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Climate-inferred distribution estimates of mid-to-late Pliocene hominins

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Abstract

During the mid-to-late Pliocene (ca. 4–3 Ma), several hominin species were present in central Sahel, eastern and southern Africa. Potential discovery of hominin remains from this period is limited by the availability of exposed Pliocene deposits and the ability to investigate them. As a result, most discoveries have been made in the Afar region of Ethiopia and in the Lake Turkana basin, thus unveiling only a portion of Pliocene hominins' probable geographical presence. In this study we provide a continental view of geographic areas potentially accessible to these hominins. To do so, we simulate the climatic envelope suitable for mid-to-late Pliocene hominin presence, using the earth system model IPSL-CM5A and the Maxent habitat suitability algorithm. The latter indicates high habitat suitability for these hominin species in semi-arid regions where annual thermal amplitude and mean annual precipitation are moderate, mostly corresponding to tropical xerophytic shrublands. Our habitat model estimates geographically continuous, suitable climatic conditions for hominins between central Sahel and northeastern Africa, but not between eastern and southern Africa. This discontinuity suggests that southern African and eastern African hominins were separated by an environmental barrier that could only crossed during particularly favourable periods or by undertaking long-range dispersal over climatically hostile habitats. During simulated periods of climate changes driven by orbital precession this climatic barrier is not present. The Turkana basin, the Laetoli region, and a large part of southern Africa remain suitable for all precession angles, suggesting that these areas may have functioned as refugia. The constant presence of these stable areas combined with the periodic establishment of corridors for dispersion can potentially explain hominin diversity in eastern Africa.

Keywords : Habitat suitability model, Niche modeling, *Australopithecus*, Africa, Pliocene, Dispersal

1. Introduction

The mid-to-late Pliocene, ca. 4–3 million years ago (Ma), was a period of global warmth with atmospheric CO_2 concentrations around 400 ppm, smaller ice sheets, reduced desert areas compared to the present, a global temperature 2–3°C warmer than the preindustrial period (e.g. Salzmann et al.; 2013; Haywood et al., 2020). Oxygen isotope ratios of benthic foraminifera and continental ice records show that this period was climatically stable, with the exception of short-lived cold episodes around 3.6 Ma and 3.3 Ma (De Schepper et al., 2014; Lisiecki and Raymo, 2005). During this period, several hominin species appear to have coexisted and fossil occurences occur in three distinct geographic areas: central Sahel (*Australopithecus bahrelghazali*: Brunet et al., 1995, 1996; Lebatard et al., 2008), eastern Africa (*Au. anamensis, Au. afarensis*: Haile-Selassie et al., 2019; *Kenyanthropus platyops*: Leakey et al. 2001; *Au. deyiremeda*: Haile-Selassie et al., 2015) and southern Africa (*Au. prometheus*: Clarke and Kuman, 2019; *Au. africanus*: Dart, 1925; Herries et al., 2013*)*. These hominins thrived in C_3-C_4 mosaic habitats (Behrensmeyer and Reed, 2013), close to freshwater sources in the form of rivers (Curran and Haile-Selassie, 2016), springs and oases (Barboni et al., 2019), or lakes (paleo-lake Turkana: Feibel, 2011; Boës et al., 2019; paleo-lake Chad: Schuster et al., 2009; Lee-Thorp et al., 2012). They may have used technology, since the oldest recovered retouched pebble assemblage discovered near Lake Turkana is dated ca. 3.3–3.2 Ma (Harmand et al., 2015).

While their exploited microhabitats appear to have been mostly dominated by the presence of freshwater and some locally sustained trees, several authors propose that they could have coped with a variety of environments (within which similar microhabitats could occur), thus leading to the idea that the genus *Australopithecus* could have been eurytopic (Bonnefille et al., 2004; Behrensmeyer and Reed, 2013). Our ability, however, to observe and investigate hominin remains from this period is limited by the availability of exposed Pliocene deposits. As a result, most discoveries have been made in the Afar region of Ethiopia and the Lake Turkana Basin, thus representing only a portion of the probable Pliocene hominin geographic distribution. Here, we aim to provide a continental view of the geographic areas potentially accessible to these hominin populations. Reconstructing the presence of freshwater sources at reduced geographic scales is speculative for chronological intervals that have a resolution of hundreds of thousands of years and regions for which detailed paleotopography is unknown. However, sources of perennial freshwater and associated gallery vegetation can occur anywhere total annual precipitation exceeds 200–300 mm and topographic depressions or river channels exist (Quade et al., 2018). This is the case during the mid-Holocene and the Last Interglacial when surface drainage was reactivated in the Sahara (e.g. Coulthard et al., 2013; Skonieczny et al., 2015), as well as in areas where precipitation is lower than that threshold, but sustained by groundwater (e.g. present-day Ounianga lakes in northeastern Chad: Kröpelin et al., 2008). C_3-C_4 mosaic habitats, similar to those occupied by hominins, are ubiquitous in African savannah environments (Marston et al., 2018) for which woody cover depends on the frequency and intensity of single rainfall events (Good and Caylor, 2011), which are not known for past periods. Although there is a link between large-scale climate and hominid microhabitats, i.e., perennial freshwater sources enable the development of mosaic habitats, we cannot mechanically calculate this.

We address these issues from a statistical point of view by employing climate envelope modeling methods to determine which large-scale climate variables are most appropriate for explaining known hominin occurrences between 4 Ma and 3 Ma and inferring their potential distributions. To do so, we employ a set of mid-to-late Pliocene climatic variables simulated with the earth system model IPSL-CM5A (Dufresne et al., 2013) to create a climatic envelope model that best matches the distribution of mid-to-late Pliocene hominin occurrences using the *kuenm* R package (Cobos et al., 2019), which uses the Maxent algorithm (Phillips et al., 2006, 2017). Via this approach, we 1) evaluate the capacity of these methods to diagnose the appropriate areas for which we possess data; 2) map potentially suitable areas currently free of paleontological remains and 3) employ a series of insolation sensitivity experiments to investigate potential dispersal between our targeted geographic regions and potential refuge areas.

2. Methods

2.1 Climate model description and setup

We use the earth system model IPSL-CM5A to simulate late Pliocene climate. Atmospheric resolution of the model is 3.75° in longitude by 1.9° in latitude, with 39 vertical levels. Mean grid spacing of the ocean model is approximately 2°, while latitudinal resolution is refined to 0.5° near the equator and 1° in the Mediterranean Sea. This model has been widely used for the study of future and past climates (e.g. Dufresne et al., 2013; Kageyama et al., 2013; Contoux et al., 2012, 2015). The boundary conditions used to force the model follow the Pliocene Model Intercomparison Project phase 1 (PlioMIP1) guidelines described by Haywood et al. (2010). They have been adapted to the IPSL-CM5A model with a modified topography, smaller ice sheets, and atmospheric concentration of CO2 fixed at 405 ppm (Contoux et al., 2012). The climate model uses PlioMIP boundary conditions designed to simulate the climate of the mid-Piacenzian (Contoux et al., 2012). Given that benthic isotope ratios show that climate variability was low from 4–2.8 Ma except for two cold outbursts at 3.6 and 3.3 Ma (Lisiecki and Raymo, 2005; Tan et al., 2017), we extrapolate that this simulation is valid for the period between 4–3 Ma, which mostly corresponds to the Piacenzian. There exists a multitude of possible orbital configurations for any period that spans several hundred thousand years, but we can only use one set of orbital parameters per simulation since we conduct equilibrium climate simulations rather than transient ones. Because the primary goal of the PlioMIP simulation was to compare the climate of the mid-Piacenzian to the preindustrial, the choice made by the PlioMIP community was to use the present-day orbital configuration. This present-day configuration is one for which eccentricity is small. In other words, climate variability linked to precession, which is the main mode of climate variability during the Pliocene, is also small. Thus, we use it as a proxy for Pliocene 'mean' climate. This simulation (Pliocene 'mean' climate) has been extensively studied and compared to other climate models in the framework of PlioMIP1 (e.g. Haywood et al., 2010; Zhang et al., 2013). We also conducted four additional Pliocene experiments in order to capture an envelope of maximum climate variability during our target period. We do so using modified orbital parameters corresponding to the period of highest eccentricity (see appendix 1) with four different precession angles (one per simulation), corresponding to the Earth at perihelion at the Northern Hemisphere summer solstice (PlioMax June) and autumn equinox (PlioMax September), and the two opposites, at aphelion at Northern Hemisphere summer solstice (PlioMin June) and autumn equinox (PlioMin September). Orbital parameters were calculated using the Analyseries software (Paillard et al., 1996).

Climatological means were calculated from the last 50 years of each simulation. Bias correction of the climate model output was obtained by using the climatic anomalies (temperature difference and percent change for precipitation, e.g. Hély et al., 2009) superimposed on Climate Research Unit climate observations at 0.5° by 0.5° (New et al., 2002). This is possible since the biases of a climate model are supposed to be stationary through different time periods (Krinner and Flanner, 2018). Our simulated climatic fields are thus downscaled from a resolution of 1.9° by 3.75° to 0.5° by 0.5°.

