. In the temperate zone of the Northern Hemisphere, wildfires are usually triggered by lightning but also depend on the availability of combustible material[42]. Consequently, the occurrence of wildfire is spatiotemporally variable: it does not occur every year in a given location. In line with this, we modeled the timing of the use of the WCP with a series of normal distributions with different mean intervals and different variances around the mean interval.

Results

We report results obtained with two versions of EMBERS, a numerical version and an analytical one. The numerical version was created to provide a clear picture of the different elements of the model. The analytical version was developed to allow faster exploration of the parameter space. An advantage of generating both versions of a model is that it enables cross-validation. We estimated the probability of a Neanderthal group losing the expertise necessary to use the WCP in a 1000-year length (L) in the face of fluctuations in (i) the mean interval between uses of the WCP (θ); (ii) variability in the intervals (ηv); (iii) the maximum number of experts in the group (*i.e.*, the maximum number of individuals with the knowledge and skills necessary to use the WCP; η^{max}); and (iv) the decay on the number of experts in the group (τ). The definitions, characteristics, and ranges of values of the parameters used in the simulations are summarized in Table 1 and discussed in detail below. When creating the two versions of EMBERS, we assumed that the parameters were independent of each other. This assumption is probably unrealistic but there are currently no data or theory that shed light on possible dependencies among the parameters. As such, we opted for the simplest assumption, which is independence among all parameters. We analyzed every combination of variables (θ, v, η^{max}, τ) for the

Table 1. Main parameters of the EMBERS model.

Parameter	Symbol	Definition	Units	Type	Values
Time Length	L	The maximum length of time modeled by EMBERS. Note that not all runs of the model get to L in the numerical version. Sometimes the ability to use the WCP is lost before L is reached. In such cases, the run ends when the ability to use the WCP is lost.	Years	Fixed	1000
Temporal Sequences	K	The number of sequences that are used for each combination of parameters in the numerical version of EMBERS. The number has to be high enough to obtain a probability distribution.	-	Fixed	111
Use Interval	θ	The mean of the normal distribution that is used to determine the intervals between uses of the WCP for a single temporal sequence and for the temporal sequences that comprise a simulation.	Years	Variable	1–20
Variability	v	A dimensionless scaling factor used to represent the uncertainty associated with the intervals between uses of the WCP.	-	Variable	0–2
Maximum Number of Experts	η^{max}	The maximum possible number of experts for a given temporal sequence. For the present study, an expert is an individual who has the knowledge and skills to use wildfire to create a campfire (*i.e.*, someone capable of using the WCP). Each temporal sequence starts with the number of experts at η^{max}, and each time the WCP is used the number of experts returns to η^{max}.	Individuals	Variable	3–60
Forgetting Time	τ	The interval it takes for the number of experts to be reduced to about a third of η^{max} ($\frac{1}{e} \approx 0.36$).	Years	Variable	1–16

values in the ranges outlined in the Materials and Methods section. For each combination of values, we computed the probability of retention, P_r.

P_r is computed differently in the numerical and analytical versions of EMBERS but the calculations depend on the same set of assumptions and parameters, such that the two versions of P_r provide comparable estimates of the probability of retaining the WCP in L for a given combination of variable values.

Figure 1 shows P_r for different values of θ and v, when η^{max} and τ are fixed at 43 and 4, respectively. The first result to note is that all the squares to the right of the blue line marking Δt^{max} show a complete loss of the WCP before L = 1000. This is expected because Δt^{max} is the time it takes for the number of experts to drop to 0 and therefore is the upper limit for retention of the ability to use the WCP in the absence of the occurrence of a wildfire. It is simply not possible for the probability of retention (P_r) to be greater than 0 if *Use Interval* (θ) is longer than Δt^{max}.

Next, even allowing for the fact that the loss of the ability to use the WCP to the right of the blue line is expected, it is evident that there are many combinations of θ and v that result in a complete loss of the ability to use the WCP during the 1000-year period modeled by EMBERS. If we focus on the combinations to the left of the blue line, approximately two-thirds of them result in the loss of the ability to use the WCP before L = 1000, while only one-third result in the retention of the ability to use the WCP up to L = 1000. Thus, Figure 1 indicates that our *in silico* Neanderthal group could lose the ability to use wildfire to make campfires even when wildfires were still occurring in its territory. Notably, Figure 1 suggests that the loss of the ability to use wildfire to make campfires was not just possible but in fact more likely than the retention of the ability.

Turning to the individual impact of the two variables, it is evident that *Use Interval* (θ) has no effect on P_r providing *Use Interval* is less than Δt^{max}. This can be seen if we move from left to right along the bottom rows of Plots A and B, where v is between 0 and 0.04. All the squares show a high probability of retention of the WCP for 1000 years, until the line showing the location of Δt^{max} is reached. Beyond the line, all the squares show a failure to retain the WCP to 1000 years. The implication of this is that the only value of θ that is relevant for estimating P_r is the one that corresponds to Δt^{max}. Another way of thinking about this is that it is Δt^{max} that dictates the boundary between the retention and loss of the WCP, rather than θ.

Unlike θ, *Variability* (v) has a substantial impact on P_r. Moving upwards on the y-axis of both panels, we can see that

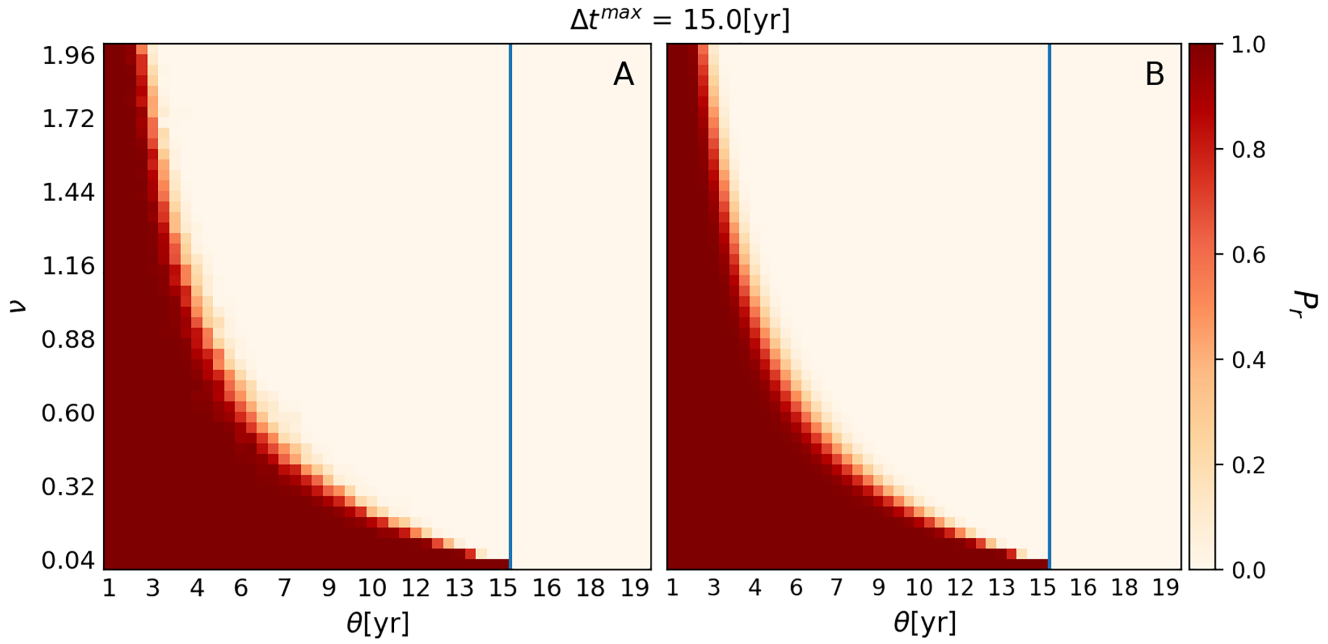

Figure 1. Plots showing *Probability of Retention* (P_r). P_r for different combinations of *Use Interval* (θ) and *Variability* (v) when *Forgetting Time* (τ) and *Maximum Number of Experts* (η^{max}) are fixed at 4 and 43, respectively. Plot **A** was generated with the numerical version of EMBERS, while Plot **B** was produced with the analytical version. Each square of the grid is color-coded to represent the probability that the WCP will be retained by the hypothetical Neanderthal group at the end of 1000 years. Dark red represents a high P_r, while cream indicates a complete loss before 1000 years was reached. The pixels shaded in lighter red and orange represent combinations of variable values that result in intermediate P_r. The lighter red-to-orange zone marks the transition between retention and loss of the WCP. The blue vertical line represents Δt^{max}, which is 15 years for the chosen set of variable values.

increasing v from 0 to 0.32 results in the boundary between retention and loss of the WCP changing from 15 years to about nine years. Then, increasing v from 0.32 to 0.88 changes the boundary to approximately five years. Further increasing v from 0.88 to 2, changes the boundary between retention and loss of the WCP to around three years. Thus, v has a non-linear impact on P_r, and the impact is such that increases in v have a much larger effect on P_r when v is small than when v is large.

We will now examine the way P_r is affected by the other two key variables, τ and η^{max}. Because τ and η^{max} affect P_r via Δt^{max} (Equation 3 in the Materials and Methods section), we will begin by examining the influence of τ and η^{max} on Δt^{max} using results from the analytical version of EMBERS.

The nature of the relationship between Δt^{max} and τ is discernible when P_r is plotted in relation to different values of v and θ. The same holds for the nature of the relationship between η^{max} and Δt^{max}. Figure 2 plots P_r in relation to a sample of different values of τ, v and θ. In Plot A, the transition zone between retention and loss is linear. Thus, when *Variability* is low (*e.g.*, v = 0.1), the ability to use the WCP can be retained in the face of a *Forgetting Time* as short as two years (τ <= 2), whereas when *Variability* is high (*e.g.*, v = 1.5), *Forgetting Time* has to be ten years or more (τ >= 10yr) for the group to retain the ability to use the WCP for 1000 years. Interestingly, the transition zone widens as v increases. This is due to stochastic processes playing an increasingly important role as *Variability* (v) and *Forgetting Time* (τ) increase. In other words, the wider the transition zone, the more chance plays a role in the retention of the ability to use the WCP in the 1000-year time.

Panel B shows the same pattern. The transition zone between retention and loss is not only linear but also widens as θ increases. The implication of the former is that the greater the value of *Use Interval* (θ), the longer the *Forgetting Time* (τ) has to be for the hypothetical Neanderthal group to retain the ability to use the WCP. For example, when θ = 4, retention happens for values of τ as low as three, whereas when θ = 14, retention only happens for values of τ equal to or greater than 12 years. Similar to Panel A, the widening of the transition zone indicates that chance plays a greater role in the retention *vs* loss of the ability to use the WCP as θ and *Forgetting Time* increase.

Figure 3 plots P_r in relation to a sample of different values of η^{max}, v, and θ. In Panel A, the transition zone between retention and loss is a positive logarithmic curve and widens as η^{max} increases. The former means if the variability (v) doubles, the number of experts has to quadruple in order to retain the ability to use the WCP for 1000 years. This effect can be appreciated by locating the values of η^{max} required to retain the ability to use the WCP in the face of values of v of 0.6 and 1.2. When v = 0.6, it is probably sufficient for the hypothetical Neanderthal group to have just 14 experts. However, when v is 1.2, the group must have 60 experts to retain the ability to use the WCP for 1000 years.

