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2016

Carotenuto, F., Tsikaridze, N., Rook, L., Lordkipanidze, D., Longo, L., Condemi, S., et al. (2016). Venturing out safely: The biogeography of *Homo erectus* dispersal out of Africa. *Journal of Human Evolution*, 95, 1-12.

<https://hdl.handle.net/10356/82274>

<https://doi.org/10.1016/j.jhevol.2016.02.005>

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Venturing out safely: The biogeography of *Homo erectus* dispersal out of Africa

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Abstract

The dispersal of *Homo erectus* out of Africa at some 1.9 million years ago is one of the most important, crucial, and yet controversial events in human evolution. Current opinions about this episode expose the contrast between those who see *H. erectus* as a highly social, cooperative species seeking out new ecological opportunities to exploit, and those preferring a passive, climate driven explanation for such an event. By using geostatistics techniques and probabilistic models, we characterised the ecological context of *H. erectus* dispersal, from its East African origin to the colonization of Eurasia, taking into account both the presence of other large mammals and the physical characteristics of the landscape as potential factors. Our model indicated that *H. erectus* followed almost passively the large herbivore fauna during its dispersal. In Africa, the dispersal was statistically associated with the presence of large freshwater bodies (Rift Valley Lakes). In Eurasia, the presence of *H. erectus* was associated with the occurrence of geological outcrops likely yielding unconsolidated flint. During the early phase of dispersal, our model indicated that *H. erectus* actively avoided areas densely populated by large carnivores. This pattern weakened as *H. erectus* dispersed over Europe, possibly because of the decreasing presence of carnivores there plus the later acquisition of Acheulean technology. During this later phase, *H. erectus* was associated with limestone and shaley marl, and seems to have been selecting for high-elevation sites. While our results do not directly contradict the idea that *H. erectus* may have been an active hunter, they clearly point to the fact that predator avoidance may have conditioned its long-distance diffusion

as it moved outside Africa. The modelled dispersal route suggests that *H. erectus* remained preferentially associated with low/middle latitude (i.e., comparatively warm) sites throughout its colonization history.

Introduction

There is general agreement that the first dispersal of humans (the ‘out of Africa 1’ event) was initiated by both intrinsic population factors (such as population expansion, better dispersal ability allowed by full bipedalism, and enhanced stone tool technology) alongside extrinsic climatic/environmental conditioning, including changing climates and the opening of geographic corridors (Shackleton et al., 1984; Tchernov, 1992; Arribas and Palmqvist, 1999; Agustí and Lordkipanidze, 2001; Flemming et al., 2003; Petraglia, 2003; Derricourt, 2006; Lahr, 2010; Abbate and Sagri, 2012; Rolland, 2013). The environment these early humans lived in must have affected their lives to a large extent. Yet, no consensus has been reached about which of the two classes of factors, intrinsic (population growth) versus extrinsic (climatic change, ecological interactions), is predominant, and whether they concurred in driving the dispersal. Environmental change obviously affects species distribution. In Quaternary large mammals it has been shown to force dispersal, prompting major adaptations or causing extinctions (Raia et al., 2012). Although *H. erectus* dispersal may simply be a direct consequence of environmental change, it appears at least reasonable that technological, and hence cultural, advancements could have decoupled

humans from at least some selective environmental pressures, thereby favouring geographic expansion, possibly through demography (Potts, 1994; Arribas and Palmqvist, 1999; Arcadi, 2006).

Homo erectus was the first hominin to venture out of Africa and over Eurasia, with several, highly-debated dispersal routes proposed to coincide with land passages connecting Africa to Eurasia during periods of sea level low-stands (Lambeck et al., 2002). There is a wide consensus that *H. erectus* evolved in Africa (but see Dennell, 2010). Its morphological diversity demonstrates variation between regional groups of a single evolving lineage with a large geographic extent, generally referred to as *H. erectus/ergaster* (Lordkipanidze et al., 2013). It is evident that *H. erectus* was fully bipedal (Lordkipanidze et al., 2007, 2013), which is consistent with the observation that this species was able to disperse over long distances. *H. erectus* is also considered to have fed more on meat than earlier hominins did (Shipman and Walker, 1989). This may link to dispersal ability, since carnivory is expected to increase locomotor demands by four to five times compared to herbivory (Pontzer et al., 2010). Behaviourally, intragroup cooperation in early *Homo* may have been important for dispersal, facilitating demographic expansion and tolerance to environmental variability (Hamilton et al., 2009).

There are plenty of competing and often controversial theories about the out of Africa 1 event. Before discoveries in Georgia and China, early archaeological evidence supported a relatively late age for the dispersal at some 1 million years ago (Ma). This bolstered the idea that the Acheulean technological innovation may have eased the

exploration of new environments (Turner, 1992). However, the earliest *H. erectus* site outside Africa is now dated with certainty at ~1.8 Ma, casting doubt on the importance of Acheulean technology as the breakthrough factor (Gabunia et al., 2002), and thus implicating ecological factors (Shipman and Walker, 1989; Leonard et al., 2000; Agustí et al., 2009). About 2 Ma, when *H. erectus* appeared, the relationship between hominins and carnivores began to change (Turner, 1992; Pushkina and Raia, 2008). Humans modified their strategy for feeding on meat, from occasional scavenging towards true predation (Croitor and Brugal, 2010; Ferraro et al., 2013). This brought about a profound transformation in human ecology. The genus *Homo* started as a member of the primary consumer, or omnivore guild, eventually becoming a top predator (Turner 1999, Pushkina and Raia, 2008). This process was not rapid and occurred alongside strong environmental/climatic changes and faunal turnovers (Raia et al., 2005; Bourlière and Howell, 2013; Feakins et al., 2013; Quinn et al., 2013; Bibi and Kiessling, 2015).