2.2 Vegetation model description and setup

We employed the BIOME4 model (Kaplan et al., 2003) to calculate vegetation in equilibrium with the Pliocene mean climate and the four orbital Pliocene climates. To do so, we calculated climate anomalies between each Pliocene experiment and the preindustrial control experiment (temperature difference and percentage of change for precipitation and clouds, e.g. Hély et al., 2009) interpolated at 0.5°x0.5°. The anomalies were then added to the 0.5°x0.5° gridded data from the Climate Research Unit (New et al., 2002). The model BIOME4 calculates vegetation types in equilibrium with climate model outputs (monthly mean precipitation, air surface temperature, cloud cover and absolute annual minimum air surface temperature). Atmospheric CO_2 concentration was fixed at 405 ppm (PlioMIP value) and soil characteristics kept at present-day values.

Biomes are assigned according to which plant functional types (PFT) are dominant, as well as the productivity and leaf area index (LAI) of each PFT. For example, when the productivity on one grid cell is dominated by the the tropical raingreen tree PFT, followed by the C_4 tropical grass and the woody desert PFT, the grid cell will be associated with tropical xerophytic shrubland biome if the LAI of the tropical raingreen tree PFT is < 4 and to the tropical savannah biome if the LAI of tropical raingreen tree PFT is > 4.

2.3 Hominin occurrence data

Predictive architectures used to estimate ecological niches or climatic envelopes rely, in part, upon the geographic coordinates (longitude and latitude) of locations where the target population has been observed. In this study, the occurrence data are the locations where fossil hominins dated from ca. 4–3 Ma have been recovered. This choice was made for several reasons. First, our climate model is representative of Piacenzian climate (ca. 3.6—2.8 Ma). This corresponds to the chronological interval to which *Au. afarensis* has been dated. Climatic envelope modeling is performed typically at the species level. However, the diversity of Australopithecus species is poorly constrained as some species, and even genera, are controversial *(Au. bahrelghazali, Au. prometheus, K. platyops*). The intra-specific and inter-specific variability of Australopithecus species is also poorly understood, such that with the recent discovery of the first complete cranium of *Au. anamensis* (Haile-Selassie et al., 2019) remains previously assigned to *Au. afarensis* were reclassified as *Au. anamensis*. Given the taxonomic uncertainty of many *Australopithecus* remains, and considering that the genus provides a working framework, we chose to simulate the climatic envelope suitable for the ensemble of Pliocene *Australopithecus* species, as well as *Kenyanthropus*. This approach is justified by the review of *Australopithecus* paleoenvironments carried out by Behrensmeyer and Reed (2013) demonstrating that these hominins are all associated with similar environments, thus suggesting that their climatic envelopes were likely similar. We excluded the more primitive *Ardipithecus*, which is older than 4 Ma, as well as *Australopithecus* species that are clearly Pleistocene in age (*Au. garhi* and *Au. sediba*) since climatic deterioration due to the Northern Hemisphere Glaciation was already well established by that time (e.g. Tan et al., 2018).

In order to have independent training and test data sets and to limit spatial auto-correlation, we eliminated multiple occurrences such that a grid cell (0.5° by 0.5°) only contained a single occurrence point (see below). As a result, we have only 18 occurrence points (Table 1) despite the fact that more than 18 paleontological sites exist. Most of these localities are tightly clustered, especially in the Awash Valley and the Turkana Basin.

Table 1. Hominin occurrence points used in this study. The sites of Assa Issie (*Au. anamensis*), Aramis (*Ardipithecus* and *Au. anamensis*), Maka and Belohdelie (*Au. afarensis*) and Bouri (*Au. garhi*) all fall in the grid cell 'Middle Awash' because of their geographic proximity.

Occurrence point	Lon (°)	Lat (°)	Age (Ma)	Age reference
Koro-Toro	19.0	16.0	3.5—3	Brunet et al., 1995; Lebatard et al., 2008
Woranso-Mille	40.5	11.5	3.8—3.3	Deino et al., 2010; Haile-Selassie et al., 2012, 2015; Saylor et al., 2019
Hadar & Dikika	40.5	11.0	3.5—2.9	Behrensmeyer and Reed 2013; Alemseged et al., 2006
Middle Awash	40.5	10.5	4.2—3.4	White et al., 1993, 2006a; Renne et al., 1999
Galili	40.5	9.5	4.5—3.5	Kullmer et al., 2008
Usno	36.0	5.5	ca. 3.4	White et al., 2006b
Shungura	36.0	5.0	3.5—3	Brown et al., 2013
Fejej	36.5	4.5	4—3.6	Kappelman et al., 1996; Fleagle et al., 1991
Koobi Fora	35.5	4.0	4.3—2.7	Brown et al., 2013
Allia Bay	36.5	4.0	4.1—3.8	Behrensmeyer and Reed, 2013
Lomekwi	36.5	3.5	3.5	Leakey et al. ,2001
Lothagam	36.0	3.0	ca. 3.5	Leakey and Walker, 2003
Kanapoi	36.0	2.5	4.2—4	Leakey et al., 1998; Ward et al., 2013
Kantis	36.5	-1.5	3.5—3.4	Mbua et al., 2016
Laetoli	35.0	-3.5	3.8—3.4	Su and Harrison, 2008
Makapansgat	29.0	-24.0	3.4—2.6	Herries et al., 2013
Sterkfontein (member 2)	27.5	-26.0	3.6—3	Bruxelles et al., 2019
Taung	24.5	-27.5	3—2.6	Herries et al., 2013

2.4 Maxent climate envelope model and kuenm R package descriptions and set-up

We use the term "climatic envelope modelling" to describe our approach. This term expresses the idea that "a multivariate space of climatic variables best matching the observed species' distribution is being estimated" (Araujo and Peterson, 2012). It does not imply a direct link with Hutchinson's theory of ecological niches, as is the case with the term "ecological niche modeling". In this study, we assume that aspects of climate determine, at least in part, species distributions, and we do not interpret the resulting predictions within a strict ecological niche framework. The output from the Maxent model is termed habitat suitability index. This term of habitat should not be interpreted in the sense of microhabitat because the climatic data that we provide Maxent are at a large scale of 0.5° (i.e. roughly 2500 km^2). The term habitat suitability index should be understood as a measure of how suitable the large-scale environment was to the targeted African Pliocene hominins.

To model the climatic envelope, we use the Maxent algorithm (Phillips et al., 2006, 2017; Phillips and Dudik, 2008), which has shown to perform well compared to other correlative predictive architectures, especially when relying on limited occurrences datasets (e.g. Phillips et al., 2006; Elith et al., 2006; Hernandez et al., 2006). Maxent requires the geographic location of sites where the target species have been observed (i.e., fossil localities) and geographically continuous environmental variables over the region of interest, which are derived from the climate model described above.

Maxent is based on the maximum entropy principle such that the estimated probability distribution is constrained by climatic characteristic associated with the known occurrence localities while it avoids assumptions not supported by the data. Maxent is not a classical presence-absence modeling method, but rather a presence-background method as real absences are not known and cannot be taken into account during the sampling of environmental variables (Guisan et al., 2017). This approach to background sampling makes Maxent suitable for making distributional predictions based on paleontological data. Maxent will compare the probability distribution associated with presence occurrences with the one associated with background points randomly sampled in the environment. The area over which this comparison will be done (i.e. the calibration area) has a great influence on model performance. Its size should be neither too small or too large (e.g. VanDerWal et al., 2009), and should be biologically meaningful to ensure that the background points represent the environmental conditions accessible to the species (Anderson and Raza, 2010; Barve et al., 2011). The calibration area encompassing all occurrences points and used in Maxent models can be found in Appendix 1. Maxent, however, is known to be sensitive to model settings (e.g. parameterization, number of variables) that affect model complexity (Warren and Seifert, 2011; Peterson et al., 2018). The more complex a model is, the more likely it will be overfitted. The more overfitted a model is, the more it will struggle to extrapolate suitable habitats outside areas where occurrences are already known (Peterson et al., 2007).