Plot B of Figure 3 shows that the relationship between η^{max} and θ is similar. The transition zone between retention and loss is not only a positive logarithmic curve but also widens as θ increases. The implication of the former is that if *Use Interval* doubles, then the maximum number of experts must quadruple in order for the ability to use the WCP to be retained until L = 1000. For example, if θ = 4, then η^{max} has to be

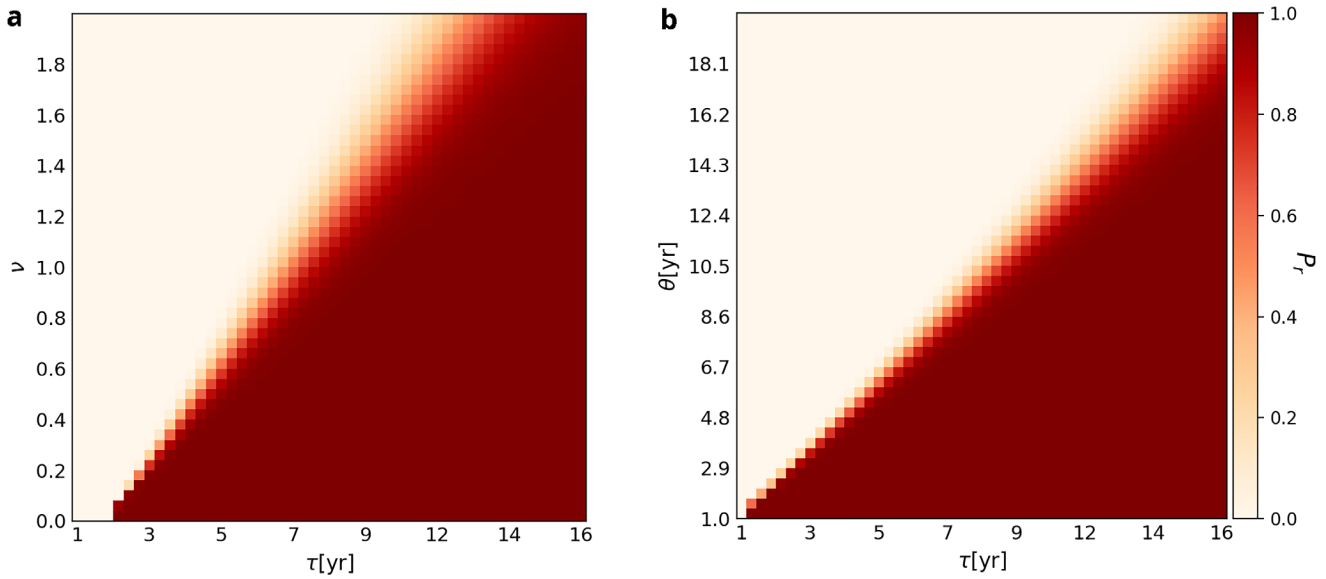

Figure 2. Probabilities of retention (P_r) associated with different combinations of *Forgetting Time* (τ), *Variability* (v), and *Use Interval* (θ). Parameter η^{max} is set at 8. θ is fixed at 4 in Plot **A**, while v is fixed at 0.3 in Plot **B**. Each square of the grid is color-coded to represent the likelihood of retention of the WCP at the end of 1000 years. The color scheme is the same as the one used in Figure 1.

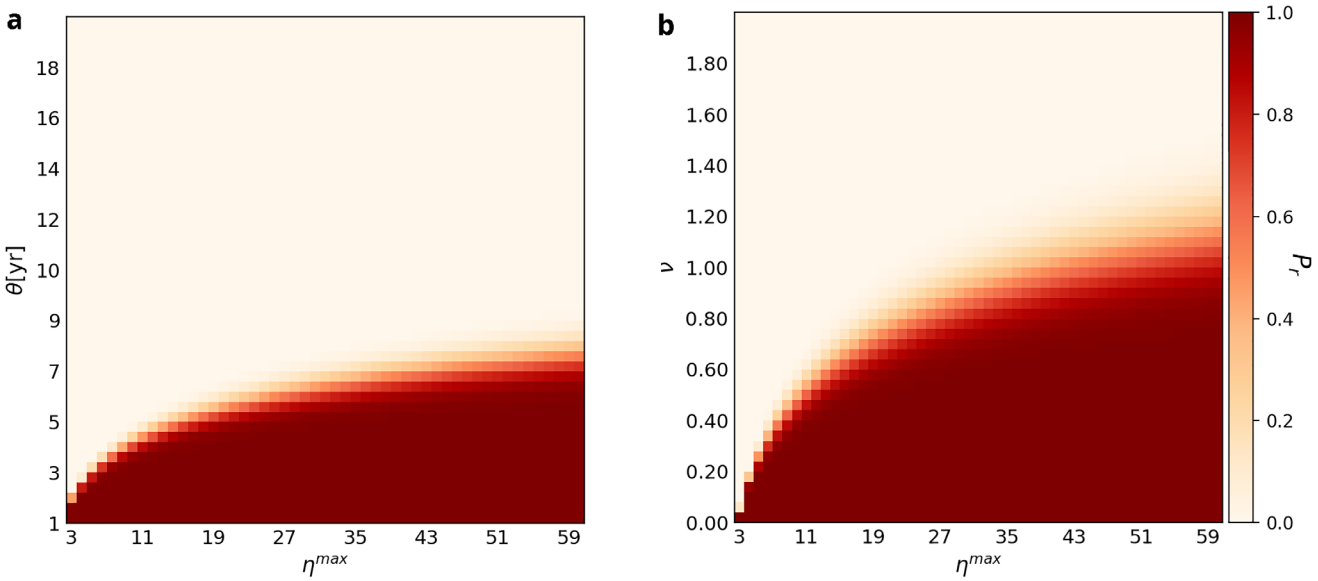

Figure 3. Retention probabilities for different combinations of η^{max} and ν and η^{max} and θ. The parameter τ is fixed at four in both panels, θ is set at 4 in Plot **A**, while ν is fixed at 0.3 in Plot **B**. Each square of the grid is color-coded to represent the likelihood of retention of the WCP at L = 1000. The color scheme is the same as in Figure 1 and Figure 2.

≥9 to retain the ability to use the WCP until L = 1000, whereas if θ = 6, then η^{max} has to be ≥30.

Figure 4 is a grid of plots that show the retention probability associated with a sample of different combinations of values of θ, ν, τ, and η^{max}. The ranges for θ and ν match those seen in Figure 1 and are used in all the plots in the grid. To make the Fig. less cluttered, only the minimum and maximum values of the ranges are shown. Each plot relates to a different combination of values of τ and $\eta^{\max}$. The ranges of values of τ and η^{max} are τ = 1, 2, 4, 8, 16, and η^{max} = 3, 6, 12, 24, 48, 60. The color coding scheme for the squares within the plots is the same as in Figure 1, Figure 3, and Figure 4. Once again, the blue lines represent the Δt^{max} for the modeled combination of variable values. Where a plot lacks a blue line, it means that the Δt^{max} is larger than the relevant maximum value of θ.

As with Figure 1, it is clear from Figure 4 that there are many combinations of τ and η^{max} that result in a loss of the ability to use the WCP during the 1000-year time span. Again, this is the case even when we consider the fact that the loss of the ability to use the WCP to the right of the blue line is expected. In 25 of the 30 panels, the number of combinations of values of τ and η^{max} that result in the loss of the ability to use the WCP before L = 1000 is greater than the number of combinations of values of τ and η^{max} that result in the retention of the ability to use the WCP up to L = 1000. Thus, like Figure 1, Figure 4 does not merely suggest it is possible that the Neanderthal group could lose its ability to use wildfire to create campfires even though wildfires are still occurring on occasion. It suggests it is more likely that the group would lose the ability than that they would retain the ability.

The impact of *Forgetting Time* (τ) on the probability of retention (P_r) can clearly be seen in Figure 4, as can the impact of *Maximum Number of Experts* (η^{max}) and the combined effect of the two variables. Focusing on the fourth row of panels from the top (the one corresponding to η^{max} = 24), we can see that the larger the value of τ (*i.e.*, the longer *Forgetting Time*), the greater the probability that the hypothetical Neanderthal group will retain the ability to use the WCP for 1000 years. Similarly, if we focus on the fourth column of panels from the left (the one corresponding to τ = 8), we can see that the probability of the group retaining the ability to use the WCP until L = 1000 increases as η^{max} increases. However, the effect of each of these variables is modified by the other variables. For example, when *Forgetting Time* is set at the shortest possible time (τ = 1) and *Maximum Number of Experts* is at fixed at the lowest possible value (η^{max} = 3), the hypothetical Neanderthal group never retains the ability to use the WCP for the 1000-year time. In contrast, when *Forgetting Time* is set at the longest possible time (τ = 16) and *Maximum Number of Experts* is fixed at the maximum possible (η^{max} = 60), the group nearly always retains the ability to use the WCP for 1000 years. Regarding the relative importance of τ and η^{max}, the impact of varying τ is greater than the impact of varying η^{max}. This can be appreciated by comparing the bottom row with the rightmost column. The change in the size of the dark red area, which denotes retention of the ability to use the WCP, is much greater as one moves from τ = 1 to τ = 16 in the bottom row than it is as one moves from η^{max} = 3 to η^{max} = 60 in the rightmost column. Thus, while both *Forgetting Time* and *Maximum Number of Experts* impact the probability of retention, *Forgetting Time* is the more influential of the two variables.

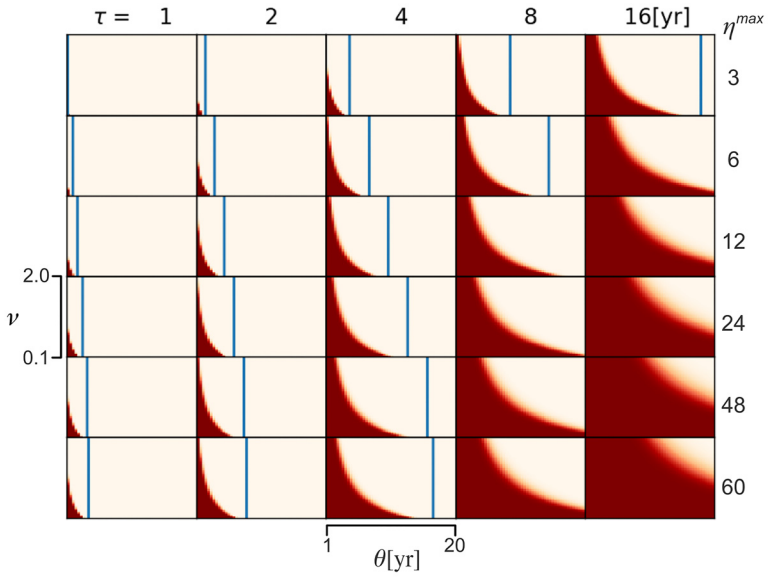

Figure 4. Multiplot showing the *Probability of Retention* (P_r). The probability of retention, P_r represented for different combinations of *Use Interval (θ)*, *Variability (ν)*, *Forgetting Time (τ)*, and *Maximum Number of Experts* (η^{max}). Each sub-plot shows P_r for combinations of θ and ν when τ and η^{max} were varied. The brackets to the left of the fourth row and the bottom of the third column show the ranges of ν and θ, respectively. For consistency, the ranges of values of τ and η^{max} are the same as those seen in Figure 1. The color-coding scheme is the same as in Figure 1, Figure 2, and Figure 3.

Discussion

The study reported here was motivated by a debate about a counterintuitive pattern documented at multiple Neanderthal-linked archaeological sites in Europe—a decrease in evidence for fire use in layers deposited in colder conditions. Sandgathe and colleagues[13–16] have proposed that this pattern indicates that European Neanderthals were unable to create fire and instead relied on wildfire to start their campfires. This hypothesis explains the decline in evidence of the use of fire in colder conditions, according to Sandgathe and colleagues[13–16], because lightning strikes are more common in temperate conditions than in cold, dry ones and therefore so are wildfires. Critics of Sandgathe and colleagues'[13–16] hypothesis have argued that it is flawed because lightning strikes would not have stopped entirely as climatic conditions deteriorated, they just would have become less frequent and more irregular[17]. It is not plausible, the critics contend, that European Neanderthals would have forgotten how to use wildfire to create campfires if they still encountered wildfire on occasion and therefore other explanations must be considered. The goal of the present study was to shed light on this debate about the plausibility of Sandgathe and colleagues' hypothesis. To do so, we developed a model that we call EMBERS.