Despite profound interest in the hominin dispersal out of Africa, ecological approaches to the investigation of the potential driving factors are still relatively scarce. Of the studies that have been undertaken, mainly focusing on hominins (Mithen and Reed, 2002; Nikitas and Nikita, 2005; Hughes et al., 2007), several were based on so-called “cellular automata models” (commonly used in spatial ecology research; Tilman and Kareiva, 1997), which seek to determine occupancy probabilities over mapped grid cells during simulated population movements from one cell to another, according to a number of ecological factors and their spatial variation. These previous studies informed the new, mammalian fossil occurrences-based approach we report here. Our aim was to understand

the ecological dynamics of the out of Africa 1 event and the probable dispersal routes followed by *H. erectus*. We tested the influence of ecological factors such as landscape characteristics, prey and predator presence, and “cultural” factors such as the availability of particular lithologies yielding stone material useful for tool making, on dispersal route. We therefore asked whether *Homo* was likely to have followed the herbivore fauna, if it was influenced by the presence of large mammalian carnivores as it is often suggested (O'Regan et al., 2011), whether it preferred a particular range of altitudes, whether available lithologies may have influenced early *Homo* movement patterns, and how these factors intermingled to shape *H. erectus* dispersal routes.

In modelling dispersal routes, we considered ecological interactions (foraging, predation, and competition), the geography of the surrounding landscapes (altitude, freshwater availability), and the factors affecting technological development, specifically the availability of lithic material suitable for tool-making. In choosing the variables in our dispersal model, we tested five competing but non-mutually-exclusive hypotheses: i) that humans actively seek regions of high herbivore occurrence probability (presumably for meat procurement); ii) that humans preferred territories densely inhabited by carnivores (in keeping with a scavenger-like behavior); iii) that humans actively avoided areas that had high probability of carnivore occurrence (to avoid either competition or predation); iv) that humans favoured specific (i.e., non-random) altitudes (to reduce energy expenditure during locomotion or to select for a particular set of temperatures); and finally v) that *H. erectus* fossil localities are linked to particular lithological classes that could have been important for tool-making. Complementary to this last hypothesis, we tested whether

freshwater procurement was important to early humans, which could have been the case in the driest regions of Africa. Our resulting model provides a new reconstruction of the geographical path taken by *H. erectus* to venture out of Africa.

Materials and methods

We prepared a dataset of 605 Pleistocene mammalian fossil localities following published literature, developing and augmenting information from the well-known web-based, accessible databases, Paleodb (www.paleodb.org), NOW (<http://www.helsinki.fi/science/now/>), and the databases provided in Raia et al. (2009) and Carotenuto et al. (2010, 2015). For each locality, we recorded the geographical coordinates, the faunal list of large mammals, and any available age information, collecting a total of 2,796 species occurrences (Supplementary Online Material [SOM] Table S1). Additionally, a subset of this database including information related to *H. erectus* occurrence was produced. Because of scientific and technological developments, such information is continually changing and always requires careful re-examination. In order to have the most up-to-date dataset, we checked for the most recent specific publications dealing with the archaeological sites considered. To produce a reliable anthropological database for each site, we therefore extracted and summarised stratigraphic, archaeological, palaeoanthropological, palaeontological, and chronological information from several sources detailed in SOM Table S2.

We emphasise that we avoided associating specific cultures with a specific hominin species, as this could be misleading (Bar-Yosef and Belfer-Cohen, 2001). Instead, we chose to define a site as *H. erectus*-bearing based on the time interval from its first appearance at around 2 Ma until the third wave of out-of-Africa dispersal (Bar-Yosef and Belfer-Cohen, 2001) dated at some 1–0.8 Ma. We consider safer to refer *Homo* remains younger than 0.8 Ma to *H. heidelbergensis*, as this is the age of that early components of Atapuerca remains that are ascribed to the last common ancestor of *H. neanderthalensis* and *H. sapiens* (de Castro et al., 1997; Stringer, 2002). Hence, our data collection was restricted to 65 *H. erectus* localities ranging in time from 1.9 to ~ 0.9 Ma (SOM Table S2). As far as it is currently known, the colonization of Europe did not start before 1.4 Ma, thus probably coinciding with the expansion of Acheulean culture in Europe, as well as in the Middle East (Bar-Yosef, 1994), and in Asia (Pappu et al., 2011). The *H. erectus* timespan was thus further divided into two consecutive dispersal waves: from Africa toward Asia from about 1.9 to 1.41 Ma, and from Southeast Europe to Central and Western Europe from ~1.4 to 0.9 Ma, separating the two portions of the database temporally, geographically, and archaeologically.

We were interested to test if and how the presence of large mammals affected the dispersal of *Homo* under the “Out of Africa 1” scenario. Possible influential factors may include active hunting of a particular species, being commensal with specific predators to facilitate scavenging, similar habitat preferences or avoidance of large carnivores to reduce competition (mutual avoidance among competitors; cf. Heithaus, 2001). Complex ecological relationships and paucity of data mean that examining these factors one by one

for specific taxa is not feasible. Instead, we took a broader approach and examined Eutherian mammals occurring in all the fossil localities in the Palearctic and Afrotropical regions and ascribed them to either “carnivore” or “herbivore” categories according to their presumed diet (as reported in www.paleodb.org and <http://www.helsinki.fi/science/now/>). We identified herbivores of potential interest to humans based on their size (those that were ~17 kg to ~ 9000 kg [estimates from Raia et al., 2012, 2013] and hence large enough to be a source of meat worth following), as well as taphonomic data (cut marks on bones or being common at archaeological sites) that indicate probable interaction with hominins (SOM Table S1). We selected carnivore genera (SOM Table S1) with body mass ranging from ~ 7 kg (an ecological cut off between large and small carnivores, according to Meloro and Elton, 2012) to ~ 255 kg (estimates taken from Raia et al., 2012, 2013). We excluded species belonging to rodents, lagomorphs, small carnivores (mustelids and viverrids), other primates, bats, soricomorphs and erinaceomorphs because their small body size prevents fossilization of most remains (Damuth, 1982).