In order to address this sensitivity and select the optimal parameterization, we employed the *kuenm* R package (Cobos et al., 2019) to produce and evaluate candidate models, as well as to perform final evaluations of the best models. We performed model calibration by testing the performance of 2210 candidate models. We produced these models using 26 distinct variable sets, made up of all unique combinations of two or more of the five climatic and vegetation variables from the Pliocene ‘mean’ climate simulation descibed below. The candidate models also employed one of 17 regularization multipliers (0.1–1 at intervals of 0.1, 2–6 at intervals of 1, as well as 8 and 10), and five feature classes or feature class combinations (q, qp, lp, lq, lqp; l=linear, q=quadratic, p=product). We based our evaluations of the candidate models' performance by first evaluating significance and predictive power using partial ROC (500 iterations, and 50% of data for bootstrapping; Peterson et al., 2008) and omission rate metrics. We then evaluated model complexity using the Akaike Information Criterion for small sample sizes (AICc) (Warren and Seifert, 2011). We retained model parameterizations that resulted in statistically significant models, resulted in omission rates lower than 5%, and ΔAICc values less than two. The parameters of these retained models were used to create final models with 10 replicates by bootstrapping. The complete *kuenm* R script that used the Pliocene 'mean' climate model is provided as an Rmarkdown document in Appendix 2. The final model was projected onto the sets of environmental conditions for each of the four precession angle configurations. During the process of model projection, we allowed free extrapolation given the response curves (i.e., response curves not truncated for at least two variables) observed during model calibration. In order to consider, the risks associated with strict extrapolation and to prevent misinterpretation of transferred areas with non-analogous conditions, we employed the mobility-oriented parity (MOP) metric (Owens et al., 2013). Following the approach suggested by Pearson et al. (2006) for small sample sizes, the simulated climatic envelope represents "regions that have similar environmental conditions to where the species is known to occur, and not as predicting actual limits to the range of a species", given that absence of proof is not the proof of absence (see Discussion). The lower threshold for hominin presence was set to the value of the lowesthabitat suitability index (fixed sensitivity; Peterson et al., 2011: p.119) score amongst the occurrence points.

The five variables used for predicting the envelope model are representative of mean climate and seasonality: Warmest Month Temperature (WMT), Coldest Month Temperature (CMT), Temperature Difference between the warmest and the coldest months (DT), Mean Annual Precipitation (MAP), and Driest Month Precipitation (DMP). Mean Annual Temperature (MAT), Wettest Month Precipitation (WMP), Precipitation Difference between the wettest and the driest months (DP) and Net Primary Productivity (NPP) were excluded from the final analysis, following the recommendations of, e.g. Merow et al., (2013), because they contributed only marginally to the definition of the climatic envelope and were highly correlated to the employed variables. The candidate models used to build the final model do not necessarily include all of the five selected variables as model overfitting increases with the number of employed environmental variables (Guisan et al., 2017).

Given the chronological uncertainty associated with hominin fossil contexts and the temporal span of the targeted period, we cannot associate specific fossils or groups of fossils with a particular orbital configuration. The most conservative choice is to use the least extreme orbital configuration—Pliocene 'mean' climate—to estimate a climatic envelope. With this configuration, eccentricity is small thereby favoring lower seasonality and lower climatic variability linked to precession. To detect suitable areas that remained stable across the four precession configurations (i.e. refugia), we thresholded the final model and each projection by reclassifying as non-suitable (i.e. 0) all grid cells with suitability scores lower than the lowest value amongst the occurrence points. Next, suitability scores were grouped into three equal categories (low-, mid- and high-suitability areas) to facilitate the reading of the models' geographic projections and prevent direct interpretations of suitability values. Finally, a binary model was computed by reclassifying all suitable grid cells as one and non-suitable cells as zero. We then compared the four obtained binary predictions with the main Pliocene 'mean' climate model to reveal temporally stable areas of suitability.

2.5 Temporal and spatial sampling sensitivity tests

In order to test the sensitivity of our climatic envelope model to the chosen temporal window with respect to occurence sampling, we replicated the approach described above by removing the oldest and most recent Australipthecus taxa from the dataset (i.e. *A. anamensis*, *A. africanus, A. prometheus*). The localities, Lomekwi, Kanapoi, Makapansgat, Sterkfontein and Taung, are removed from model computation, resulting in the loss of all South African occurrences. The map of habitat suitability corresponding to this sensitivity test is available in Appendix 1. As recommended for small occurrence datasets (Pearson et al., 2006; Shcheglovitova and Anderson, 2013), we used a delete-one jackknife approach (or leave one out approach) to evaluate the influence of individual occurence on predictive variability. We removed one locality from the dataset, computed the model with $n - 1$ localities in *kuenm* and repeated this process until every locality have been removed once (i.e. n separate models for *n* observed localities). The *n* projections of these *n* models, as well as a consensus of all projections, are available in Appendix 1.

3. Results

3.1 Climate model validation

First, we assess the validity of the climate model at hominin sites by comparing paleoenvironmental reconstructions to the biome simulated with the BIOME4 model using IPSL-CM5A climate variables (see Supplementary Material). Vegetation reconstructions at hominin sites describe a seasonal, dry mosaic of woodland, shrubland and grassland (Behrensmeyer and Reed, 2013 and references therein), with small-scale more mesic environments sustained by local water resources (e.g. microhabitats sustained by rivers, lakes and springs; see Barboni et al., 2019). The BIOME4 model indicates tropical xerophytic shrubland, tropical savannah, or tropical deciduous woodland at 16 of the 18 hominin localities (Fig. 1, see also Methods). In the BIOME4 model, productivity is higher in tropical deciduous woodland (Kantis locality) than in tropical savannah (Usno and Laetoli localities), and in tropical savannah than in tropical xerophytic shrubland (e.g. Awash Valley, Koro-Toro locality), but the same plant functional types are present in these three biomes. These biomes describe a mix of tropical raingreen trees, C_4 tropical grass, and woody desert plant functional types (C_3 and C_4) that correspond to a warm, seasonally dry climate, which is in good agreement with the mosaic of woodland, bushland and grassland inferred from vegetation reconstructions, although local-scale water sources are invisible to the model.

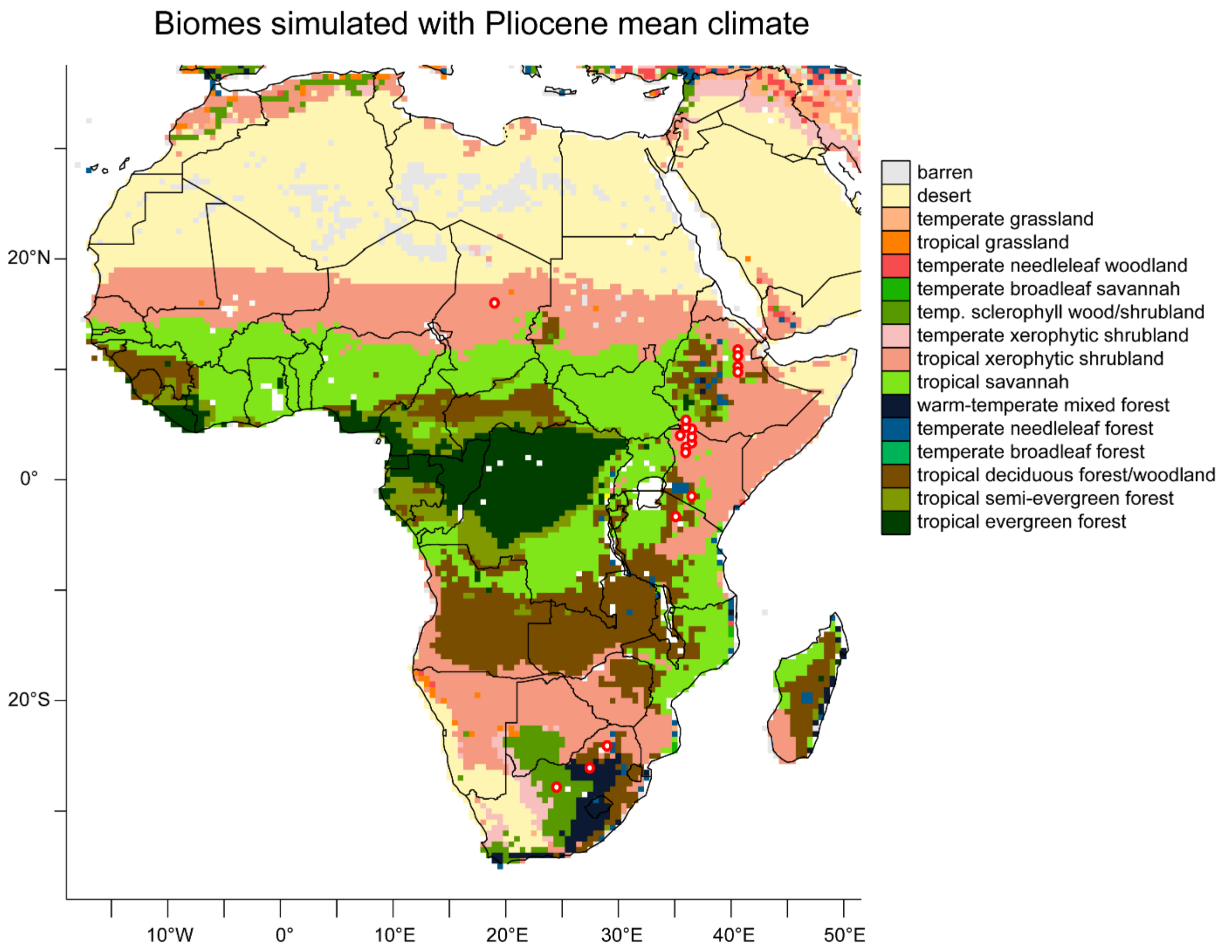

Figure 1. Vegetation simulated with BIOME4 for the Pliocene mean climate. Red circles are the 18 hominin occurrence points.