EMBERS estimates the probability of a hypothetical group of Western European Neanderthals losing the knowledge and skills required to use wildfire to create a campfire, *i.e.*, the ability to use the wildfire-use cultural package (WCP). Specifically, it estimates the probability of losing the WCP in a 1000-year period in the face of variation in (*i*) the maximum number of individuals able to use the WCP (*Maximum Number of Experts*); (*ii*) the rapidity of decay of the group's ability to use the WCP (*Forgetting Time*); (*iii*) the time between uses of the WCP (*Use Interval*); and (*iv*) the uncertainty associated with the preceding variable (*Variability*). In the study, we grounded EMBERS in the empirical world by utilising values for *Maximum Number of Experts* that were drawn from studies that have estimated Neanderthal group size, and values for *Forgetting Time* that were taken from studies dealing with the loss of procedural-motor skills. In a similar vein, we utilised values for *Use Interval* and *Variability* that reflect the known temporal dynamics of wildfires in the Northern Hemisphere's temperate zone. In order to cross-validate the results, and for computational efficiency, we created two versions of EMBERS, a numerical version and an analytical version.

The results yielded by the two versions of EMBERS were consistent: The loss of the ability to use wildfire to create campfires is a more likely outcome than retention of the ability when the variable parameters were assigned values that approximate the conditions assumed by Sandgathe and colleagues[13–16], i.e., when the frequency and regularity of wildfires declines. In fact, the results indicate that the loss of the ability to use wildfire to create campfires is a more likely outcome than its retention for a large majority of the potential combinations of values of the four variables. Thus, our study supports the plausibility of Sandgathe and colleagues'[13–16] hypothesis. Continuing to encounter wildfire would not necessarily have ensured that the Neanderthal groups were able to maintain the ability to use wildfire to create campfires. The speed of decay of procedural-motor skills is such that, for groups that depended on access to wildfire to start their campfires, it would only

have taken a relatively small decline in the frequency and regularity of wildfires for the groups to have lost the relevant cultural knowledge.

The foregoing results are, of course, dependent on EMBER's assumptions. Yet, there is no reason to believe that these made the results unreliable. We made seven main assumptions when creating EMBERS: (*i*) the primary cause of wildfire is lightning; (*ii*) campfires last for only a short period, *i.e.*, a few days or weeks; (*iii*) the process of using wildfire to create and curate a campfire is sufficiently complex that it must be the product of social learning and cultural transmission; (*iv*) the WCP involves procedural-motor skills and therefore undergoes exponential decay like the procedural-motor skills whose retention has been investigated in present-day *H. sapiens*; (*v*) the hypothetical Neanderthal group permanently loses the WCP if the number of experts drops below 1; (*vi*) the number of experts recovers instantly to the selected value for *Maximum Number of Experts*, after a use of the WCP; and (*vii*) the values of the parameters do not change within a given simulation. Assumptions *i, ii, iii*, and *iv* are grounded in empirical evidence. The remaining three assumptions are harder to defend, but it is unlikely that they biased the results in favor of loss of the ability to use the WCP. Assumption *v* increases the probability of the WCP being lost, but assumptions *vi* and *vii* promote retention of the WCP. So, if assumptions *v*, *vi*, and *vii* biased the results in a particular direction, they probably did so in favor of retention of the ability to use the WCP.

The results are also dependent on the values selected for the variable parameters. The values for the four variables were chosen in light of findings of empirical studies, and where it was necessary to make a call about the values at either end of the range for a variable, we selected values likely to result in a higher probability of retention. Thus, if anything, the values we selected for the variables biased the results in favor of retention of the ability to use the WCP.

It appears, then, that we can invest reasonable confidence in the finding that it is more likely that the ability to use the WCP would be lost than retained in conditions akin to those experienced by European Neanderthal groups during cold, dry periods of the Pleistocene. This means that our study suggests Sandgathe and colleagues'[13–16] explanation for the pattern of fire evidence at Pech de l'Azé IV, Roc de Marsal, and several other Neanderthal sites in Europe is plausible. That is, it suggests the decline in fire evidence at the sites in question after climatic conditions worsened *could* be due to the Neanderthals who occupied them being unable to create and curate fire and having to rely on wildfire to create campfires. Contrary to what critics have argued[17], continuing to encounter wildfire would not necessarily have ensured that the Neanderthal groups were able to maintain the ability to use wildfire to create campfires. The speed of decay of procedural-motor skills is such that it would only have taken a small decline in the frequency and regularity of wildfires for the groups to have lost the relevant cultural knowledge.

As mentioned in the Introduction, implausibility due to wildfire being less frequent rather than non-existent in cold conditions is not the only grounds on which Sandgathe and colleagues'[13–16] hypothesis has been criticized. Two other criticisms can be identified in the literature. One is that there are better explanations for the empirical finding that Sandgathe and colleagues[13–16] developed their hypothesis to explain—i.e., the dramatic decrease in evidence for fire use in layers deposited in colder conditions at multiple Neanderthal-linked sites in Europe[17,43]. (The other criticism is that there is archaeological evidence that demonstrates Neanderthals were able to create fire at will[12,44]. While these criticisms are not directly relevant to the goal our study, which was to assess the plausibility of Sandgathe and colleagues'[13–16] hypothesis, we will briefly comment on them.

Alternative explanations for the decline in fire evidence highlighted by Sandgathe and colleagues[13–16] have been put forward by Henry[43] and Sorensen[17]. Henry[43] focused on the economics of fire creation and use and proposed that the Neanderthal groups in question stopped making fire because the calories they expended collecting the resources needed to create and maintain a fire had started to exceed the extra calories obtained from cooking food compared to eating it raw. Although we believe Henry was right to draw attention to the fact that the costs of making fire need to be considered alongside its benefits, we do not think her explanation for the pattern of fire evidence is better than the one put forward by Sandgathe and colleagues[13–16]. The reason for this is that Henry's hypothesis assumes that the knowledge and skills required to create, maintain, and transport fire can linger unused for long periods of time and still be available when conditions change and the benefits of using fire start to exceed the costs again. This assumption is problematic. The relevant knowledge and skills can be expected to be subject to decay just like the knowledge and skills involved in CPR. Hence, a Neanderthal group that stopped making fire for an extended period of time because it had become uneconomic would likely lose the ability to create fire at will, just like the hypothetical Neanderthal group on which EMBERS focused lost the ability to use the WCP in many of the temporal sequences. Thus, the economic view of fire use promoted by Henry is incomplete. It is important to consider the costs and benefits of using fire, but that is not enough. The cultural processes involved, especially cultural loss, have to be considered too.

Sorensen[17] argued that the decline in fire evidence highlighted by Sandgathe and colleagues[13–16] can be explained by the relevant Neanderthal groups adapting to colder, drier conditions by using smaller, short-lived fires for specific tasks. They would have done so, he argued, because woody fuel is less abundant in colder, drier conditions. According to Sorensen[17], the use of short-lived fires would have resulted in a significant decline in evidence for fire. This 'ephemeral fire hypothesis' was rejected by Sandgathe and colleagues[15] on the grounds that the artifact density at some of the relevant sites was so

high that even small, short-lived, infrequent fires would have left burned artifacts. There are other problems with the ephemeral fire hypothesis. One is that it is inconsistent with the available ethnographic evidence, which, as we explained earlier, indicates that hunter-gatherers prefer to transport embers between camps rather than restarting fires from scratch[9]. Another problem is that the ephemeral fire hypothesis, like Henry's[43] economic hypothesis, presupposes that the knowledge and skills required to start a fire can be maintained by a group for any length of time. As the analyses reported here show, this is not a reasonable assumption. The relevant knowledge and skills can be expected to have decayed, and to have done so rapidly, if the group did not use them. Thus, even if the other problems with the ephemeral fire hypothesis are ignored, the ephemeral fire hypothesis is, like Henry's[43] hypothesis, incomplete. Cultural loss has to be considered.

The other criticism of Sandgathe and colleagues'[13–16] hypothesis that can be identified in the literature is that it cannot be correct because there is evidence that indicates Neanderthals were able to create fire at will. This criticism has appeared in two studies[12,44] —Sorensen *et al.* (2018) and Brittingham *et al.* (2019). Sorensen *et al.*[12] claimed to have found microwear evidence that Mousterian bifaces (one of the key components of the Mousterian of Acheulean Tradition [MTA] as defined by François Bordes[45]) were used to create fire. Sorenson *et al.* (2018)[12] argued that Neanderthals used MTA bifaces in conjunction with chunks of pyrite (FeS_2) to produce fire. Specifically, they argued that Neanderthals struck pieces of pyrite against the flat/convex surfaces of MTA bifaces to produce sparks capable of setting tinder alight. They based this claim on a comparison between microwear they identified on a sample of MTA bifaces and microwear they generated in replicative experiments. This is an interesting hypothesis, but, Sorensen *et al.* (2018)[12] did not identify any evidence of pyrite on the bifaces they examined. Nor did they adequately investigate alternative causes of the damage they documented on the flat/convex surfaces of the bifaces in their sample. Equally problematically, Sorenson *et al.* (2018)[12] did not blind the experiments: the experimental microwear was created by a person who knew what they needed to produce to support the authors' preferred explanation for the microwear on the archaeological artifacts, which means the results of the experiments are unreliable. Given these problems, Sorenson *et al.*'s (2018)[12] claim is unconvincing.

Brittingham *et al.* (2019)[44] approached the problem of trying to identify evidence that Neanderthals were able to create fire at will in a different way. They analyzed polycyclic aromatic hydrocarbons (PAHs) at the Armenian Middle Palaeolithic site of Lusakert Cave. PAHs are organic compounds that are produced when organic material is burned. Heavy PAHs are a major component of burned wood PAH emissions, while light PAHs are a major component of wildfire PAH emissions. Brittingham *et al.* (2019)[44] reported finding no association between the abundance of heavy PAHs and the abundance of light PAHs. Instead, they found that the abundance of heavy PAHs was correlated with the density of Middle Palaeolithic artifacts. They concluded from this that the Neanderthals who occupied the site must have been able to create fire from scratch and therefore were not dependent on wildfires to create their campfires. On the face of it, Brittingham *et al.*'s (2019)[44] results represent a substantial challenge to Sandgathe and colleagues'[13–16] hypothesis—and by extension this study. However, the data that Brittingham *et al.* (2019)[44] present in their Figure 1 shows a positive correlation between the abundance of heavy PAHs and a proxy of environmental temperature, δD_{Wax}. This correlation indicates that heavy PAHs were more abundant in warmer conditions than in colder conditions. If heavy PAHs are indicative of campfires, as Brittingham *et al.* (2019)[44] contend, then their data are in line with Sandgathe and colleagues'[13–16] hypothesis rather than inconsistent with it. Thus, Brittingham *et al.*'s (2019)[44] study does not in fact challenge Sandgathe and colleagues'[13–16] hypothesis.

In sum, then, the other two criticisms of Sandgathe and colleagues[13–16] hypothesis are no more compelling than the claim that the hypothesis is implausible because Neanderthals would still have encountered wildfire when conditions became colder and drier.

Although the EMBERS model was developed to evaluate a hypothesis regarding the pyrotechnological abilities of European Neanderthals, none of the assumptions it makes is specific to European Neanderthals, or even Neanderthals in general. The assumptions hold for any group of hominins relying on wildfire to create campfires in Europe, including groups of *Homo sapiens*. Indeed, given that lightning is the primary cause of wildfire worldwide, and that the frequency and predictability of lightning strikes vary through time in all regions of the world, the assumptions hold for any group of hominins reliant on wildfire to create campfires. One implication of this is that we should be prepared for the possibility that, prior to the development of the ability to make fire from scratch and a means to keep that knowledge from vanishing, the use of fire was often a temporary phenomenon. It may have been common for hominin groups to gradually develop the ability to use wildfire to create campfires via cumulative cultural evolution and then rapidly lose the ability due to a change in the local wildfire regime. This in turn implies that wildfire-dependent hominin groups may have found it difficult to persist after migrating into higherlatitudes unless they had other means of coping with cold temperatures such a high basal metabolic rate or clothing.