To reconstruct potential main routes of movement across Africa and Eurasia, we modelled the ecological and physical scenarios that we identified as most likely to be influential in *H. erectus* dispersal, and tested which of those scenarios significantly affected *H. erectus* locality distribution.

The ecological scenario

One of our aims was to assess whether there was a statistically significant association between large mammal occurrence and the geographic distribution of *H. erectus* prior to using this information in dispersal route reconstruction. To do this, we first needed to reconstruct the spatial distribution of the herbivores and carnivores in our sample. As the fossilization process does not have the same probability everywhere, the set of occurrences of a fossil species do not necessarily represent its real geographic range. Thus, we used a method to reconstruct the probabilities of taxon occurrence. Indicator Kriging (IK, a specialized version of the general method known as Kriging [Matheron, 1963]) is a spatial interpolation method able to produce a map showing the probability that a variable has a specific value, even in non-sampled geographic locations. In general, Kriging interpolation is used to reconstruct the value of a spatially distributed variable where there are no sampling points. It is based on the first law of geography, according to which "everything is related to everything else, but near things are more related than distant things" (Tobler, 1970). In Kriging, this law is mathematically formalised by a function that expresses the relationship of the distances between sampling points and the values of a variable they bear. This relationship produces an empirical semi-variogram, which is fitted to a mathematical model to describe the spatial structure of the variable.

For the herbivores and carnivores in our database, we drew, separately and for the two temporal intervals (from 1.9 to 1.41 and from 1.4 to 0.9 Ma), a total of four probability maps of occurrences by performing IK. To do so, for each group we scored as 1 those fossil localities where we recorded the occurrence of at least one large herbivore (or carnivore)

species and 0 otherwise. This way, for each temporal bin, we produced two binary matrices of occurrence, one for herbivores and another for carnivores. We used the binary matrix as entry data for IK and interpolated the probability of occurrence over a raster grid with a cell resolution of about 5 km at the equator. The cell resolution was computed as half the mean distance between the nearest points (fossil localities), as proposed in Hengl (2006), by using the package “plotKML” (Hengl et al., 2015) run into the R software (R Core Team, 2015). This method provides grid cells filled with a comparable number of sampling localities.

We performed IK and fitted the empirical semi-variograms in R by using the “automap” package (Hiemstra et al., 2008), which estimates model parameters via generalized least squares (GLS) and chooses the model that fits best the empirical semi-variogram by reduced maximum likelihood estimation (REML; Kitanidis, 1983; Christensen, 1993). In the resulting grid maps, cells are scored according to a continuous variable ranging from 0 to 1, along with latitude and longitude values to identify their geographic position. In these maps, a cell including a fossil locality with herbivore occurrence but surrounded by some cells where there are no herbivores, will have a sampling probability lower than 1. This is because the value at each point location is reconstructed by taking into account the neighbouring localities’ probability optimised by model fitting of the empirical semi-variogram. In contrast, a locality where there are no recorded herbivores can still score >0 . This means that maps generated via IK yield an estimate of the local probability density of herbivore (or carnivore) occurrence.

We estimated the goodness of fit of the chosen model for fitting of the empirical semi-variogram by performing a cross validation test for each of the computed maps. By the "leave-one-out" approach, we estimated the value at a known location (the 0 or 1 value of a particular fossil locality) by using the semi-variogram model, this time considering all localities other than the one under scrutiny, and compared the estimated value to its known value. We repeated this procedure for all the fossil localities with the related map. We used the new estimate to compute the root mean squared error (RMSE), which tells how good the semi-variogram model is in predicting known values. The closer the RMSE is to zero, the better the IK prediction. Further, as we dealt with fossil localities, which are not evenly distributed in space, we produced error maps showing the spatial distribution of the sampling bias affecting the prediction. Error maps, computed for the reconstructed herbivore and carnivore occurrence probability maps separately, give no information about the reliability of the reconstructed value in non-sampled locations, but can be used to infer the confidence of the predicted variable value. After these maps were drawn, we used them to extract the probability of carnivore and herbivore occurrence related to *H. erectus* fossil localities.

The geographic (abiotic) scenario

To model the physical landscape that *H. erectus* might have encountered during its dispersal, we reconstructed the altitudinal map of Africa and Eurasia during the temporal range of the fossil localities in our database (from about 1.9 to 0.9 Ma). We computed a mean altitudinal map by averaging the actual (worldclim.org) and the Pliocene elevation

(Sohl et al., 2009) maps at 2 x 2 decimal degrees cell resolution. As this map was the result of a mathematical operation, we needed to locally update the coastline variation and the presence of land bridges by considering further information provided by the recent geomorphological literature dealing with this topic. Actually, four main possible passages are consistently hypothesised from Africa to Eurasia: Gibraltar strait, BaB El-Mandab strait, the Messinian strait, and the Sinai land connection. Today, there is no clear evidence supporting any but the Sinai passage, which has connected the two continents since the Miocene (Lahr, 2010). For this reason, we limited the possible passage of *Homo* out of Africa to the Sinai connection. During Pleistocene glaciations, sea lowstands exposed the Sunda Shelf, thereby connecting Southeast Asia to the Indonesian archipelago islands (Hall, 2009). This allowed dispersal towards Java, where *H. erectus* remains dated at 1.57 Ma (Kaifu, 2010) were found. Because of the coarse-grained resolution level of the Pliocene altitudinal map provided by Sohl et al. (2009), the cells localizing the Sunda Shelf had missing values and, thereby, we arbitrarily corrected these cells by assigning them the smallest existing neighbouring cell value, thus using a conservative approach to correct our map.