3.2 Hominin climatic envelope estimations and robustness

At a regional scale, the highest habitat suitability areas reconstructed by the climatic envelope model are located in tropical eastern Africa, except over eastern Somalia and western Ethiopia (Fig. 2). The Turkana Basin, areas west of Lake Victoria, as well as a region covering southern Somalia, eastern Kenya and northern Tanzania (including Laetoli and coastal regions, hereafter called the SKT region), and finally western Eritrea, northern Somalia-Djibouti and eastern Ethiopia (including the Awash valley) are the most climatically suitable regions for *Australopithecus*. Three other regions show reasonable habitat suitability indices. The first is a latitudinal corridor at ca. 15°N, covering Africa from the Atlantic coast to the Red Sea, at roughly the latitude of Lake Chad. This Sahelian corridor suggests a probable continuity of environmental conditions between the Awash valley and the Lake Chad region, with the potential for population dispersals within this corridor. The second area of interest is located in South Africa, southwestern Angola, Botswana, non-coastal Namibia, southern Mozambique, and southeastern Zimbabwe. This area is not connected to eastern Africa in our model, suggesting that population dispersals to or from this southern African area would not have been possible under mean Pliocene climate conditions. The last area is located on the African Mediterranean coast, including the locality of Ain Boucherit, where no Pliocene hominins have been recovered to date, but where stone artefacts and cut-marked bones dating to ca. 2.4 Ma are documented (Sahnouni et al., 2018). Our geographic coverage also includes southern regions of Eurasia (e.g. Yemen, Israel, Jordan, parts of southern Europe) for which habitat suitability attains values suggesting that mid-to-late Pliocene hominins could have survived in these regions if they had been accessible. After *kuenm* calibration process, the final model meeting significance and complexity requirements (of 2210 candidate models) is based on two of the five available variables: the temperature difference between the warmest and the coldest month (DT) and mean annual precipitation (MAP). All hominin occurrences are located in regions where annual precipitation is below 800 mm/yr with a marked dry season and limited annual thermal amplitude (up to 15°C; Fig. 3) inside semi-arid zones (BS in the Köppen-Geiger classification, Peel et al., 2007).

Sensitivity tests on the occurrence data (i.e., leave one out approach) reveal that habitat suitability in the Sahelian corridor is not governed by a single locality, not even Koro-Toro located in central Sahel, while the suitable area in northern Africa is a result of climatic similarities to occurrence points located in eastern Africa (e.g. the Middle Awash) or in southern Africa (e.g. Taung; see Suppl. Fig. 1). The Allia Bay locality in Kenya has the strongest influence on suitability scores in the Sahelian corridor, but even its removal is insufficient to make this pattern disappear. The consensus map (see Suppl. Fig. 1), which combines all the sensitivity tests, demonstrates the robustness of the depicted pattern for hominins in Pliocene ‘mean’ climate (Fig. 2) by preserving the three main areas of suitable habitats (i.e. eastern, southern Africa, and the Sahelian corridor).

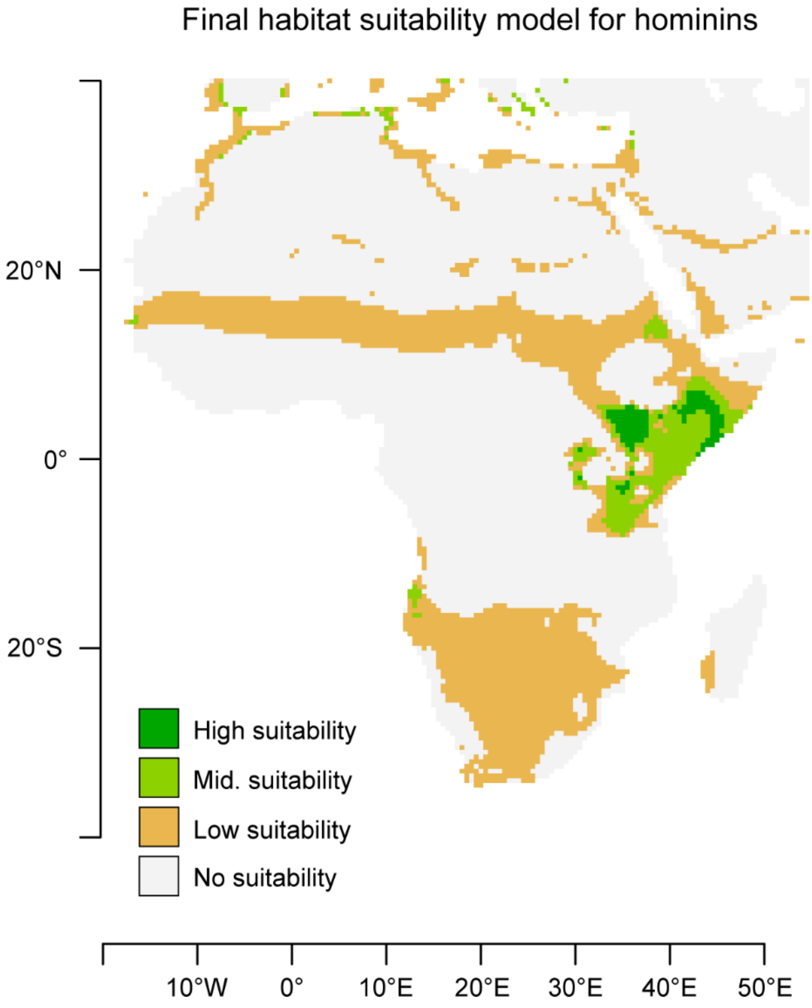

Figure 2. Habitat suitability index for hominins under the Pliocene mean climate scenario. All values above the lowest presence threshold are shown (see Methods). Low suitability regroups cells with habitat suitability values ranging from 0.08–0.36; middle suitability range from 0.36–0.63; and high suitability is assigned to cells with values over 0.63. The final *kuenm* model is based on the DT and MAP variables.

The sensitivity test conducted via temporal sampling (i.e. the removal of youngest and oldest species; see Suppl. Fig. 2) demonstrates the robustness of the climate envelope modeled with all selected occurrences (Fig. 2). We performed this test without the three localities from South Africa and nevertheless the same areas remain suitable for hominins. The main differences between this sensitivity test and the main model are the absolute suitability values in suitable areas. In southern Africa, the eastern coast depicts middle and high suitability in the sensitivity test while in the main model these areas are associated with low suitability scores. In northern Africa and the European Mediterranean coast, suitability values are higher in the test, while conversely the areas of middle and high suitability in eastern Africa are more geographically limited than in the main model.

Our results show that eastern and southern Africa were not connected, with respect to suitability, under Pliocene mean conditions. However, we know that *Australopithecus* was present both in eastern and southern Africa, indicating that either: 1) climate variability allowed them to cross this environmental barrier; or 2) they were able to reach/occupy both regions because their niche was in fact broader or because they attempted long-range dispersal across climatically unsuitable areas. In an effort to evaluate the first hypothesis, we further examined potential geographic variability of suitable areas for mid-to-late Pliocene hominins caused by orbital precession changes.