The present study also has implications for the ongoing effort to develop an adequate theory of cultural evolution[46]. In the last 25 years, researchers working in the field of cultural evolutionary studies have discussed cultural loss, but they have done so primarily in the context of trying to elucidate the relationship between cultural complexity and demography (e.g., 47–56). Little attention has been paid to the importance of cultural loss relative to cumulative cultural evolution, or to the specific mechanics of cultural loss. The results yielded by EMBERS indicate that this is unfortunate. That the loss of the WCP was more common than its retention suggests that

cultural loss has the potential to be a highly influential process, and that we need to change how we think about cultural evolution. We should view humans and other cultural species as having to constantly contend with the decay of their knowledge and skills and treat the maintenance of existing cultural traits as at least as great a challenge as the invention and transmission of new ones. Regarding the mechanics of cultural loss, EMBERS shows that memory decay is critically important. The rate of memory decay varies by the type of cultural trait (e.g., procedural skills tend to be forgotten faster than perceptual skills[57] but in the absence of ways of countering memory decay, all cultural traits will degrade and eventually be lost, resulting in a reduction in cultural richness and/or complexity. This implies that memory decay should be recognized as a key cultural evolutionary process alongside copying error, guided variation, and the various types of cultural transmission that have been recognized. An obvious corollary of this is that the main ways of countering memory decay should also be treated as important phenomena by cultural evolutionary theorists. So far, memory decay and ways of countering it have received little attention in the cultural evolutionary literature. We have only been able to identify three recent relevant publications—Wakano and Kadowaki[58], which included a rate of loss of skill; Ammar *et al.*[59], which focused on the related process of forgetting (*i.e.*, deliberate, active erasure of knowledge); and Morin[60], which did not explicitly discuss memory decay but did discuss techniques that human groups employ to retain traditions, including repetition and redundancy. Based on the results of the present study, there is, we suggest, good reason for researchers interested in cultural evolution to increase the number of studies dealing with cultural loss and ways of retaining knowledge and skills. As part of this effort, it would be sensible to tap into the work being carried out by researchers interested in cultural preservation[61–63], the role of oral traditions in cultural maintenance[64–66], children's play and oral storytelling in small-scale societies[67–70], and the role of memory in human affairs[71–74]. Some of the recent work on culture in non-human animals is also likely to be helpful[75–77].

With respect to future directions, in the next phase of our work we intend to extend EMBERS to explore a more complex scenario than the one examined in the present study. To reiterate, we assumed that the WCP was gradually lost by memory decay turning experts into non-experts. However, memory decay is not the only way that a group can lose experts. They can also be lost suddenly via death, as the Polar Inuit example discussed in the Introduction demonstrates, or migration. This raises the possibility that the present study overestimated the probability of retention of the WCP because we did not allow the relevant knowledge and skills to be lost by the sudden disappearance of individuals as well as by memory decay. Conversely, the observation that some of the groups who had forgotten how to make fire obtained embers from neighbouring groups raises the possibility that a wildfire-dependent hominin group could counter the effects of a change in the local wildfire regime by obtaining embers from another group. As we modeled an isolated Neanderthal group, EMBERS may have underestimated the probability of retention of the WCP. Unfortunately, it is not obvious how to think about the scale of the effect of including two processes leading to the loss of the WCP versus the scale of the effect of including two sources of embers. It requires another modelling study that extends EMBERS such that (i) the WCP is lost by both memory decay and the death/migration of experts, and (ii) the Neanderthal group is part of a network of groups and therefore may be able to obtain an ember from a neighbouring group, if one of them has a campfire in the relevant time frame (cf. Derex and Mesoudi, 2020; de Pablo *et al.*, 2022).

Another possibility for future research was suggested by Prof. Michael Chazan in his review of the present paper. Prof. Chazan suggested that we should consider the impact of the loss of the WCP on other dimensions of Neanderthal culture, especially their stone tools. The idea here is that the WCP would have been deeply integrated with other cultural behaviours and therefore its disappearance via forgetting would have resulted in reorganization of other parts of the Neanderthal cultural repertoire. We share this intuition and agree that it would be interesting to investigate whether the decline in fire evidence at the relevant Neanderthal sites is associated with changes in archaeological evidence that can be plausibly linked to subsistence or thermoregulation, such as the extent to which animal bones were processed to extract grease and the frequency of the remains of fur-bearing animal (see 78). However, it is worth noting that studies of cultural transmission in contemporary societies imply that the degree of integration and packaging among cultural traits is context-dependent[79–81]. So, a failure to find a correlated change in, say, the extent to which animal bones were processed to extract grease would not necessarily be surprising, nor shall it be ruled out without proper study.

Lastly, it would be useful to connect the results of the present study with the literature on disaster management. As we explained earlier, researchers have noted for over a century that even obviously useful knowledge and skills are prone to loss[64–67,71,73,82–84], but as far as we have been able to ascertain, ours is the first study to explore the impact of variation in the periodicity of a type of environmental event (wildfire) on the maintenance of knowledge and skills associated with such events (the use of wildfire to create campfires). What our study suggests is that the retention of knowledge and skills associated with a given type of environmental event is extremely sensitive to changes in the variability of the timing of the events in question. Even a small increase in variability can result in the reduction of knowledge and skills below the critical threshold. While we focused on the occurrence of wildfires and the ability to use wildfire to create campfires, it seems likely that the effect will hold for knowledge and skills associated with many other types of environmental events. This has implications for understanding a range of hominin behaviors in the past, but it also has implications for humans living in the present. Most notably, it implies that knowledge and skills that have been developed to mitigate environmental

disasters like floods and droughts are at risk of loss if the occurrence of such disasters becomes more variable. This in turn implies that measures designed to counter the decay of knowledge and skills in the realm of disaster management (e.g., annual practice days) need to track changes in the variability of the relevant events. Similarly, historical mitigation and adaptation measures — developed long ago and since forgotten — should probably be considered more seriously in thinking about future disasters[85–87]. Assessing whether these intuitions are correct—and exploring whether there are other implications of EMBERS for disaster preparedness and management—would, we think, be another worthwhile undertaking.

Materials and methods

The numerical version of EMBERS

We created two versions of EMBERS, a numerical version and an analytical version. In this section, we outline the numerical version and justify our estimations of the parameter ranges based on the available literature and practical considerations.

Main parameters and operations

To generate the n temporal sequences that comprise a numerical simulation, EMBERS performs three operations: It (i) determines the timing of uses of the WCP in each temporal sequence; (ii) establishes the amount by which the hypothetical Neanderthal group's ability to use the WCP decays between uses; and (ii) decides whether the group will recover the ability to use the WCP or lose it permanently. (iv) Subsequently, the n temporal sequences are used to estimate the probability of the group losing the ability to utilize the WCP during each simulation. In this section, we will explain how each of these operations is carried out.

Determining the timing of uses of the WCP

Each temporal sequence of a simulation comprises a series of intervals, which are measured in units of years. The first interval of each temporal sequence is the time between the start of the temporal sequence and the initial use of the WCP. The other intervals in a temporal sequence are the time between two uses of the WCP. Intervals are labelled as i and defined as Δt_i^k.

For each temporal sequence, Δt_i^k intervals are drawn from the positive values of a normal distribution generated with the following expression:

$$\mathcal{N}(\theta,[v\cdot\theta]^2), \tag{1}$$

where θ is the mean in units of years and v is a parameter we call *Variability*, which is a dimensionless scaling factor used to represent the uncertainty associated with the intervals between uses of the WCP.

EMBERS generates $2L/\theta$ values of, Δt_i^k *i.e.*, $i \in \left[1, \frac{2L}{\theta}\right]$, for a given temporal sequence. For an unbiased normal distribution, there are, on average, L/θ intervals. Thus, generating $2L/\theta$ values of Δt_i^k ensures that the sum of the intervals will equal or exceed L. The consecutive draws of Δt_i^k for a temporal sequence are independent of each other.

Because the intervals that comprise a temporal sequence are drawn from a normal distribution, the intervals will vary in length even though the same θ and v are used to generate them. Most of the intervals will be close to the θ selected for the temporal sequence, but some will be substantially shorter, and others will be much longer (Figure 6). The probability of drawing a Δt_i^k value that is very short or very long compared to θ is dependent on v. And the value of Δt_i^k is, in turn, dependent on the value of v selected for the temporal sequence. The larger the value of v, the greater the probability of drawing Δt_i^k that deviates greatly from θ.

While the values of θ and v are held constant for the temporal sequences included in a single simulation, the values of θ and v are varied between simulations. The effect that different values of θ and v have on the time between uses of the WCP (or other complex practices) is illustrated in Figure 5, which shows a segment of a sequence of uses generated with the aid of a normal distribution with θ = 8 and v = 0.2 and a segment of a sequence of uses based on a normal distribution with θ = 2 and v = 2.

We created K=111 simulations using different combinations of values for θ and v to explore the impact of different values for *Use Interval* and different levels of the variability associated with *Use Interval*. We employed values of θ between 1 and 20[yr] and values of v between 0.1 and 2.0.

We set the lower limit of θ at 1[yr] because our aim was to model the use of the WCP (and other complex practices) in the temperate zone following natural annual cycles. We set the upper limit of θ at 20 [yr] to represent the use of the WCP as a once-in-a-generation event. This was, we reasoned, the longest interval between uses consistent with a strong test of Sandgathe and colleagues'[13,15,16] hypothesis.

The v values we selected were intended to represent a spectrum of wildfire regimes in the temperate zone of the northern hemisphere (or other spectrum of variable uses, like wale strandings, Pinetree blossoming or El Niño/La Niña events), which run from relatively predictable to highly erratic[88,89]. The lower limit of v corresponds to a variability of 10% of θ. This means that if, for example, θ is four years, the variability is 0.4 of a year. Such a level of variability results in just minor departures from the mean interval of four years. Specifically, it results in around 16% of the intervals between uses being ≥4 years. The upper limit of v corresponds to a variability of twice of θ. This results in a much greater departure from the interval specified by θ. Returning to the previous example, if θ = 4 and v = 2, then approximately 16% of the intervals between uses will be ≥12 years, so a relatively frequent event (on average) might experience long periods without use once every six times.