In addition to the altitudinal information, we also included in the analyses a recently developed global lithological map (Hartmann and Moosdorf, 2012). We used this raster map to investigate whether the availability of particular lithologies influenced the occurrence of *H. erectus*, which would be consistent with the idea that energy-inexpensive tool stone procurement mattered to early humans. The map was provided at a resolution of about 0.5 decimal degrees at the equator, showing the geographical distribution at the

surface of the most important lithological classes in the three general categories of sedimentary, volcanic, and metamorphic rocks (see Hartmann and Moosdorf, 2012 for further details about the lithologies). The map of Hartmann and Moosdorf (2012) also includes the geographical distribution of the most important water bodies of the world (mainly internal seas and the largest and oldest lakes). It is not easy to assess whether the lithological outcrops shown in this map are the same as those present in the time period considered in this study. A way to test for chronological consistency of the outcrop geological composition is to consider only data that fall in tectonically stable regions. To this aim, we downloaded from the Earthquake Hazard Program of the USGS website (<http://earthquake.usgs.gov/earthquakes/search/>) the geographic coordinates along with the magnitude of the last 45 years of earthquakes recorded in both the Afrotropical and the Palearctic regions. Then, we computed the mean magnitude in a ~50 km grid cell resolution (SOM Fig. S1) and extracted the mean magnitude sampled by our fossil localities in a 10 km wide radius search circle. In all the analyses involving lithologies and water bodies, we excluded the localities with a mean sampled magnitude higher than four, assuming that a higher mean magnitude is proof of intense tectonics (hence strong possible modification of the landscape geology). As done for the lithologies, we needed to be sure that water bodies we were considering in the analyses were as old as the oldest documented occurrence of *H. erectus*. As reported in Maslin et al. (2014) the most important East African lakes, where most African *H. erectus* fossil localities were found, existed at least since the Pleistocene and possibly since much longer.

The ecological and environmental correlates of H. erectus distribution

To accomplish our goals, we used the maps of herbivore and carnivore presence probability for the two temporal intervals and the maps of mean altitude and lithology/water body distribution. As explained above, the herbivore and carnivore maps were made of a grid whose cells were given an estimated probability value (from 0 to 1), whereas the reconstructed altitude comprised the averaged values of the actual and Pliocene maps. As regards lithologies, we used a grid whose cells indicate the spatial distribution of surface rocks (outcrops) and of large water bodies.

To verify our five hypotheses, we performed a set of bootstrap resampling tests on each variable separately. All the bootstrap resamplings, but the one performed on the lithological map (see below), consist of the following steps. First, we superimposed all the *H. erectus* fossil localities to each of the grid maps and computed the mean of the values (herbivore and carnivore occurrence probability and mean altitude) sampled in these localities (real mean). Second, we superimposed all the fossil localities in our record to the same map and sampled the corresponding values. From this latter sample, we drew a random subset of values with the same number of fossil localities including evidence of *H. erectus* and computed the mean (simulated mean of herbivore and carnivore occurrence probability and mean altitude). For each grid map, and for both the considered temporal intervals, we repeated this procedure 999 times, thus generating a simulated random distribution of mean values of the selected variables. Then, to test the hypotheses described above, we measured the frequency that the real mean occurred in the random distribution of the simulated means. Specifically, if we hypothesized that *H. erectus* “preferred” high

values of a specific variable, we explicitly tested whether the corresponding real mean had a probability of occurring in the random distribution of simulated means higher than chance (i.e., a probability higher than 95%). When dealing with lithologies and water bodies, we modified the above procedures lightly. At first, for each temporal bin, we considered Africa and Eurasia separately because the two continents have different predominant lithologies (African territories are mainly composed of metamorphic rocks and unconsolidated sediments, whereas Eurasia is more heterogeneous). Second, as rocks are categorical variables, we considered the frequency of sampling each class in each iteration (instead of the mean value) and then tested if the sampled frequencies had higher or lower probabilities than chance.

Besides this, we tested the relationship between herbivore and carnivore probabilities of occurrence and the altitudinal distribution of *H. erectus* localities by performing, for each temporal interval, two separate generalised linear model (GLM) regressions, taking the two mammalian groups as predictive variables.

*The least cost routes computation of *H. erectus* dispersal*

A least-cost path is the minimum cost track that a species can walk through for minimizing energy consumption, after specifying a particular function for energy preservation. To compute the least cost paths of *H. erectus* out of Africa, we first needed to simplify *H. erectus* historical patterns of geographical distribution by only considering the

most important steps in colonizing new territories. Indeed, by taking into account the whole fossil record of a species, we can misinterpret the results because a species can continue to dwell in a region even if it expanded further into new territories, thus masking the real temporal sequence of dispersal events. To overcome this problem, we superimposed a grid with a cell resolution of about 500 km to the total geographical extent of *H. erectus* fossil localities and sampled only the oldest locality for each cell (SOM Fig. S2).

All of these localities had different geographic coordinates but, sometimes, very similar estimated ages, thus hampering the construction of a single hypothesis for *H. erectus* dispersal. To cope with this, we first sorted the localities in a chronological order and then considered, when dealing with localities with the same estimated age, the order of all localities providing the minimum cumulative straight-line path distance. For special cases when, for instance, a locality C with age 1.5 Ma is nearer to the an older locality A with age 2 Ma than its chronologically closer locality B with age 1.7 Ma, we admitted a bifurcation and preferred to reconstruct two different and disconnected routes, like the paths from A to B and A to C, assuming that two waves of dispersal started from the oldest locality A. This procedure allowed us assume that *H. erectus* did not travel an unreasonably long way between very spatially near localities. This happened mainly when reconstructing the dispersal route over Europe because of the chronological and spatial proximity of *H. erectus* localities found there. The selected ordination of localities was then considered for the computation of the least-cost route of dispersal from Africa towards Eurasia.

The calculation of the least-cost routes implies the computation of a conductance map, which is a grid map in which cells are given an index of conductance (i.e.,

permeability) indicating how favourable the walk through was. The index of conductance is a function of the variables chosen (herbivores, carnivores, altitude map, or lithologies) to draw the least cost route.

To compute the conductance index, we used the empirical frequency distribution of *H. erectus* localities occurring in discrete probability value intervals of 0.1, as regards herbivore and carnivore maps, and in discrete ranges of altitudes (200 m wide intervals). The simple function we used is summarized as follows:

$$CI_{(x, y)} = f(He_{i,z})$$

where $CI_{(x, y)}$ is the conductance index computed for the cell with coordinates x and y , and $f(He_{i,z})$ is the frequency of *H. erectus* (He) localities in the interval “ i ”, including the value of the variable “ z ” of the considered cell.