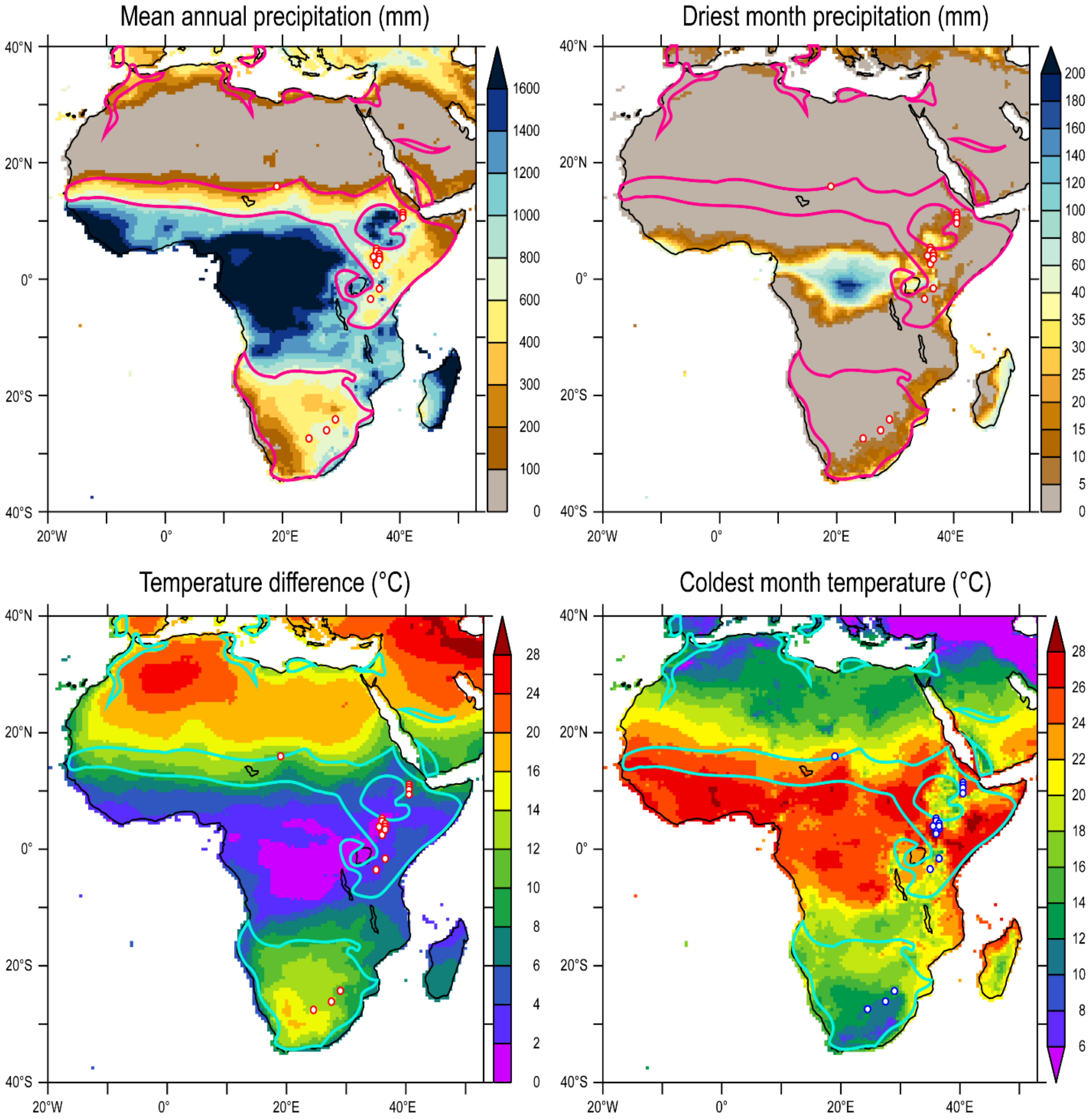

Figure 3. Mean annual precipitation (MAP), driest month precipitation (DMP), temperature difference between the coldest and warmest months (DT), and coldest month temperature for the Pliocene (CMT). Areas suitable for hominins from figure 2 are outlined. MAP and DT are the variables composing the "best" parameter setting selected after model calibration.

3.3 *Orbitally driven climate variability and potential dispersals*

We projected the climatic envelope estimated from Pliocene mean climate conditions onto four Pliocene climate scenarios simulated with summer and autumn insolation maxima and minima (Figure 4, Suppl. Fig. 3-6). This provides examples of the potential ability of Pliocene hominins to disperse

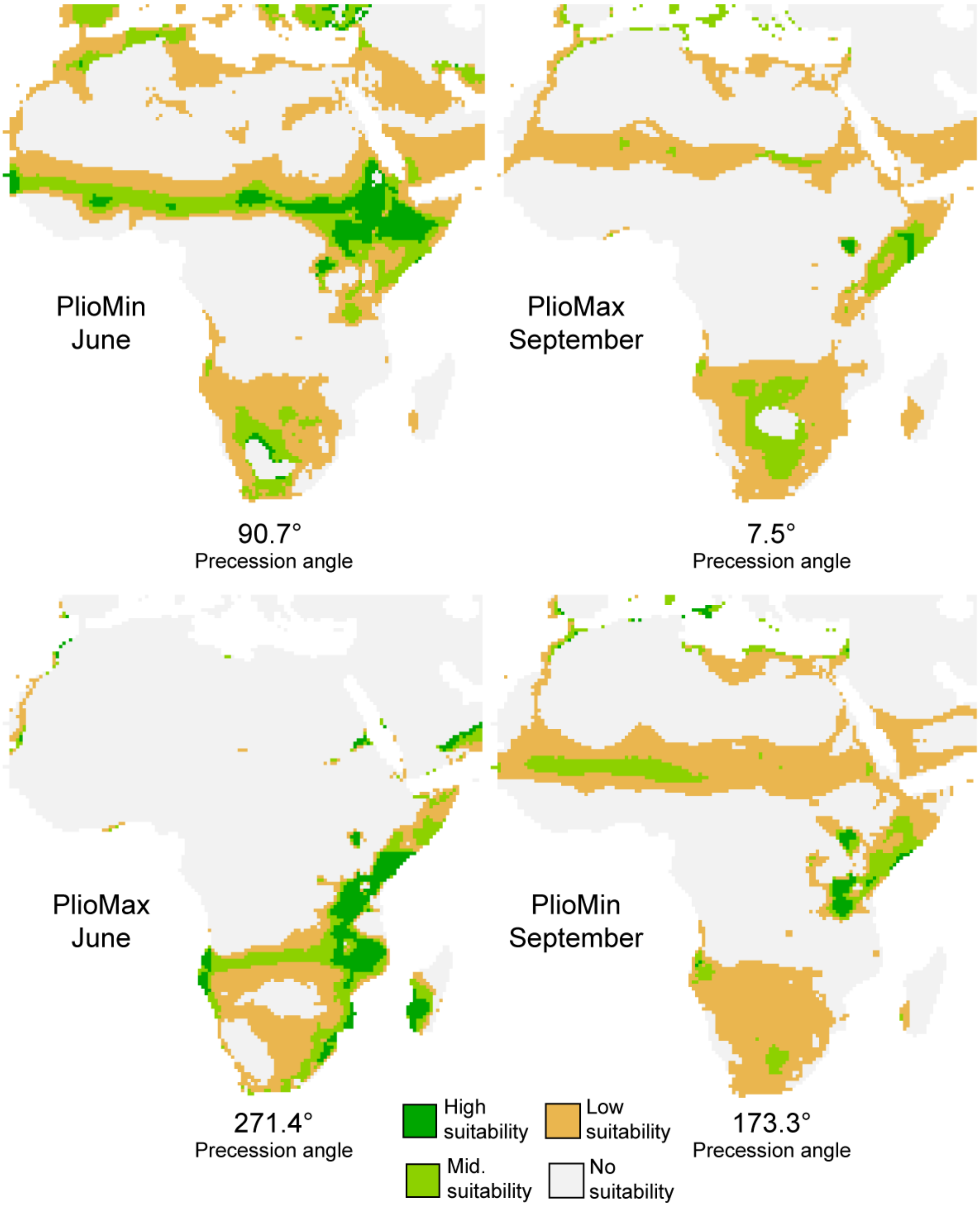

Figure 4: Projections of the final model computed with the Pliocene mean configuration onto four orbital precession configurations (see Methods). PlioMax June with a precesion angle of 271° is the most distant configuration from Pliocene 'mean' climate (i.e. 100.04°), whereas PlioMin June is the closest (90.74°).

geographically during specific climate scenarios driven by orbital precession variability—dispersals that would not necessitate them changing the environmental conditions they exploited.

During periods of boreal summer or autumn insolation maxima (PlioMax June simulation and PlioMax September simulation, respectively), the Afar region and a large portion of eastern Africa are unsuitable, except for the Turkana region and the SKT region (including the Laetoli and coastal regions) (Fig. 4). During these periods, the tropical rain belt is located further north. The Sahelian band of suitability is shifted north of Koro-Toro (Suppl. Fig. 5) into the present-day Sahara for PlioMax September, and it is totally absent for PlioMax June. There remains a large unsuitable area between Laetoli (the southernmost eastern African site) and Makapansgat (the northernmost southern African site) for three of the configurations. However, in the PlioMax June projection (i.e. boreal summer maxima), a continuous zone of middle and high climatic suitability between eastern and southern Africa emerges (Fig. 4, bottom left), which would have allowed hominin dispersal to/from the south. Variations in precession angle could therefore be a potential factor controlling the emergence of corridors permitting the dispersion of ancient hominins between eastern and southern Africa along the Kingdon line (Kingdon, 2003; Joordens et al., 2019). During periods of boreal summer insolation minima (Fig. 4, top left, PlioMin June), the habitat suitability indices becomes high in the northern part of the African rift, particularly in the Ethiopian highlands, down to the Baringo locality and also extend down to Laetoli through the SKT region. Suitability in the Sahelian band increases strongly and shifts southward following the tropical rain belt. Three areas remain above the lowest presence threshold for all orbital configurations and can therefore be considered true core areas or refugia (Fig. 5)—the Turkana Basin, the SKT region, and a vast portion of southern Africa. To the contrary, the Sahelian band and the Awash Valley remain suitable in some, but not all, of the four climate scenarios.