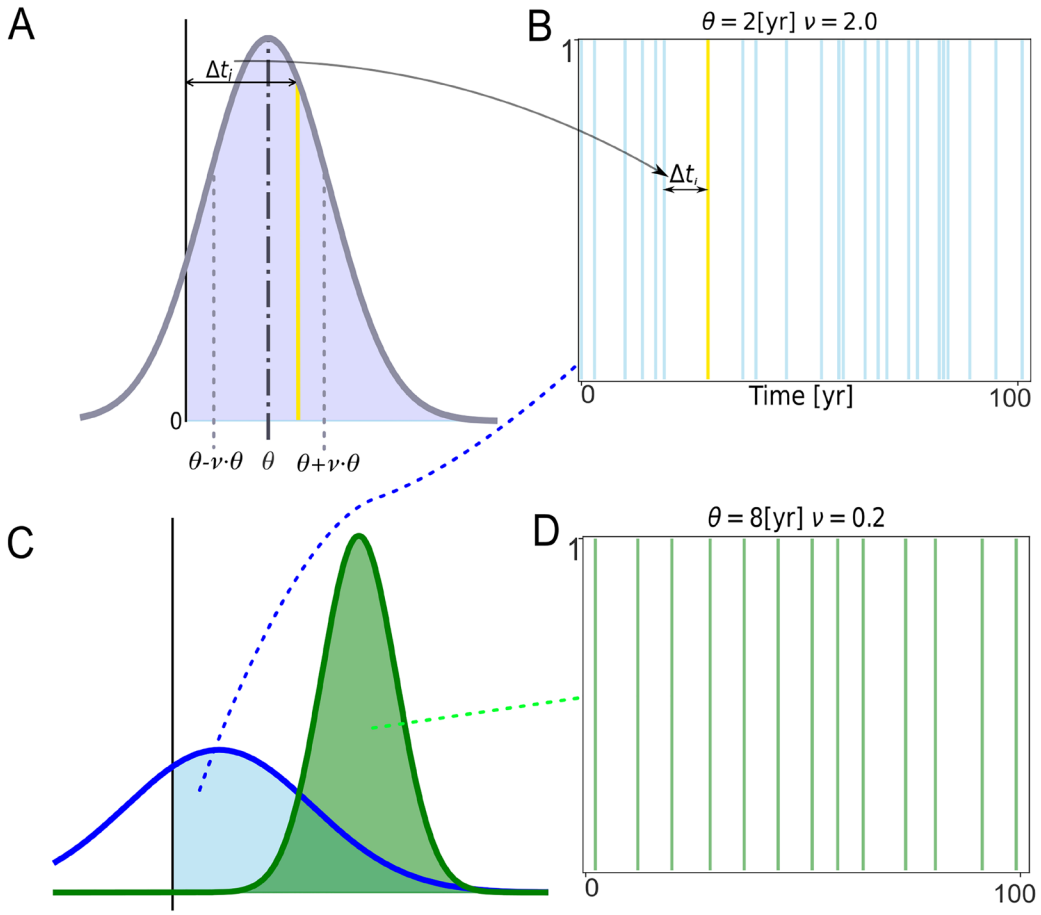

Figure 5. Diagram illustrating how intervals between uses of the WCP (Δt_i^k) are determined and different temporal sequences for two Normal Distributions. The intervals are drawn from the positive values of a normal distribution. The θ and ν of the normal distribution are held constant for all the intervals in a temporal sequence and for all the temporal sequences in a simulation but are allowed to vary among simulations. Panel **A** illustrates the selection of a single value of Δt_i. The normal distribution in **A** has a θ of 4 and a ν of 1. The grey dotted lines correspond to the standard deviation of the normal distribution ($\theta \cdot \nu$). The violet shaded area corresponds to the positive values of the normal distribution. The yellow line represents a focal use of the WCP (or any other complex practice), while the black line, marked with 0, represents the preceding use of the WCP. Panel **B** shows where the focal use of the WCP fits in a 100 year-run of the simulation. The blue vertical lines represent other uses of the WCP in that sequence. The intervals associated with these uses of the WCP were drawn from the blue normal distribution in Panel **C**. Panels **B** and **D** show the impact of different values of θ and ν. The sequences in **B** and **D** were generated from the positive values of the normal distributions (green and blue shaded areas) shown on panel **C**. The green one has $\theta = 8$ and $\nu = 0.2$, while the blue one has $\theta = 2$ and $\nu = 2$. The positive values of the two distributions yield sequences of uses of the WCP that have different statistical properties. Most significantly for present purposes, the uses of the WCP in panel **D** are more regular than those in panel **B**.

Establishing the decay of experts in a

For each interval (Δt_i^k), the numerical version of EMBERS computes the number of group experts, denoted as $\eta(\Delta t_i^k)$. In line with the assumption that the number of experts decreases exponentially when not practicing, $\eta(\Delta t_i^k)$ is defined as:

$$\eta(\Delta t_i^k) = \eta^{max} exp(-\Delta t_i^k / \tau), \quad (2)$$

where η^{max} is the maximum number of experts for a given temporal sequence, and τ is *Forgetting Time* (Figure 7). To reiterate, an expert is someone with the knowledge and skills to use wildfire to create a campfire (or any other complex skill). *Forgetting Time* is the interval it takes for the number of experts to be reduced to about one-third of η^{max} ($\frac{1}{e} \approx 0.36$ to be exact). The bigger the value of τ, the longer it takes for the number of experts to decrease to 0.36 of η^{max}. For example, if η^{max} is 20, a τ of two years means that, if two years pass without WCP use (or other complex practice), only seven individuals will be able to use the WCP, whereas a τ of eight years means that, it takes eight years without a use of the WCP for the number of experts to decline to seven.

As with the values of θ and ν, the values of τ and η^{max} are constant among the temporal sequences that comprise a simulation

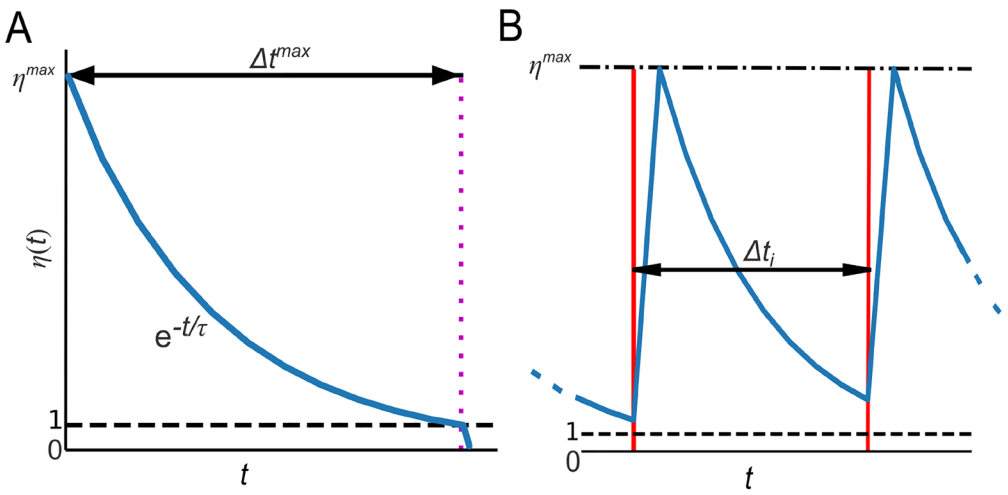

Figure 6. The decay and recovery of the hypothetical group's ability to use the WCP. Panel **A**: the number of experts η over time (blue line) begins at η^{max} and then decays exponentially until a use of the WCP occurs or the number of experts drops below the specified minimum threshold (black dashed line). The time it takes for the number of experts to drop below the minimum threshold is denoted by Δt^{max}. In the diagram, Δt^{max} is marked by the magenta dotted line. Panel **B** represents a segment of a single run of a temporal sequence, the red lines are uses of the WCP (or any other complex practice). The black double-ended arrow shows the interval between the first use of the WCP and the second use (Δt_i) as seen in Figure 5. The black dashed and dotted line and the black dotted line represent the maximum possible number of experts (η^{max}) and the minimum threshold for the number of experts, respectively. Moving from right, starting at t = 0, we see that the number of experts decreases exponentially. Then, after the first use of the WCP, the number of experts increases rapidly to η^{max}. Subsequently, the number of experts begins to decay again and does so until the second use of the WCP. At that point, the number of experts once again increases rapidly to η^{max}, before beginning to decay once more.

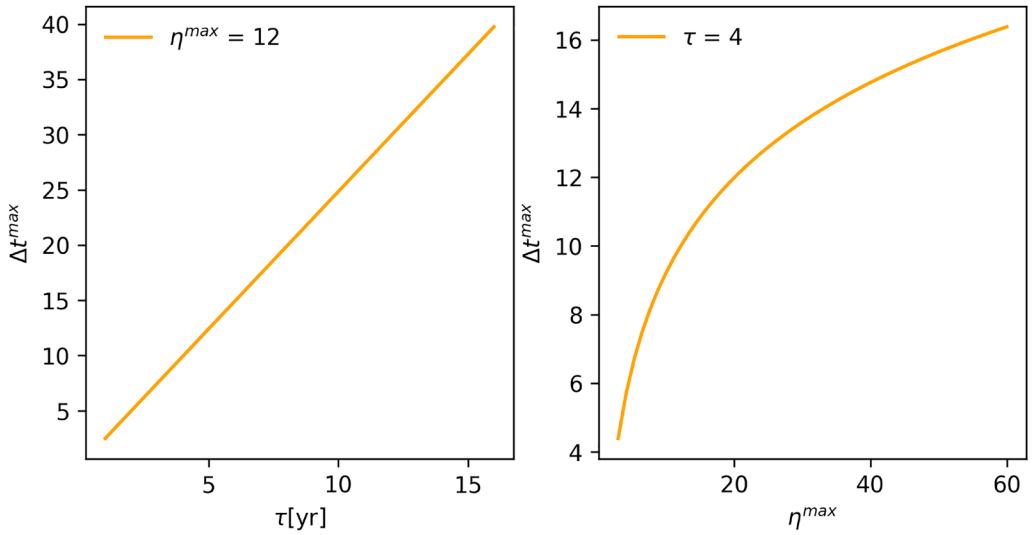

Figure 7. (**A**) Relationship between *Maximum Time* (Δt^{max}) and *Forgetting Time* (τ), and (**B**) *Maximum Number of Experts* (η^{max}). Plot **A** shows that Δt^{max} is linearly dependent on τ, when η^{max} = 12. Plot **B** shows that Δt^{max} is logarithmically dependent on η^{max}, when τ = 4. The relationships are of the same type (*i.e.*, linear and logarithmic) when other values of η^{max} and τ are selected.

but vary among simulations. We varied η^{max} between 3 and 60, and τ between 1 and 16 years. The minimum and maximum values for η^{max} are consistent with the ancient DNA-derived estimates of the size of Neanderthal groups[24,90,91]. Assuming that the hypothetical Neanderthal group comprised 60 individuals (including elderly and children), we conceptualized values of η^{max} close to three as modeling the WCP as highly specialized knowledge and skills, and values of η^{max}

close to 60 as modeling the WCP as widely distributed knowledge and skills. That everybody in the group was skilled in the WCP, even babies, is an extreme scenario, but is the most conservative consideration possible for the sake of the WCP retention (or other cultural practices) in our model.

The lower and upper limits of the range of values of τ were based on estimates of the rate of decay we derived from data presented in studies that have investigated the loss of procedural-motor skills[39,92–95]. Procedural-motor skills, consisting of a set of well-established sequences that have to be repeated in a certain, specific order, like CRP, with a clear beginning and end, are the ones that best reflect the WCP due to the sequential nature of fire-caring, building camp-fires from embers and long term fire-curation, plus the right use of materials and kinds of tinder and woods[8,27,30,31]. We fitted exponential curves to the decay data reported in the studies and then inferred τ values. The estimated τ ranged from two months to four years (refer to extended data- Table S1[96]). We opted for a lower limit for τ of one year rather than two months because we were interested in the impact of variation in the intervals between uses of the WCP at the annual scale, plus the bigger the τ, the more conservative our analysis is. For the upper limit of τ, we selected 16 years because it allowed us to investigate the effect of slower decay rates than the maximum ones found in the literature for procedural-motor skills[94], also making our analysis more conservative.

Deciding whether a group will use it or lose it

For all the temporal sequences generated with the numerical version of EMBERS, we used one person as the *Minimum Threshold* for the retention of the use of the WCP (or any other complex skill). We did so because, as we discussed earlier, the actions necessary to use wildfire to start a campfire in a temperate zone must be carried out in the right order. A corollary of this is that at least one person in the hypothetical Neanderthal group must know the right order of the actions for the group to be able to retain the ability to use the WCP. Thus, in the temporal sequences generated with the numerical version of EMBERS, the WCP was deemed permanently lost if the number of experts dropped below one.