For the creation of the conductance indices based on lithological and water body maps, we used a different procedure because they are categorical variables. We created a grid map for each categorical variable where each cell recorded its distance to a specific lithology (or to the water body class). Then, if, for example, we recorded a positive association with a particular lithology, the value of the related conductance index was the inverse of the distance to this variable (i.e., cells near to the specific lithology have higher conductance values than those far away). In the opposite case, the conductance index has values proportional to the distance to lithology. The conductance maps were built by averaging all the specific conductance indices computed for a particular temporal interval or region. Then we used the Dijkstra’s algorithm (Dijkstra, 1959) for least-cost route path, originally conceived to solve connection problems in graph theory. This algorithm

minimizes the cost of moving from the first (starting) node (in our case a grid cell) to the last (finishing) one by iteratively looking for the node (cell) combination with the minimum cumulative cost (1/conductance). For each of the two route paths (i.e., towards Eastern Asia and Central and Western Europe), we computed a mean conductance map by using all the maps that verified our ecological and geographical hypotheses, as explained above.

Results

*Ecological and environmental correlates of *H. erectus* distribution*

Based on the maps we produced, the IK was a good predictor of occurrence probability in known localities for the older (1.9 to 1.41 Ma) temporal interval (RMSE = 0.0016 and RMSE = 0.0032 for herbivores and carnivores, respectively). For this temporal interval, the bootstrap resampling of the herbivore map indicates that localities with evidence of *H. erectus* presence indicated that the probability of hominins associating with herbivores was no higher than expected by chance (mean sampled value of herbivore probability of occurrence = 0.985, C.I. 95% = 0.990, $p = 0.111$). For carnivores in this temporal interval we found that localities of *H. erectus* sampled lower values than expected by chance, conforming to the hypothesis that *H. erectus* and carnivore occurrences are disjointed (hypothesis III; mean sampled value of carnivore probability of occurrence = 0.122, C.I. 5% = 0.299, $p = 0.001$). In SOM Figure S3, we report the error map of the

carnivore occurrence probability distribution used for the least-cost route of dispersal. In addition, our results show that *H. erectus* localities did not sample higher altitudes than predicted by chance (mean sampled altitude = 877.43 meters, C.I. 0.95% = 968.16 m, $p = 0.169$).

For the second temporal interval, the interpolation method we used provides evidence in favor of data quality, with RMSE as low as <0.01 for both herbivore and carnivore data. During this interval (from 1.4 to 0.9 Ma), neither herbivore nor carnivore occurrence probability maps were significantly associated with human presence (herbivores: mean sampled value of occurrence probability = 0.903, C.I. 95% = 0.971, $p = 0.682$; carnivores: mean sampled value of occurrence probability = 0.340, C.I. 5% = 0.253, $p = 0.526$). Bootstrap resampling indicates *H. erectus* localities occur at higher than expected altitudes (mean sampled altitude = 1037.122 meters, C.I. 0.95% = 976.379 m, $p = 0.02$).

By using the analysis for the chronological consistency of the lithological map, we found that 19 % of the localities sampled a mean magnitude higher than 4. Therefore, we excluded these localities in all the analyses performed with lithological and water body maps. The bootstrap resampling tests showed that, during the older temporal interval, the *H. erectus* localities in Africa are positively linked to water bodies (measured frequency = 10, $p < 0.01$, CI 95% = 6), whereas no rock types were preferentially selected. Conversely, we recorded a statistically significant association with unconsolidated sediments in Eurasia (measured frequency = 3, $p = 0.038$, CI 95% = 3). In the lithological map provided by Hartmann and Moosdorf (2012), in the class "unconsolidated sediment" (examples being

sands, mud, alluvial and lacustrine deposits, dunes, beach sands, and colluviums), the authors considered all those geologically young, not yet consolidated sediments usually of Cenozoic age. All grain sizes are represented in this category. In the younger temporal interval, we again found no significant link between *H. erectus* African locality lithologies or water bodies. However, in Eurasian localities, mixed sedimentary rocks are sampled more often than expected by chance (measured frequency = 4, $p = 0.041$, CI 95% = 4). "Mixed sedimentary rocks" represent all those sediments where carbonate is mentioned but not dominant. Mixed sedimentary rocks are usually a combination of different rock types (e.g., interlayered sandstone and limestone). Another classical representative rock in that class is shaley marl (Hartmann and Moosdorf, 2012). Unconsolidated sediments and mixed sedimentary rocks are both likely to yield loose chert, which is ideal for tool making (Miall, 1981).

Regarding the relationships between mammalian fauna and the elevation distribution of *H. erectus* localities, for the older temporal interval the GLM regression between ln-transformed altitude and herbivore occurrence probability is negative but not significant (slope = -2.549, $p = 0.847$, AIC = 34.137), whereas the relationship between altitude and carnivores is negative and significant (Fig. 1a; slope -1.157, $p < 0.01$, AIC = 37.296). During the younger temporal interval (from 1.4 to 0.9 Ma), the relationship between altitude and herbivore occurrence probability values is positive but not significant (slope = 0.573, $p = 0.328$, AIC = -23.957), whereas with carnivores it is negative and significant (Fig. 1b; slope = -1.116, $p < 0.01$, AIC = 9.713).

The least cost routes computation

We produced conductance matrices according to the results of the bootstrap resampling. That is, for the older temporal interval, we built a complex model based on probability of carnivore occurrence for Africa and Eurasia, the map of the distances to the water bodies for the African continent, and the map of the distances to unconsolidated sediments in Eurasia. For the younger temporal interval, the complex model includes altitude and the map of the distances to mixed sedimentary rocks for Eurasia.