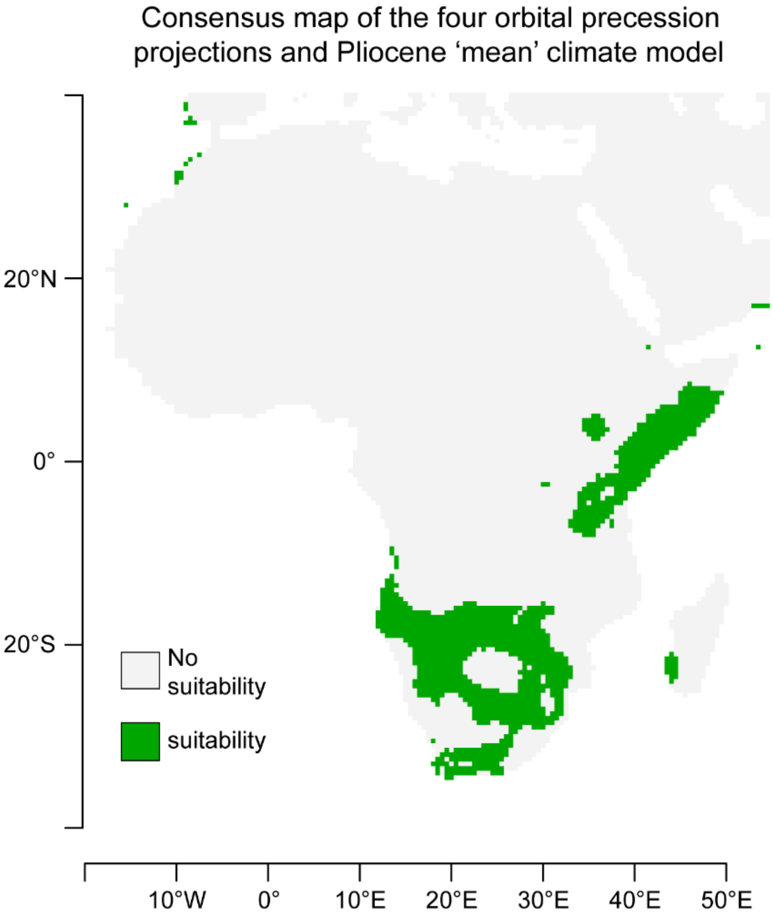

Figure 5: Refuge areas. Consensus map based on the final climatic envelope's suitable areas estimated with Pliocene 'mean' climate (Fig. 2), as well as with the four orbital precession configurations (Fig. 4).

4. Discussion

4.1 Australopithecus *in semi-arid climate*

From the late Miocene onwards, early hominins were not found in sites sampling densely forested environments nor shadowless plains, but instead are known from more or less wooded, mosaic habitats (see Sponheimer 2013). The earliest known hominin, *Sahelanthropus tchadensis*, lived in a Sahelian-like mosaic landscape close to lake settings (Vignaud et al., 2002; Le Fur et al., 2009; Blondel et al., 2010; Novello et al., 2017). The early Pliocene hominins *Ardipithecus ramidus* and *Ardipithecus kadabba* are also thought to have lived in an open, wooded savannah biome (Levin et al., 2008; White et al., 1994, 2009; Cerling et al., 2011), within which they occupied localized forested micro-habitats sustained by springs (WoldeGabriel et al., 2009; Barboni et al., 2019). However not all early hominids are associated with savannahs, *Orrorrin* lived in an open deciduous forest, punctuated by very wet areas (Bamford et al., 2013; Senut, 2020).

By the late Pliocene, *Australopithecus* occupied open landscape environments. Pliocene hominin localities of the Lower Awash Valley and the Turkana Basin had mammal communities corresponding to a climate for which precipitation was low (inferior to 800–1000 mm/yr) and temperature seasonality was pronounced (Robinson et al., 2017). Our model suggests that these populations occupied regions characterized by a semi-arid climate (dry and seasonal with moderate thermal amplitude) and environments that would have been more or less wooded depending on surface and sub-surface water availability. Blumenthal et al. (2017) postulate that variable climatic conditions in the Turkana Basin, within the range of present-day environments, were already present at 4.2 Ma, suggesting that the region's hominins were already occupying (semi-)arid areas with soil temperatures of approximately 30–35°C (Passey et al., 2010). Sponheimer (2013) also states that the australopithecine masticatory apparatus was adapted to abrasive food already by 4 Ma, implying that they could rely on (although perhaps only seasonally) xerophytic tubers which are found in arid environments and can contain up to 70% water. A re-examination of Turkana *Au. anamensis* has shown that C_4 biomass composed up to 30% of their diet, suggesting increased foraging in open landscapes already by 4 Ma (Quinn, 2019). An increased proportion of C_4 foods in the hominin diet occurs at 3.8 Ma (Uno et al., 2016), and *Au. bahrelghazali* was also dependent of C_4-derived resources (Lee-Thorp et al., 2012). At Hadar, *Au. afarensis* was a mixed C_3/C_4 feeder and coped with ecological changes via "… a highly varied intake of C_4 foods" (Wynn et al., 2016). Recent dental analyses of *Au. africanus* also reveal that this species faced seasonal dietary stress (Joannes-Boyau et al., 2019). Finally, our results show that the climate envelope of mid-to-late Pliocene hominins largely overlaps with semi-arid climates, but also includes more temperate climates. This agrees with Behrensmeyer and Reed (2013) who consider that *Australopithecus* could survive "considerable seasonal temperature" variations, thus suggesting that they possessed enhanced thermoregulatory capacities (Lieberman, 2015). This is a step towards the genus *Homo*, which appears to have been adapted to even more arid climates (DiMaggio et al., 2015; Robinson et al., 2017).

4.2 Hypotheses on the paleobiogeography of Australopithecus

Dispersal events during the Pliocene are thought to have strongly influenced the paleobiogeography of *Australopithecus* (Foley et al., 2013). Our results support this hypothesis by indicating that australopithecines in Chad, eastern Africa and South Africa faced similar climatic conditions. However, dispersal between eastern Africa and southern Africa appears to have been possible only during periods of extreme summer insolation (PlioMax June), when the Lake Malawi basin would have been dry enough to create continuous semi-arid environments (Fig. 4 and Suppl. Figure 5). To the contrary, *Au. bahrelghazali*, *Au. afarensis*, and *K. platyops* could have dispersed between the Turkana Basin, Laetoli and the SKT region, the Awash Valley and central Sahel—with the Turkana basin and the SKT region remaining suitable during periods of extreme insolation forcing. Isolation of some regions (e.g., the Turkana Basin and SKT regions serving as refugia), induced by climate and vegetation changes driven by orbital forcing, would have isolated animal populations (including hominids) and reduced gene flow, thus fostering allopatric speciation by vicariance. This would explain the highest levels of species diversity in eastern Africa in that distinct species could develop during periods when the two regions were not connected, and later disperse during periods when they were environmentally linked. Comparing the habitat suitability map to the vegetation model (Figs. 1 and 2), it is evident that areas of suitability correspond primarily to those where the simulated biome is tropical xerophytic shrubland (represented in pink in Fig. 1), although the two maps are not strictly superimposable. This environment is typically present along woodland margins (fringe environments), corresponding to the hypothesis that *Australopithecus* was an edge (or ecotonal) adapted genus (Sussman and Hart, 2015), as suggested for early Pleistocene *Paranthropus robustus* (Caley et al., 2018).

According to our results, the coastal regions of southern Somalia and eastern Kenya would have been suitable even during extreme insolation changes (Fig. 5). This region is included in the extent of the coastal mosaic forest proposed by Kingdon (2003) and Joordens et al., (2019) (the coastal ape hypothesis). However, our vegetation model does not reproduce forest in this area, but rather tropical xerophytic shrubland (this biome does contain the tropical raingreen tree plant functional type); our model also supports the hypothesis that *Australopithecus* did not live in forest contexts, but rather in semi-arid zones. Small-scale patches of gallery forest could have been favoured by local conditions in this area, without being visible in the model, since the coastal forest at present only measures a few tens of kilometres of width at its maximum extent. The fact that occurrence points of Pliocene *Australopithecus* are located in semi-arid areas, which were already semi-arid areas during the Pliocene, does not mean that these species were restricted solely to these areas, since it remains possible that fossils have not been observed elsewhere. Our model, which effectively indicates areas where remains have been recovered, does predict that this region of southern Kenya and northern Tanzania had some tropical trees, and was climatically favourable for *Australopithecus* during the Pliocene even across climate changes linked to orbital precession variability.