Because the minimum threshold for the number of experts is one, it is possible to compute the maximum length of time a group can retain the WCP without using it. We refer to this variable as *Maximum Time* or Δt^{max}. It is defined as the interval between the start of the exponential decay process described in the last section and $\eta(\Delta t) < 1$. Therefore, we derive the expression for this interval as:

$$\Delta t^{max} = \tau \; ln \; (\eta^{max}). \tag{3}$$

In Figure 6, we illustrate the *Maximum Time* (interval between the origin and the magenta line, highlighted by black arrows) as the point where the number of experts drops below one. If the interval between uses exceeds *Maximum Time,* the number of experts drops below one. In other worlds, the *Minimum Threshold* links the *Maximum Number of Expert* (η^{max}) and *Forgetting Time* (τ) through *Maximum Time,* as depicted by Equation 3.

Interestingly, Δt^{max} has a linear relationship with *Forgetting Time* (τ) but a logarithmic relationship with *Maximum Number of Expert* (η^{max}). The correlation plot presented in Panel A of Figure 7 sheds light on the relationship between *Forgetting Time* (τ) and Δt^{max}, as seen in Equation 3. It plots the values of Δt^{max} that were obtained when Δt^{max} was fixed at 12, against the corresponding values of τ. Correlation plots generated from other pairs of values of Δt^{max} and τ show that Δt^{max} is always linearly dependent on τ.

Given the foregoing, the recovery *vs* loss decision operation can be described in the following manner. Each temporal sequence begins with the number of experts at $\eta\ (0) = \eta^{max}$. This number starts to decay immediately. Whether or not the decay process continues depends on a use of the WCP occurring before the number of experts drops below 1, *i.e.*, $\Delta t_1 > \Delta t^{max}$. If this happens, the number of experts rapidly returns to η^{max} (Figure 8). However, if the number of experts drops below one, the sequence ends and a permanent loss of the WCP is recorded. The process of decay and recovery repeats each i interval until either the number of experts drops below one (Figure 8) or 1000 years has passed.

Formally, the recovery *vs* loss decision operation can be represented by the following expression:

$$\eta(t_i^k) = \begin{cases} \eta^{max} & if\ \eta(\Delta t_i^k) \geq 1 \\ 0 & if\ \eta(\Delta t_i^k) < 1, \end{cases} \tag{4}$$

where is η^{max} the maximum number of experts for the simulation and $\eta(\Delta t_i)$ is the number of group members capable of using the WCP at the end of a given interval (see Equation 1). The expression indicates that EMBERS calculates $\eta(\Delta t_i^k)$ for each Δt_i^k. If $N(\Delta t_i) < 1$, then the temporal sequence ends and a loss of the WCP (or any other complex practice) is recorded, $n_l^k = 1$. However, if $\eta(\Delta t_i^k) \geq 1$, then $\eta(\mathrm{t_i^k})$ recovers to η^{max}. If the temporal sequence reaches time $t_i^k = 1000$, then $n_l^k = 0$.

The loss *vs* retention operation can be summarized with the following expression:

$$n_l^k = \begin{cases} 1 & if\ \eta(t_i^k = 1000) = 0 \\ 0 & if\ \eta(t_i^k = 1000) > 1, \end{cases} \tag{5}$$

where n_l^k counts for the number of losses l for each time series k. We opted to treat the recovery process as rapid partly because it is the simplest option but mainly because it reduces the probability of the WCP being lost, which meant that the analyses is the most conservative against loss, i.e. a stronger test of Sandgathe and colleagues[13–16] hypothesis.

Estimating the probability of loss for each simulation

The final operation of the numerical version of EMBERS estimates the probability of the hypothetical Neanderthal group losing the ability to use the WCP (or any other group keeping

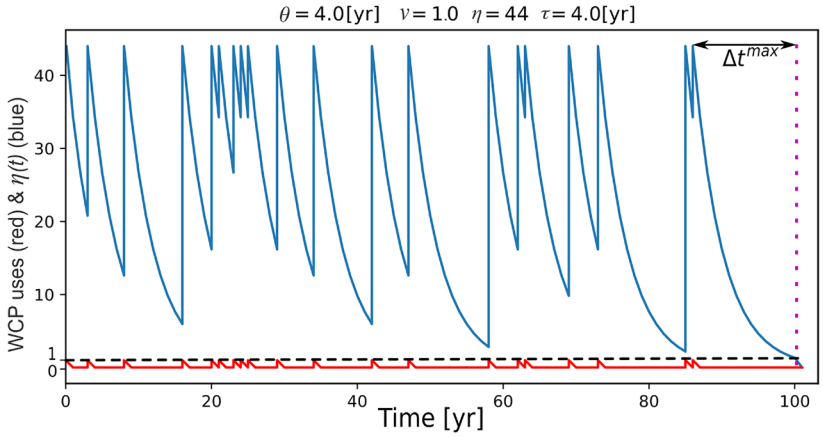

Figure 8. Dynamics of the process of the loss and recovery of experts. The number of experts is tracked by the blue line. The spikes in the red line at the bottom represent uses of the WCP (or any other complex practice). The threshold for retention of the ability to use the WCP (1 expert) is marked by the black dashed line towards the bottom of the panel. Starting at t = 0, the number of experts begins at η^{max}, decays exponentially until the WCP is used, and then recovers back to η^{max}. This process continues until the year 100, when *Use Interval* becomes larger than Δt^{max} and $\eta(t)$ drops below the group's threshold for retention of the ability to use the WCP. At this point, the run comes to an end.

a complex practice) prior to 1000 years elapsing. The variability in the intervals that comprise a temporal sequence is important here. That the values of Δt_i^k for a temporal sequence will rarely be the same means there will be variability among the set of temporal sequences that comprise a simulation with respect to whether the use of the WCP is retained for 1000 years. This variability is used to estimate the probability of the loss of the WCP for a given simulation and therefore for the unique combination of values of the four key parameters (θ, v, η^{max}, τ) employed in the simulation. For each simulation, EMBERS calculates n_l, which is the number of temporal sequences experiencing a loss of the ability to use WCP before L = 1000. Formally n_l can be defined as the sum of the n_l^k values:

$$\mathrm{n}_l = \sum_{k=0}^{K} n_l^k. \tag{6}$$

Thereafter, n_l is divided by the total number of temporal sequences included in the simulation (K). The resulting quotient is EMBERS' estimate of the probability of retaining the WCP before L = 1000, for the simulation and, more importantly, for the unique combination of values of θ, v, η^{max}, and τ utilised in the simulation. Formally we can express this probability as:

$$P_r(\theta, v, \eta^{max}, \tau) = 1 - n_l / K, \tag{7}$$

where (θ, v, η^{max}, τ) is the unique combination of *Use Interval* (θ), *Variability* (v), *Maximum Number of Experts* (η^{max}), and *Forgetting Time* (τ).

Algorithm for the numerical version. Each simulation was based on a particular combination of values for the four key variables (θ, v, η^{max}, τ) and involved the creation of K independent temporal sequences ($k \in [0, K]$). The simulations were run with the following algorithm:

1. Compute a $\mathcal{N}(\theta, [v \cdot \theta]^2)$.

2. Generate n Δt_i^k, $k \in$ [0, K] sequences from the positive values of the distribution.

3. For $k \in$ [0, K] and for $i \in [1, 2L/\theta]$ do:

   3.1 If $\Delta t_i^k > \Delta t^{max}$, then the k *temporal sequence* is counted as a loss and ends, $n_l^k = 1$, $k = k+1$.

   3.2 If $\Delta t_i^k < \Delta t^{max}$, then the i time increases as $t_i = t_{i-1} + \Delta t_i$, $t_0 = 0$.

   3.3 If $t_i > L$, then the series ends, $n_l^k = 0$, $k = k+1$.

4. When $k = K$, $\mathrm{n}_l = \sum_{k=0}^{K} n_l^k$, $P_r(\theta, v, \eta^{max}, \tau) = 1 - n_l/K$.

The analytical version of EMBERS

In this section we outline the analytical version of EMBERS. This version represents a different solution to the problem of estimating the probability a group losing a complex practice in L, given different combinations of values of the four key variables, θ, v, η^{max}, and τ. Analytical solutions are only possible for some systems, but when they are feasible, they have the advantage of being quick to compute.

Main parameters and operations

The analytical version of EMBERS employs the same values for L and the key variables as the numerical version of the model (Table 1). It also employs the maximum time function utilized in the numerical version of EMBERS, Δt^{max} (see Equation 3).

In computing the solution for each set of variable values we utilize the *Probability of Discontinuity* (P_d), which is the average probability that the group loses a complex practice after each use. Because the values for *Use Interval* are derived from a normal distribution (Figure 5), we can easily compute P_d with the aid of the error function (erf), which provides the probability that a value is bigger or smaller than a given threshold. In EMBERS, the threshold is the maximum time Δt^{max}, and the distribution of values is given by $\mathcal{N}(\theta, [v \cdot \theta]^2)$. Therefore, the probability that any given interval is bigger than Δt^{max} is:

$$P_d(\mathcal{N}(\theta,[\theta\cdot v]^2),\Delta t^{max}) = \frac{1}{2}\left[1-\mathrm{erf}\left(\frac{\Delta t^{max}-\theta}{\theta\cdot v\sqrt{2}}\right)\right]. \quad (8)$$

Next, we define the *Probability of Retention* (P_r), which is the probability that no interval between potential uses is longer than Δt^{max} for the time length L. For simplicity, we assume that the number of intervals in L is the ratio between L and the mean θ. Given this, the probability that at least one of the intervals in L is longer than Δt^{max} is simply 1 minus P_d to the power of the number of intervals. Accordingly, P_r is defined as:

$$P_r(P_d, L/\theta) = 1 - P_d^{L/\theta}. \quad (9)$$

It is important to note that, because P_d is the average discontinuity probability in each interval, the more intervals in L, the lower the probability of retention (P_r).

Data and materials availability

All data are available in the main text or the supplementary materials. Supplementary materials can be found together with the code in the following: https://github.com/andreuandreu/EMBERS/tree/v3.2.

Archived software and supplementary material available from Zenodo: andreuandreu/EMBERS: https://doi.org/10.5281/zenodo.15722063[96].

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Version 2

Reviewer Report 07 January 2026

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✔ **Gabriela Amorós**
University of Murcia, Murcia, Spain

This paper offers a thoughtful and timely reassessment of a long-standing assumption in Neanderthal research: that habitual fire use necessarily implies habitual fire-making. By explicitly modelling the ecological availability of wildfire under different climatic and vegetational scenarios, the authors move the debate away from technological dichotomies and toward a more realistic landscape-based perspective. In my view, this shift is both necessary and overdue.
Recent developments increasingly emphasize that Neanderthal lifeways unfolded within highly heterogeneous landscapes, where vegetation structure, fuel continuity, and fire regimes would have varied substantially across space and time. In this broader context, the model presented here aligns well with recent landscape-scale and palaeoecological approaches highlighting the role of ecological thresholds and environmental constraints in shaping human fire use (Refer ref no.1).
I find particularly thought-provoking the paper's implicit warning against asymmetric reasoning in the archaeological record. The absence of clear fire-making technologies is often treated as a deficit, whereas the systematic acquisition of fire from natural sources is seldom explored quantitatively. By demonstrating that repeated fire use could, under certain conditions, be sustained without habitual ignition, the authors provide a productive reframing that encourages greater interpretive caution and conceptual flexibility.
This contribution does not seek to close the debate on Neanderthal fire use, but rather to reopen it on firmer ecological and theoretical grounds. As such, it represents a stimulating and welcome addition to ongoing discussions on Neanderthal adaptability and human–environment interactions.
GABRIELA AMORÓS, University of Murcia

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Is the work original in terms of material and argument?
Yes

Does it sufficiently engage with relevant methodologies and secondary literature on the topic?
Yes

Is the work clearly and cogently presented?
Yes

Is the argument persuasive and supported by evidence?
Yes

If any, are all the source data and materials underlying the results available?
Yes

Does the research article contribute to the cultural, historical, social understanding of the field?
Yes

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: Ecosystems of Neanderthals, Palaeoecology, Palaeobotany, Paleoart, Visual Arts, Science Education

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Reviewer Report 07 January 2026

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Michelle Scalise Sugiyama
University of Oregon, Eugene, USA

I have no further comments.