Figure 2a shows the least-cost route map for the dispersal of *H. erectus* from East Africa throughout East Eurasia (the oldest temporal interval). According to this map, *H. erectus* moved throughout Africa starting from Kenya (East Turkana, 1.89 Ma) and then going towards South Sudan, Sudan, and Egypt. Along this route, according to our dispersal model, *H. erectus* moved between two areas with a low to medium probability of meeting carnivores (Fig. 2b; the territories of the Rift Wally and the Sinai passage), although we detected somewhat large (>0.5) prediction error values (SOM Fig.S3). This dispersal route is highly influenced by the presence of water bodies, i.e., the East African Lakes, like Turkana and Nasser (along the Nile River). Outside Africa though the Sinai passage, *H. erectus* reached Georgia (Dmanisi) at 1.77 MA. This route is influenced by a very low probability of meeting carnivores (with a medium level of error prediction, SOM Fig. S3) until reaching Georgia, where we reconstructed a carnivore encounter probability of about 0.9 (Fig. 2b) and a very low level of prediction error (SOM Fig. S3). In these regions, the geographical distribution of unconsolidated sediments in the Fertile Crescent had a positive

influence in computing the least cost path of dispersal (Fig. 2c). The reconstructed route connecting Georgia to the nearest fossil locality in eastern Eurasia (Yuanmou, 1.7 Ma) runs along the southern coast of the Caspian Sea, touches the territories of today's Azerbaijan, Iran, Afghanistan, and Pakistan, and moves south to the Himalayas, eventually reaching the Yunnan Province via what is today India, Bangladesh, and Burma. This part of the route is influenced by mid to low probability values of meeting carnivores, reaching the lowest values when arriving in the territories surrounding Yunnan (Fig. 2b), with variable prediction errors (SOM Fig. S3). The reconstructed dispersal path touches the territories of Pakistan and Rajasthan, which are relatively rich in unconsolidated sediments (Fig. 2c). In our reconstruction, the Zhongyuan (the Chinese Central Plain around the Yellow River) was a very large area of settlement where a dispersal wave towards Indonesia (Sangiran on the island of Java, 1.57 Ma) started. In this region are several localities, such as Renzidong (1.7Ma), Longgudong (1.25 Ma), Xiaochangliang (1.36 Ma), and Donggutuo (1.1 Ma). Here the carnivore occurrence probability is very high (Fig. 2b), with a low prediction error (SOM Fig. S3). The passage through this area is mainly influenced by the presence of unconsolidated sediments found in the wide flood plains where several Chinese rivers exundate (Fig. 2c). The route towards Sangiran is characterised by a mid/high probability of encountering carnivores (Fig. 2b; with high to mid prediction errors, SOM Fig.S3). Important in determining this dispersal route is the presence of unconsolidated sediments in Thailand and in the flood plains of Eastern Java. The cumulative distance walked through by *H. erectus* in the reconstructed scenario was about 25,000 km.

For the temporal interval from 1.4 to 0.9 Ma, our model considered the reconstructed elevation map and the distribution of the mixed sedimentary rocks. The route (Fig. 3a) for *H. erectus* arrival in Central and Western Europe starts from Ubeidiya (1.4 Ma), in the territories of modern-day Israel, where it is possible to encounter several deposits of mixed sedimentary rocks (the characteristic limestone and sandstone formations in Israel; Fig. 3b). The route connecting Israel to Turkey, according to our model, is mainly influenced by altitude (Fig. 2c), and *H. erectus* dispersed over the Anatolian Plateau, touching the localities of Dursunlu (1.21 Ma) and Kocabas (1.1 Ma). According to the chronological order of the European localities, the successive steps in this reconstructed dispersal route are the two localities in Spain (Fuente Nueva, 1.35 Ma, and Sima del Elefante, 1.20 Ma). This route is characterized by the particular topography of Central Europe, drawing a path crossing the Balkan Alps, the Dinaric Alps, the Alps, and the Pyrenees. All these territories provide many opportunities to encounter deposits of unconsolidated sediments. Because of the very close age estimations of the remaining European localities, it was not possible to reconstruct with confidence any unique and unidirectional path. As a consequence, we identified “waves” of dispersal from the Levant (Ubeidia, 1.4 Ma) to Central (Vallonet, 0.95 Ma) and Southern Europe (Pirro Nord, 1.16 Ma) that overlap with each other (in Fig. 3a, red lines indicate routes that were repeatedly used for dispersal). For this route, the computed cumulative distance walked was about 15,400 km.

Discussion

During the late Pliocene, around 3 Ma, aridity increased globally (Shackleton et al., 1984; deMenocal, 1995; Bobe and Behrensmeyer, 2002). Soon after 2.5 Ma, at the onset of the Quaternary, 41 ka glacial cycles caused the so-called "Late Pliocene climate crush" (Bartoliet al., 2005), accompanied by (still) lower precipitation and increased seasonality (deMenocal, 2004; Mosbrugger et al., 2005). In East Africa, grasslands replaced closed mesic woodlands (Potts, 2013; Berkeet al., 2015), expanding towards south-eastern Eurasia (Vrba, 1985; Dennell, 2010; Cerling et al., 2011). The mammalian fauna responded greatly to these changes, experiencing intense faunal turnover and dispersal at this time (Behrensmeyer et al., 1997; Arribas and Palmqvist, 1999; Raia et al., 2005; Bibi and Kiessling, 2015).