5. Conclusions

During the mid-to-late Pliocene, different hominin species are identified in Africa at localities that are geographically separated (central Sahel, eastern Africa and southern Africa). When using a climatic envelope model, the estimated areas suitable for mid-to-late Pliocene hominins cover most of eastern Africa, the Sahelian corridor from the Atlantic coast to the Red Sea, large portions of southern Africa, and a restricted portion of the African northwestern Mediterranean coast. The climatic envelope associated with these areas is predominantly characterized by strongly seasonal precipitation and annual thermal amplitude up to 15°C, in accordance with the two variables selected by the kuenm R package to create the final model (i.e., mean annual precipitation and thermal amplitude between coldest and warmest month). The estimated envelope is geographically continuous between eastern Africa and the Lake Chad region, while a similar pattern is not observed between eastern Africa and southern Africa, suggesting that this environmental barrier was crossed during periods of extreme summer insolation maxima or that hominins had a broader climatic envelope than the one estimated with our occurrence data. The Turkana Basin, the region covering southern Somalia, eastern Kenya and northern Tanzania (including Laetoli and coastal regions), and a vast portion of southern Africa remain suitable during periods of orbital variability, contrary to the Sahelian corridor and the Awash valley. Those refugia are located in eastern and southern Africa and are only connected during certain orbital configurations, potentially explaining the diversity of hominin species observed in eastern Africa at that time.

Further studies could improve our results, notably, due to the scarce nature of presently available data, but this is certainly a long-term perspective. For the immediate future, the increased capability of climate models to simulate Pliocene conditions via PLIOMIP2 (Haywood, 2020; Tan et al., 2020; Zhang et al., 2020) warrants pursuing.

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Climate-inferred distribution of mid-to-late Pliocene hominins

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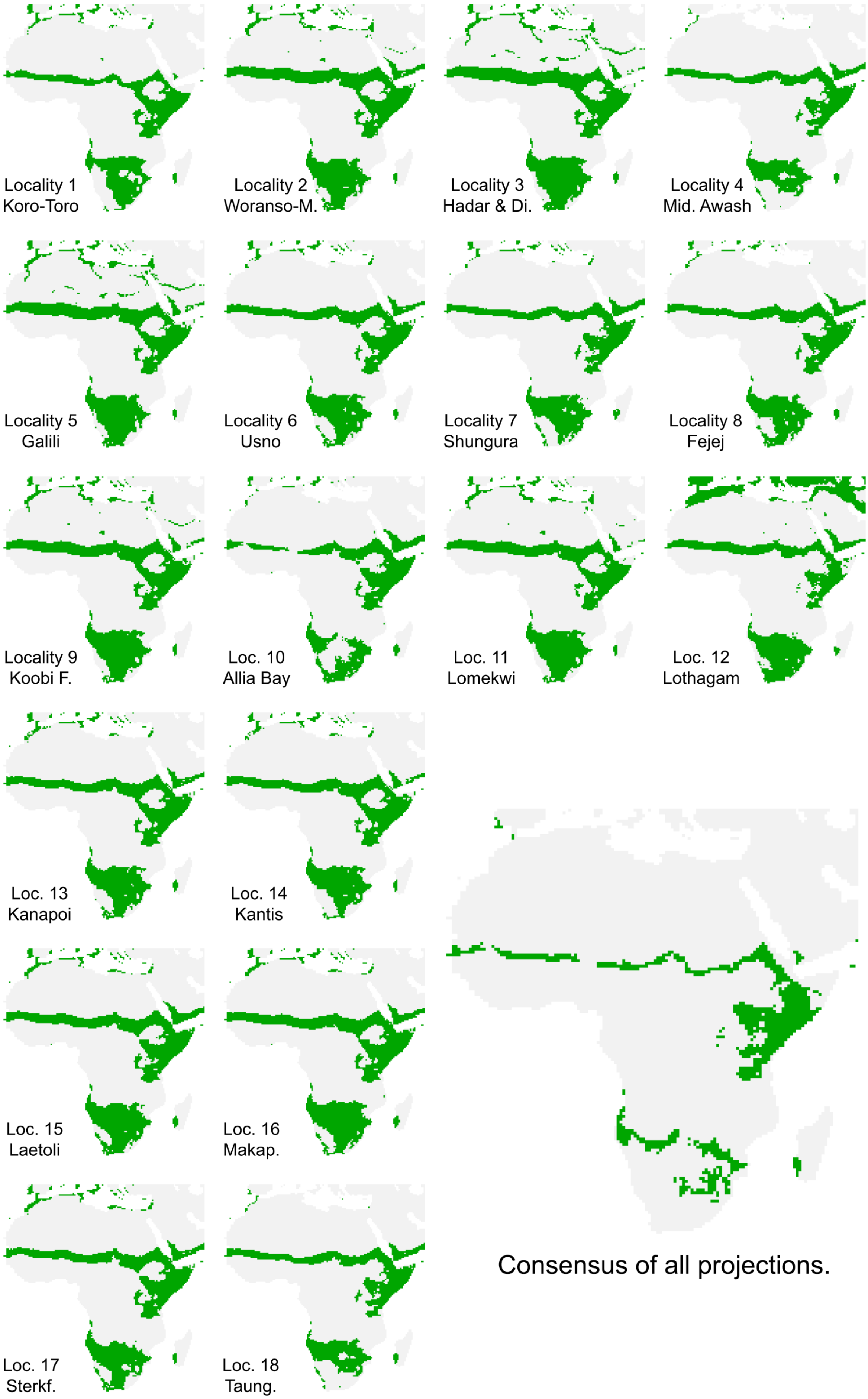
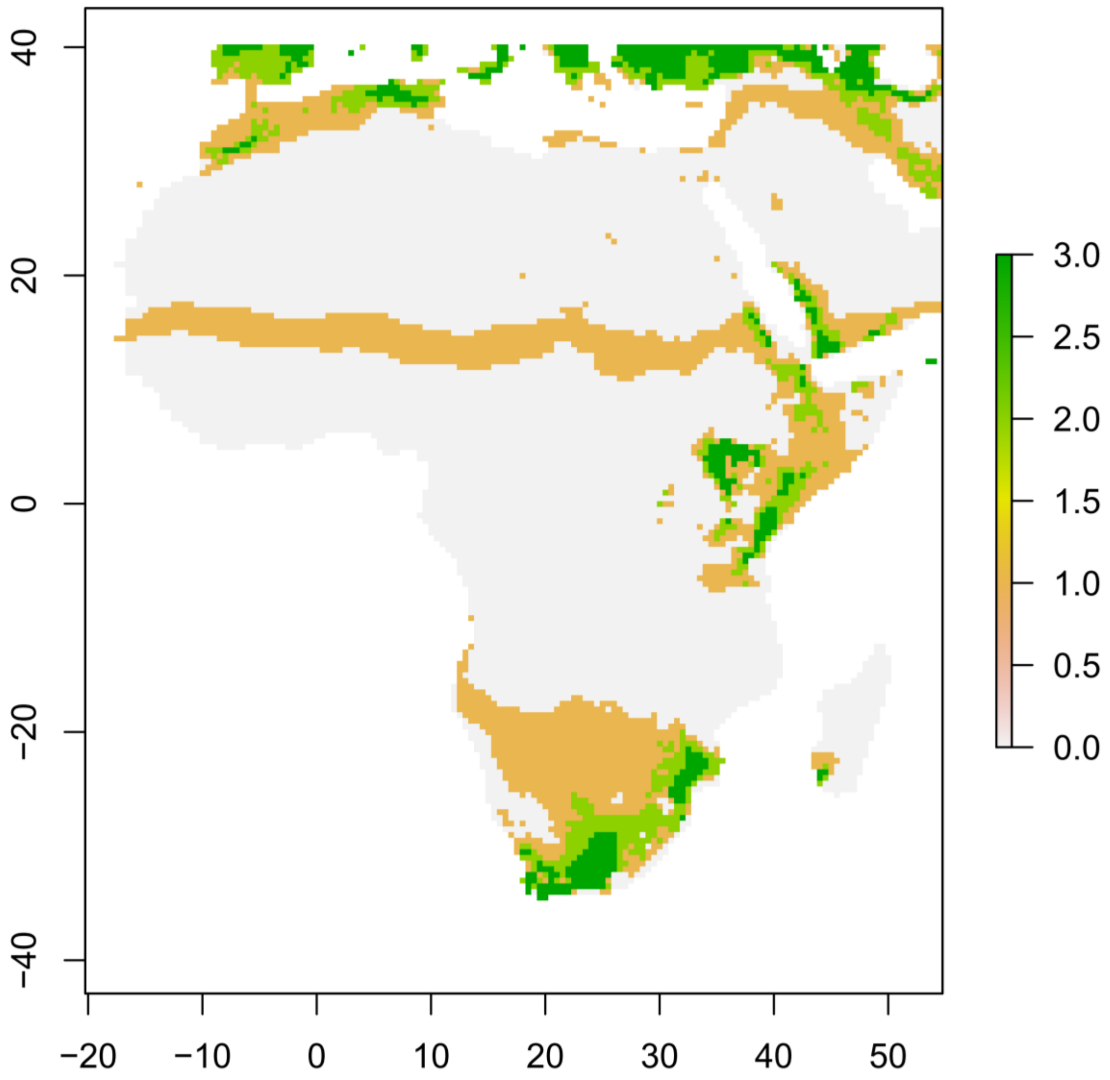
Appendix 1