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: The hunting-and-gathering ecological niche, including: cultural transmission

and cumulative culture; evolution of teaching/learning; traditional ecological knowledge; evolution of symbolic behavior; oral tradition; evolution of play

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Reviewer Report 06 January 2026

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José Luis Guil-Guerrero
University of Almeria, Almería, Andalusia, Spain

Title: Use it or lose it: A model-based assessment of the hypothesis that European Neanderthals relied on wildfires to create their campfires
Journal: Open Research Europe
Global evaluation
This article presents a sophisticated and carefully argued modelling assessment of the "wildfire hypothesis" for Neanderthal fire use. The EMBERS model is comprehensively delineated, internally consistent, and firmly rooted in ethnographic and cognitive literature. The study provides compelling evidence that the loss of wildfire-dependent fire-use knowledge is both plausible and likely under realistic conditions, thereby reinforcing the validity of Sandgathe et al.'s hypothesis. However, the work sometimes overstates the strength of inferences, conflates plausibility with explanatory sufficiency, and relies on assumptions that deserve tighter archaeological and ecological anchoring.
Conceptual issues
-The central conceptual concern is the equation of the modelled cultural loss with the archaeological absence of fire. While the model shows that fire-use expertise may be lost despite occasional wildfire encounters, it does not directly demonstrate that such loss would necessarily produce the specific archaeological signatures observed. This issue is recognised, but not yet fully resolved (pp. 10–12).
-Secondly, the Wildfire Cultural Package (WCP) is regarded as a cohesive, cumulative solution, where the loss is essentially binary (see pages 4 to 5 for further details). Components of fire use (e.g. ember transport, fuel selection, fire maintenance) may degrade asynchronously. This simplification may exaggerate the likelihood of total loss.
-Thirdly, it is important to note that the assumption of group isolation (pp. 4–6, 12) is crucial to the results but is archaeologically weakly constrained. While genetic data are cited, social contact sufficient for ember exchange could occur without substantial gene flow.
-Fourthly, the model assumes that memory decay is the primary loss mechanism. However, it should be noted that demographic shocks, seasonal mobility and ecological knowledge transmission may interact non-linearly with forgetting. These factors will be addressed in future work, but are central to the use of fire.

Issues by sections
-Page 2 (Abstract & Results)
It has been noted that the statement 'losing the ability to use wildfire was more likely than retaining it' risks misinterpretation. The model demonstrates the loss of expertise rather than the loss of fire use itself. This distinction should be clarified at the outset.
-Page 4 (Model setup).
The model only considers lightning-caused wildfires, but there are other natural ignition sources to consider, such as peat fires and human-mediated ember persistence. This simplification biases results towards loss without quantifying its effect.
-Pages 5–6 (Assumptions on expert recovery).
It is evident that the instantaneous reset of expert numbers after each successful use of the WCP is unrealistic and internally inconsistent with the emphasis on fragile transmission. This assumption strongly favours retention, yet this is not explored parametrically.
-Pages 7–9, (Results)
It is important to note that the repeated claim that loss is "more likely than retention" could be misread as a real-world frequency statement, rather than a statement conditional on parameter space sampling. It is important to reiterate the conditional nature of this probability.
-Pages 10–11 (Critique of alternatives)
The dismissal of economic and ephemeral-fire hypotheses relies heavily on the assumption that unused skills inevitably decay rapidly. While there may be some truth to this for certain procedural skills, it is more of an assertion than a demonstration when it comes to fire-making specifically.
Suggestions for improvement
1. The authors should explicitly map model outcomes to archaeological expectations, clarifying what degree and duration of cultural loss would plausibly result in the observed reduction of fire proxies.
2. The WCP should be partially decomposed, allowing for graded loss of fire-related competencies rather than an all-or-nothing threshold.
3. Incorporating limited intergroup contact or ember exchange in sensitivity tests would substantially strengthen the realism of the conclusions.
4. The paper would benefit from a clearer separation between plausibility testing and hypothesis validation. This would avoid any language that could be interpreted as confirming the wildfire hypothesis rather than bounding its feasibility.

Is the work original in terms of material and argument?

Yes

Does it sufficiently engage with relevant methodologies and secondary literature on the topic?

Yes

Is the work clearly and cogently presented?

Yes

Is the argument persuasive and supported by evidence?

Partly

If any, are all the source data and materials underlying the results available?

Yes

Does the research article contribute to the cultural, historical, social understanding of the field?
Yes

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: Palaeonthropology, Food Technology, Wild Edible Plants

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.

Version 1

Reviewer Report 08 November 2025

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?

Michelle Scalise Sugiyama
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[2] University of Oregon, Eugene, USA

This important article calls out a serious shortcoming in the study of cumulative culture evolution: the lack of attention to memory decay and means of countering it. Consequently, little is known about the frequency with which knowledge decay occurred in past hominin environments or the conditions that contributed to it. To explore these questions, the article uses existing research on Neanderthal fire use. Oddly, several Middle Paleolithic Neanderthal sites exhibit a pronounced decrease in evidence of fire use during colder periods. A possible explanation for this decline is that Neanderthals were incapable of producing fire from scratch and instead relied on wildfire embers for ignition. Because lightning strikes and consequent wildfires are less frequent under cold, dry conditions, Neanderthals living during these periods would have had fewer opportunities to make fire, raising the intriguing possibility that this knowledge decayed during colder periods (and, presumably, was re-discovered during warmer periods when wildfires were more frequent).

The authors use formal modeling to investigate this process, coding for four mechanisms of knowledge/skill loss: variability in use, interval between uses, memory decay, and number of experts. Two important takeaways from this effort are that (1) loss was more likely than retention and (2) many combinations of variability and use interval led to a total loss of fire-making knowledge over the 1000-year period modeled. In light of these findings, the authors stress the

need for greater attention to memory decay and ways of countering it in cultural evolutionary research, claiming that they "have only been able to identify three recent relevant publications" (11).

This claim raises two issues of concern. First, why limit the search to recent publications? In my own research, I have reaped insights from work published decades ago. For example, despite their flaws—or perhaps because of them--Bartlett's (1932) experiments using "The War of the Ghosts" tale are highly instructive. Without a thorough search of the literature, the authors cannot be certain that memory decay and means of countering it have not been productively addressed elsewhere.

This brings us to the second issue, which concerns the nature and scope of research on cumulative culture evolution. The authors are correct that evolutionary scholars (i.e., scientists who study hominin or hominid evolution) have largely ignored an important component of cultural transmission: the media used by oral cultures to encode and transmit knowledge, and the mechanisms and strategies used to prevent knowledge decay and corruption. Their critique of this omission is valid, as is their call for "researchers interested in cultural evolution to increase the number of studies dealing with … ways of retaining knowledge and skills" (11). However, their conceptualization of "relevant publications" appears to be extremely narrow—so narrow that it excludes recent research that expressly addresses this issue (e.g., Nowell 2021; Scalise Sugiyama 2024; Scalise Sugiyama & Reilly 2023). Moreover, the authors do not follow through on their critique by directing readers to the vast body of research on the challenges posed by oral transmission of communal knowledge and/or strategies used to surmount them (e.g., Hagar 1900; Lord 1960; Berlin & O'Neill 1981; Ong 1982; Minc 1986; Cruikshank 1990; Rubin 1995; Basso 1996; Johnson 1998; Sobel & Bettles 2000; Barber & Barber 2004; Ludwin et al. 2007; Kelly 2015; Clarke 2018; Curran et al. 2019; Scalise Sugiyama 2021, 2022). A related body of research examines the role of play in the entrainment and maintenance of physical skills (e.g., Bock & Johnson 2004; Petersen 2004; Scalise Sugiyama et al. 2018). While most of this research is not "cultural evolutionary theory" in the strict sense used by the authors, it is most certainly research on "ways of countering memory decay" and "the maintenance of existing cultural traits" (11). This work is the logical starting place for cultural evolutionary theorists seeking to develop models that incorporate the mechanics of cultural loss and means used to prevent it.

These omissions are all the more perplexing given that one of the co-authors, Riede, has published several articles on the role of play in cultural evolution, including the use of toys for teaching. One of these studies, which examines the cross-cultural pervasiveness of string figures in hunter-gatherer societies, argues that "games and pastimes like string figures *allow individuals to freely practice manual dexterity and cognitive skills*" (Kaaronen et al. 2024:9; my emphasis). In light of the present paper's "use it or lose it" argument, the failure to mention play as a means of countering knowledge/skill loss is a missed opportunity.

In their discussion of directions for future research, the authors note that their model may actually have *overestimated* the probability of retention of pyrotechnical knowledge because it did not factor in the possibility of acquiring embers from neighboring groups. I encourage the authors to pursue this question in future research, as in my own work I have encountered numerous references to the borrowing (or acquisition) of fire from neighbors or other villages. Significantly, this information is often found in stories, which are widely recognized as an important means of preserving and transmitting accumulated communal knowledge in hunter-gatherer and other oral

cultures. The following passage from a Wasco tale illustrates this practice:

Towards midnight of the following day the fire went out, and in the village the fires went out in every house. Next day the father said to the eldest boy, “Go over to Tenino [a neighboring village] and get fire.” The two boys started. Towards sundown they reached Tenino .... Their father had made a stick of cedar-bark for them with little cracks in it, good to hold fire; they crept up to the fire and lighted this stick. (Sapir 1909:243)

As this example indicates, the mechanisms used by hunter-gatherers to maintain existing cultural traits are right under our noses, and are well-documented ethnographically. To detect them, cultural evolutionary theorists need to broaden their search parameters.

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Is the work original in terms of material and argument?

Yes

Does it sufficiently engage with relevant methodologies and secondary literature on the topic?

Partly

Is the work clearly and cogently presented?

Yes

Is the argument persuasive and supported by evidence?

Yes

If any, are all the source data and materials underlying the results available?

Yes

Does the research article contribute to the cultural, historical, social understanding of the field?

Yes

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: Hunter-gatherer ecology and cultural adaptation, including: cultural transmission and cumulative culture; teaching/learning; traditional ecological knowledge; evolution of symbolic behavior; oral tradition; evolution of play

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have

significant reservations, as outlined above.

Author Response 21 Nov 2025

Andreu Arinyo i Prats

Response to Reviewer 2 (Prof. Michelle Scalise Sugiyama) We thank Reviewer 2 for her thoughtful review. We appreciate the time and care she devoted to engaging with our paper. Below we provide responses to the main points she raised.

1. Focus on recent publications

1.1. Reviewer comment The reviewer questions why our literature review was restricted to recent publications.

Response: We suspect our phrasing may have caused some confusion here. Our intention was not to disregard earlier scholarship. Rather, our goal was to highlight the fact that *within the field of cultural evolution studies*, there has been limited recent engagement with the issue of cultural loss in the last few decades. We have tried to clarify this point in the revised version of the Discussion. The start of the relevant paragraph now reads as follows: "The present study also has implications for the ongoing effort to develop an adequate theory of cultural evolution [43] . In the last 25 years, researchers working in the field of cultural evolutionary studies have discussed cultural loss, but they have done so primarily in the context of trying to elucidate the relationship between cultural complexity and demography (e.g., 44–53). Little attention has been paid to the importance of cultural loss relative to cumulative cultural evolution, or to the specific mechanics of cultural loss" We believe the revised section better communicates our intent. Before moving on to the next point, it is worth noting that elsewhere in the paper we do reference a wide range of earlier and foundational work — starting with Rivers (1912) and including little-known studies focused on CPR and military skills, from the 1970s and 1980s.