The *H. erectus* skeleton was optimized to preserve energy during long-distance locomotion (Ruff, 2006, 2008; Pontzer et. al., 2010). This suggests that it could be viewed as adapted to dispersal alongside other megafauna. In fact, our model indicated that there was no particular connection between *H. erectus* and the spatial distribution of either herbivores or elevation during the older temporal interval (from ~1.9 to ~1.41 Ma). However, there was a significantly negative relationship between the presence of *H. erectus* and the density of large carnivores. Such a negative association, and the negative relationship between carnivore occurrence probability and elevation (Fig. 1a), suggests that carnivore avoidance was important to *H. erectus*. Some authors argue that human dispersal may have been conditioned by the structure of the large carnivore guild (Turner, 1992; Arribas and Palmqvist, 1999). There are models that envision early humans as "obligatory marginal scavengers" (Shipman, 1986; Binford, 1988; Blumenschine, 1995; Brantingham,

1998; Treves and Palmqvist, 2007), unable to coordinate food processing and mainly focusing on a plant-based diet. Others consider these early humans to be hunters or confrontational scavengers (Isaac, 1984), strongly oriented towards meat procurement. Several authors tend to synthesize these two contrasting views, suggesting either occasional hunting by humans or aggressive scavenging (Brantingham, 1998; Stiner, 2002; Dominguez-Rodrigo and Pickering, 2003; Ferraro et al., 2013). Whatever the case, a tight association between humans and carnivores seems to be the natural outcome of an emphasis on indirect meat provisioning. In contrast to this, our data suggest that, rather than taking advantage of large carnivore kills, humans either avoided carnivores, or simply moved passively together with the large herbivore fauna. Under the “predator protection” hypothesis (Hart and Sussman, 2009), carnivore species are expected not to occur significantly with humans, which probably used group living as a basic protective strategy against predators, either to detect and avoid them, to increase the ability to chase them away (Treves and Naughton-Treves, 1999), or to defend profitable resources (Palmqvist et al., 1996). Our data are consistent with such predator avoidance hypotheses, although the (geographical) scale of our observation is probably coarse enough to suggest caution with this interpretation, especially as we also note co-occurrence of large carnivores and *Homo* at several sites, including Youanmu (Zhu et al., 2008), Gongwangling (Norton et al., 2010), Dmanisi (Vekua and Lordkipanidze, 2008), and Ubeidya (Bar-Yosef and Tchernov, 1972).

The younger interval is marked with human entrance into Europe, coinciding with the appearance of the Acheulean culture in the Near East (at Ubeidya; Bar-Yosef, 1994). Unlike the older time interval, the geographic distribution of this hominin species is no

longer associated with carnivores. Yet, surprisingly *H. erectus* started to significantly prefer moderate to high altitudes (around 1000 m). Given the negative association between carnivore density and altitude (Fig. 1b), this may suggest that humans either changed their strategy to avoid predators (choosing high elevation sites where carnivores are rarer), or started to fend them off more effectively. Some authors argue that large early Pleistocene predators drove scavenging-dependant humans to sporadic dispersal over Europe (Turner, 1992; Martinez- Navarro and Palmqvist, 1996; Palmqvist et al., 1996; Arribas and Palmqvist, 1999; Palombo, 2010). Yet, by the end of the Villafranchian period, large carnivore populations started to decline in Europe (Croitor and Brugal, 2010). At this time, humans became behaviourally more flexible, hence able to cope with different environments. Their diet also became more variable, with a greater proportion of meat included, which is expressed in manifest hunting since the middle Pleistocene (Croitor and Brugal, 2010). Probably, a flexible semi-scavenger and semi-hunter *H. erectus* may have taken advantage of this new situation as soon as predation pressure languished. However, it was *H. heidelbergensis* to fully occupy Europe, later than *H. erectus* entrance there (Rightmire, 2001).

We find it very interesting that human actively selected for mixed sedimentary rocks and unconsolidated sediments outside Africa. These kind of outcrops are typically rich in easily collected, ready-to-use flint (Miall, 1981), which is the main tool stone for Eurasian *H. erectus* (Shea, 2010). Our results suggest that the procurement of raw materials for tool making probably was a factor in conditioning the presence (and arguably the path of dispersal) of *H. erectus* outside Africa. In contrast, in their African cradle, *H. erectus*

individuals significantly made for the old and massive Rift Valley lakes. This is arguably important where and when increasing aridity started to take its toll, in the so-called “Savannahstan” environment (Dennell, 2010). The robustness of these results must be judged alongside consideration of possible taphonomic bias. Unconsolidated sediments and mixed sedimentary rocks are rare overall in human occupied sites, and flint stone is rare in African outcrops (where we did not find any association to any rock type). Hence, the preference for places yielding this kind of material in Eurasia is probably genuine (Shea, 2010). On the other hand, most eastern African earlier sites refer to fluvial or lacustrine deposits, which means the preference for large water bodies in the older temporal interval might be an artefact rather than real. However, the Rift Valley lakes are among the oldest and largest inland water systems of the world, and paleosol records of early Pleistocene savannah flora at the Nachukui Formation, Turkana Basin, indicate strong preference for wooded habitats to access water for early hominins (Quinn et al., 2013).

To depict the least-cost path of *H. erectus*, we used significant ecological and geographical interactions as specific variables to define the energy consumption function. According to our temporal intervals, we conducted two sets of maps: for the earlier interval (1.9–1.41 Ma) towards Asia, we mapped one least-cost path by considering a complex model combining the carnivore occurrence probability, the map of the distance to the water bodies, and the distribution of the unconsolidated sediments in the energy consumption functions (Fig.2a). A second map (Fig.3a) was computed by using the altitude and the mixed sedimentary rocks distribution in the energy consumption function. It depicts the most likely path taken by *H. erectus* during second interval (1.4–0.9 Ma).

Despite a lively debate about the likelihoods of alternative pathways is active in the scientific literature, we conditioned the early Pleistocene *H. erectus* dispersal out of Africa through the Sinai landbridge. Whereas most researchers agree with this, others favour a North African corridor, via the Gibraltar strait (Arribas and Palmquist, 1999; Flemming et al., 2003; Abbate and Sagri, 2012) or even an East African horn passage, via Bab el-Mandab strait and into the Arabian Peninsula (Lahr, 2010; Abbate and Sagri, 2012). However, there are many arguments against these theoretical passages. Critically, there is no available evidence that would prove the water-crossing ability of humans before the late Pleistocene, despite the periodic lowering of the water level in the Red Sea (Tchernov, 1992; Straus, 2001; Petraglia, 2003; Derricourt 2006; Rolland 2013). Indeed, most palaeontological and palaeoceanographic information is not supportive of any animal migration via Gibraltar and Bab el-Mandab during the early Pleistocene (Mithenand Reed, 2002; O' Regan et al., 2002, 2011; Fernandes et al., 2006; Lahr 2010). We additionally ignored the hypothetical corridor connecting Sicily to North Africa in keeping with the arguments presented in Villa (2001).