2. Overly narrow scope of the cited literature

2.1. Reviewer comment The reviewer suggests that our conceptualization of relevant publications is too narrow and results in the exclusion of several pertinent works on oral transmission, communal knowledge, and strategies for preventing memory decay.

Response: We agree that many of the studies cited by the reviewer offer valuable insights into the way by oral cultures preserve and transmit knowledge. We omitted them for the sake of brevity but accept that we went too far. To rectify the situation, we have amended the fourteenth paragraph of the Discussion. Its final sentence now directs the reader to studies dealing with memory loss and retention in other fields of study. The sentence in question reads as follows: As part of this effort, it would be sensible to tap into the work being carried out by researchers interested in cultural preservation (Chaplin-Kramer *et al.*, 2022; Aguilar and Webb, 2024; Arinyo-i-Prats, Turner and Latosky, 2025), the role of oral traditions in cultural maintenance (Scalise Sugiyama, 2021, 2024; Scalise Sugiyama and Reilly, 2023), children's play and oral storytelling in small-scale societies (Scalise Sugiyama, 2017; Langley, 2018; Riede *et al.*, 2018; Nowell, 2023), and the role of memory in human affairs (Arthur and Day, 2019; Corbett *et al.*, 2020; Kusumastuti *et al.*, 2022; Olivier, 2024). Some of the recent work on culture in non-human animals is also likely to be helpful (Brakes *et al.*, 2019; van Dooren *et al.*, 2024; Oestreich, Barlow and Hersh, 2025).

3. Role of play in maintaining skills and knowledge
3.1. Reviewer comment The reviewer highlights the omission of research on the role of play in skill acquisition and maintenance, noting its relevance to our "use it or lose it" framework and citing examples such as Bock and Johnson (2004), Petersen (2004), and Scalise Sugiyama et al. (2018). The reviewer also points out that one of us has published on this very topic.
Response: We appreciate this observation. We are indeed aware of the importance of play in cultural transmission and skill retention and have previously published on related themes. However, our search of the ethnographic literature found little direct evidence for children's participation in fire foraging, ember transport, or fire maintenance — the specific focus of our study. For this reason, we chose not to expand on the topic in depth to preserve the paper's focus. Nevertheless, we have suggested that cultural evolutionary theorists should engage with the work on children's play, at the end of the fourteenth paragraph of the Discussion.

4. Misinterpretation of model limitations regarding ember acquisition
4.1. Reviewer comment Reviewer 2 notes that we argued that our model may have *overestimated* the probability of pyrotechnical knowledge retention because it did not factor in ember acquisition from neighbouring groups. She encourages us to explore this possibility further.
Response: As we explain towards the end of the Discussion, we intend to explore this issue in a future modeling study. The problem is that our decision not to factor in the possibility of ember acquisition from neighboring groups is potentially counterbalanced by our decision not to model the loss of experts via death and migration. While the former can be expected to have led us to overestimate the probability of loss of the WCP, the latter can be expected to have led us to underestimate the probability of loss of the WCP. However, because the dynamics of these processes are likely to be complex, we cannot say anything more concrete about their probable impact on the results of the study at this stage. Elucidating the impact of the two variables on the probability of loss of the WCP will require additional, dedicated modeling work.

5. General remarks and integration of suggested literature
5.1. Reviewer comment Reviewer 2 provides a helpful list of literature on oral transmission, skill retention, and memory maintenance, noting that our discussion could benefit from engaging with this body of work.
Response: We agree that citing more papers on oral transmission, skill retention, and memory maintenance would have been desirable, but we were keen to keep the text concise and focused. We still are, so we haven't added all of the literature highlighted by the reviewer. Instead, we have selected what we consider to be the most relevant of the studies for inclusion.

6. Concluding remarks
Once again, we thank Reviewer 2 for her review. Her comments helped us improve the clarity, scope, and precision of our manuscript. We think the revised version now more accurately conveys our intended arguments and better acknowledges previous work. We believe the paper is now ready for the final stage of the publication process and hope that Reviewer 2 agrees.

Competing Interests: No competing interests were disclosed.

Reviewer Report 30 August 2025

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Michael Chazan
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Arinyo-i-Prats et al. provide a welcome contribution to the argument that obligate cooking is an emergent aspect of genus Homo rather than a precondition for the evolution of a hominin with increased brain size (see discussion in Chazan 2017). This article builds on the observation by Sandgathe and colleagues that in French Middle Paleolithic sites with a deep stratigraphic sequence there are fluctuations in the intensity of the signal for the use of fire as reflected in the frequency of burnt lithics. Moreover, it is precisely in periods of colder climate conditions, when one would assume fire would be most useful, that this signal is weakest. Sandgathe proposes that this pattern reflects the reliance of Neanderthal on natural fires, which are less frequent in cold periods due to a decrease in the frequency of lightening strikes. Arinyo-i-Prats carry out a simulation to see whether loss of technical knowledge could account for this pattern. Not surprisingly they find that there would be loss of technical knowledge over time that could lead to a loss of acquired skill. This simulation brings attention to the social aspect of the use of fire that is often neglected in discussions that focus on diet and energetics.

I can offer two comments on this discussion. The first is that there is a lack of clarity in the authors' use of nomenclature about the type of engagement with fire under consideration. This is often described as 'use of wildfire' whereas the topic of this article is actually the maintenance of fire and the tending of fire in a way that facilitates cooking and other aspects of pyrotechnology. The evidence from our research at Wonderwerk Cave demonstrates that the use of wildfire dates back at least to the Acheulean, but there is an important distinction between the technical knowledge needed to collect wildfire as opposed to the complex operations needed to maintain fire (Berna et al. 2012). The maintenance of fire is not clearly evident at Wonderwerk or other sites with Acheulean evidence for the use of fire.

The second point stems from the type of model adopted for the transmission of knowledge found in this article. Transmission of knowledge is seen in this article as the passing along of packets of information and seems to occur in a world devoid of other technologies and social relations. It would be interesting to see the authors expand the scope of their work to include stone tools. In the Middle Paleolithic we often see relatively minor variation in lithic technology which speaks not only to transmission of skill and knowledge but also on the way stone tools (and this would be

even more true of fire) are deeply embedded in social life and other technical domains, particularly food preparation. What is lost in Arinyo-i-Prats et al.'s discussion of knowledge transmission are the traditions that constrain the choice of technical strategies. A shift in the use of fire would require a very considerable loosening of cultural norms of behavior. The 'forgetting' the authors describe would require a reorganization of food preparation and elements of social structure that would have been quite profound. This aspect of the integration of technical and social aspects of hominin adaptation is somewhat lost by the kind of modeling presented here. Nonetheless, the authors do succeed in shifting our focus in a productive manner and in pointing to areas of further research. This work builds constructively on the observations by Sandgathe and colleagues make a strong case that not only was obligate cooking not characteristic of the earliest members of our genus, it was not even essential to the adaptations of Neanderthals, whose cranial capacity overlaps with that of modern humans.

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Is the work original in terms of material and argument?

Yes

Does it sufficiently engage with relevant methodologies and secondary literature on the topic?

Yes

Is the work clearly and cogently presented?

Yes

Is the argument persuasive and supported by evidence?

Partly

If any, are all the source data and materials underlying the results available?

Yes

Does the research article contribute to the cultural, historical, social understanding of the field?

Yes

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: Archaeology and human evolution. I do not have expertise in the technical aspects of the simulation presented in this article.

I confirm that I have read this submission and believe that I have an appropriate level of

expertise to confirm that it is of an acceptable scientific standard.

Author Response 21 Nov 2025

Andreu Arinyo i Prats

Response to Reviewer 1 (Prof. Michael Chazan) We thank Reviewer 1 for the time and care he devoted to reviewing our paper. Below we respond to his two points of critique.

1. Nomenclature and scope of the Wildfire Cultural Package

1.1. Reviewer 1 comment "The first is that there is a lack of clarity in the authors' use of nomenclature about the type of engagement with fire under consideration. This is often described as 'use of wildfire' whereas the topic of this article is actually the maintenance of fire and the tending of fire in a way that facilitates cooking and other aspects of pyrotechnology. The evidence from our research at Wonderwerk Cave demonstrates that the use of wildfire dates back at least to the Acheulean, but there is an important distinction between the technical knowledge needed to collect wildfire as opposed to the complex operations needed to maintain fire (Berna et al. 2012). The maintenance of fire is not clearly evident at Wonderwerk or other sites with Acheulean evidence for the use of fire."

Response: There appears to be a misunderstanding here. As we explain in the section of the paper titled "Key assumptions of the model", we modeled the impact of several variables on the retention of the Wildfire Cultural Package or WCP. We did not conceptualize the WCP as limited to "the maintenance of fire and the tending of fires in a way that facilitates cooking and other aspects of pyrotechnology". Rather, we conceptualized it as *all* the knowledge and skills that a Neanderthal group would have needed to collect and use wildfire. In the paper, we highlighted several of the actions that are necessary to use wildfire to start a campfire in a temperate zone, but this was not supposed to be an exhaustive list, which is why we prefaced the list with "[t]hese actions include". That said, we accept it is possible that, as Prof. Chazan suggests, "there is an important distinction between the technical knowledge needed to collect wildfire as opposed to the complex operations needed to maintain fire", and we will consider subdividing the WCP and modelling the elements of the package separately in a future extension of the present study. A key problem we will have to overcome, we suspect, is grounding the parameters for each of the elements of the package in the empirical literature.

2. Impact of loss of fire on other cultural traits

2.1. Reviewer 1 comment "The second point stems from the type of model adopted for the transmission of knowledge found in this article. Transmission of knowledge is seen in this article as the passing along of packets of information and seems to occur in a world devoid of other technologies and social relations. It would be interesting to see the authors expand the scope of their work to include stone tools. In the Middle Paleolithic we often see relatively minor variation in lithic technology which speaks not only to transmission of skill and knowledge but also on the way stone tools (and this would be even more true of fire) are deeply embedded in social life and other technical domains, particularly food preparation. What is lost in Arinyo-i-Prats et al.'s discussion of knowledge transmission are the traditions that constrain the choice of technical strategies. A shift in the use of fire would require a very considerable loosening of cultural norms of behavior. The 'forgetting' the authors describe would require a reorganization of food preparation and elements of

social structure that would have been quite profound. This aspect of the integration of technical and social aspects of hominin adaptation is somewhat lost by the kind of modeling presented here."
Response: This is an interesting point, one that deserves to be explored in detail in a future study. We share Prof. Chazan intuition but we're aware of empirical studies that suggest that situation may be more complicated than he and we imagine. To address this point, we have added the following paragraph to the future directions section of the Discussion: " Another possibility for future research was suggested by Prof. Michael Chazan in his review of the present paper. Prof. Chazan suggested that we should consider the impact of the loss of the WCP on other dimensions of Neanderthal culture, especially their stone tools. The idea here is that the WCP would have been deeply integrated with other cultural behaviours and therefore its disappearance via forgetting would have resulted in reorganization of other parts of the Neanderthal cultural repertoire. We share this intuition and agree that it would be interesting to investigate whether the decline in fire evidence at the relevant Neanderthal sites is associated with changes in archaeological evidence that can be plausibly linked to subsistence or thermoregulation, such as the extent to which animal bones were processed to extract grease and the frequency of the remains of fur-bearing animal (see Collard *et al.*, 2016). However, it is worth noting that studies of cultural transmission in contemporary societies imply that the degree of integration and packaging among cultural traits is context-dependent (Cavalli-Sforza *et al.*, 1982; Guglielmino *et al.*, 1995; Jordan, 2014). So, a failure to find a correlated change in, say, the extent to which animal bones were processed to extract grease would not necessarily be surprising, nor shall it be ruled out without proper study.

3. Concluding remarks
Once again, we thank Reviewer 1 for his comments, which we found both stimulating and helpful. We believe the paper is now ready for the final stage of the indexing process and hope that Reviewer 1 agrees

Competing Interests: No competing interests were disclosed.