According to our data, *H. erectus* went through “Savannahstan” (Dennell, 2010), a grassland biome that spread around Southwest Asia and eastern Africa at some 1.8 Ma (Hughes et al., 2008; Lahr, 2010; Abbate and Sagri, 2012). The first documented arrival in Eurasia of early humans is at Dmanisi. The palaeoenvironment at this site is reported as mixed woodland, dry and relatively warm (Gabunia et al., 2001). Our map (Fig.2a) depicts *H. erectus* moving to the Caucasus via the Levantine corridor, possibly together with additional African immigrants (Belmaker, 2010). The extensive floodplains of the Early

Pleistocene ancestors of the Indus, Ganges, and their major outfalls should have been attractive areas for *H. erectus*, as shelter from the large predators and a resource rich area, but difficult to colonise successfully because of the landscape changes during monsoonal rains (Bar-Yosef and Belfer-Cohen, 2001).

Our results further suggest several possible routes of diffusion of *H. erectus* around the Palearctic-Oriental biogeographic boundary in Southeast Asia (Norton et al., 2010). Java was the terminus of dispersal, dated to 1.5 Ma, for *H. erectus* in Southeast Asia. Plio-Pleistocene boundary tectonics accompanied by increased volcanic activity formed the emergent Sunda and Sahul Shelves, including the islands of the Indonesian Archipelago. Glaciation, deglaciation, and the accompanying sea level fluctuations greatly affected land mass configurations in Southeast Asia. During the Pleistocene, the Sunda and Sahul shelves were episodically largely exposed forming huge land connections between the Asian mainland and the islands of Sumatra, Java, and Kalimantan, creating the so-called Sundaland (Voris, 2000). This corridor served as a land bridge and migration route for *H. erectus* and other vertebrate fauna from the Asian mainland to Java (Zaim, 2005). Again, in this older time interval, the movements of *H. erectus* seem to coincide with those of many other large mammals.

For the second interval, our data suggest that humans accessed Southern Europe through the Bosphorus passage (Ryan et al., 2003; Muttoni et al., 2010), exposed during the Pleistocene, probably by the so-called Cassian sea level fall (Arribas and Palmqvist, 1999). Sites such as Fuente Nueva and Sima del Elefante in Spain are the terminals of arrival through Eastern and Central Europe, after a travel that lasted for about 50 ka. In the map

shown in Figure 3b, we reconstructed more than one dispersal wave starting from the Levantine Rift Valley, which had a tropical biota that was very similar to those of the African savanna, where hominins lived (Por, 2004), thus probably acting as an attractive pole for propagules. The chronological proximity of Central and Southern European localities testifies that these territories were colonised at nearly the same time, thus resulting in a favourable area for settlements. The ages of European sites also testify that humans arrived there later, after colonising Southeast Asia. The climatic harshening of Central Europe during the Pleistocene possibly scourged any adventurer or, at least, made it difficult to establish long-lasting settlements due to the derived increase of the dispersal's cost over these territories. Humans probably entered Europe from settlements in the Levant and after the diffusion of Acheulean technology, which possibly allowed them to undertake high costly explorations of new territories by better exploiting animal resources (Carbonell et al., 2010).

Our study focuses on the ecological and behavioural attributes of the dispersal of *H. erectus* out of Africa. We found that such species dispersal is best viewed in the context of the large primary consumers dispersal first started at 2.5 Ma, and triggered by intense climate change. Contrary to any other species, though, *H. erectus* was able to modify its behaviour, making for high altitudes and for landscapes littered with usable stone material once he colonised Europe and started to exploit the Acheulian culture outside Africa.

Acknowledgements

The backbone of this article is part of the doctoral thesis of one of the authors (NT), carried out at the University of Florence (Doctorate in Earth Sciences, XXVII national cycle, 2012-2014). We are grateful to Stefano Tavani, Stefano Vitale, and Emma Ruggiero for their assistance with the geological analyses and inferences. We thank Jens Hartmann and Nils Moosdorf, who kindly gave us access to the raw data to build their map and assisted us with its interpretation. The Italian participation at the Dmanisi International Research Project is supported by the Italian Foreign Ministry (DGSP-VI grants to LR). Hannah O'Reagan, Jordi Agustí, one anonymous reviewer and the Editor Sarah Elton, provided us with fruitful deep advice on the manuscript content and presentation.

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Figure legends

Figure 1. Plot of the relationship in *Homo*-populated localities between altitude and (a) carnivore probability of occurrence in the older temporal interval (from 1.9 to 1.41 Ma), and (b) carnivore probability of occurrence in the younger interval (from 1.4 to 0.9 Ma).

Figure 2. The least-cost route reconstruction of *H. erectus* dispersal over Africa and Eastern Eurasia during the older temporal interval (from 1.9 to 1.41 Ma) displayed over the computed conductance map (a). The same path is displayed over the carnivore occurrence probability map (b), and over the map of the distances to the water bodies (Africa) and unconsolidated sediments (Eurasia) (c). Eastern routes towards localities with age less than 1.41 Ma (slate-grey lines) were computed by using the conductance map of the younger temporal interval (from 1.4 to 0.9)

Figure 3. The least-cost route reconstruction for *H. erectus* dispersal over Europe during the younger temporal interval (from 1.4 to 0.9 Ma) displayed over the reconstructed conductance map (a). The path is always westward and the three different coloured lines represent different possible waves starting from bifurcations (see the text) when the same route is walked through again. The same path is displayed over the map of the distances to the mixed sedimentary rocks (b) and over the reconstructed mean altitude map (c).