Supplementary Figures 1 to 8

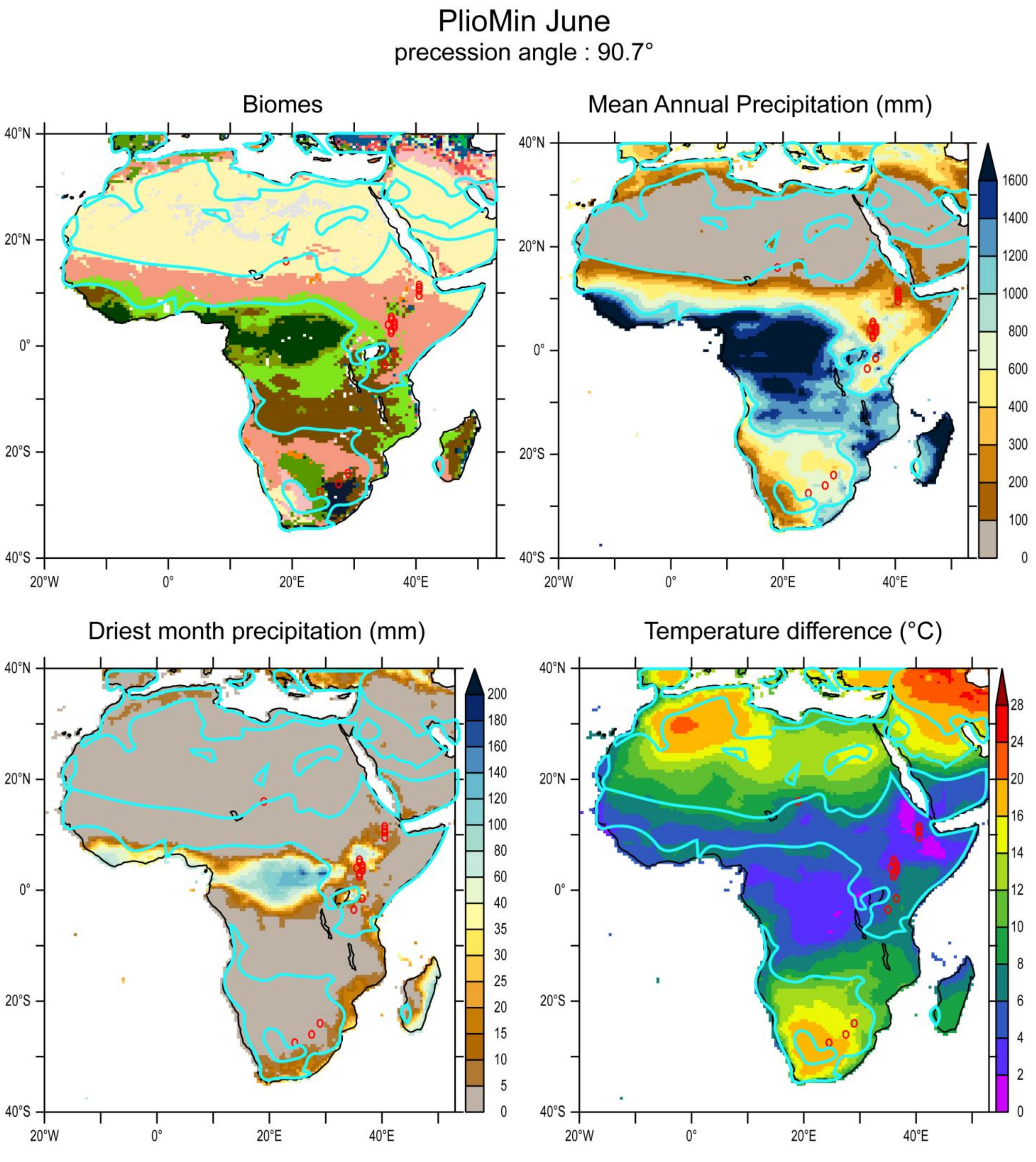
Supplementary Table 1



Supplementary Figure 1. Binary map (green for suitable areas) for the 18 jackknife kuenm final models. Named locality is removed, number refers to Table 1. Map in the bottom right is the consensus map of the 18 final models.



Supplementary Figure 2. Sensitivity test on temporal window of sampling. Au. *anamensis*, Au. *prometheus* and Au. *africanus* are removed resulting in the removal of the three localities from southern Africa. HSM obtained with KUENM and Maxent algorithms. Climatic layers are Pliocene ‘mean’ climate.



PlioMin June

precession angle : 90.7°

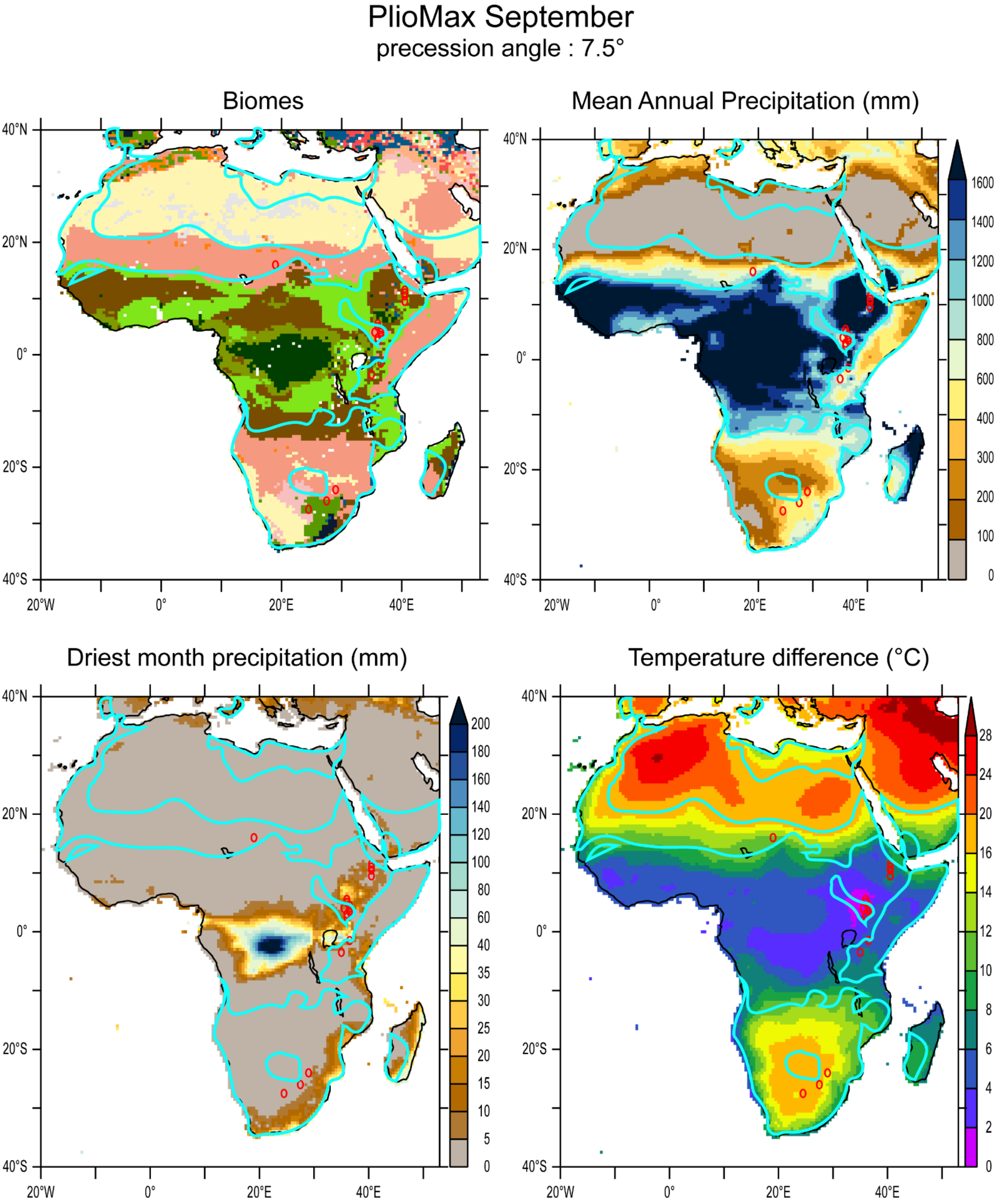
Biomes

Mean Annual Precipitation (mm)

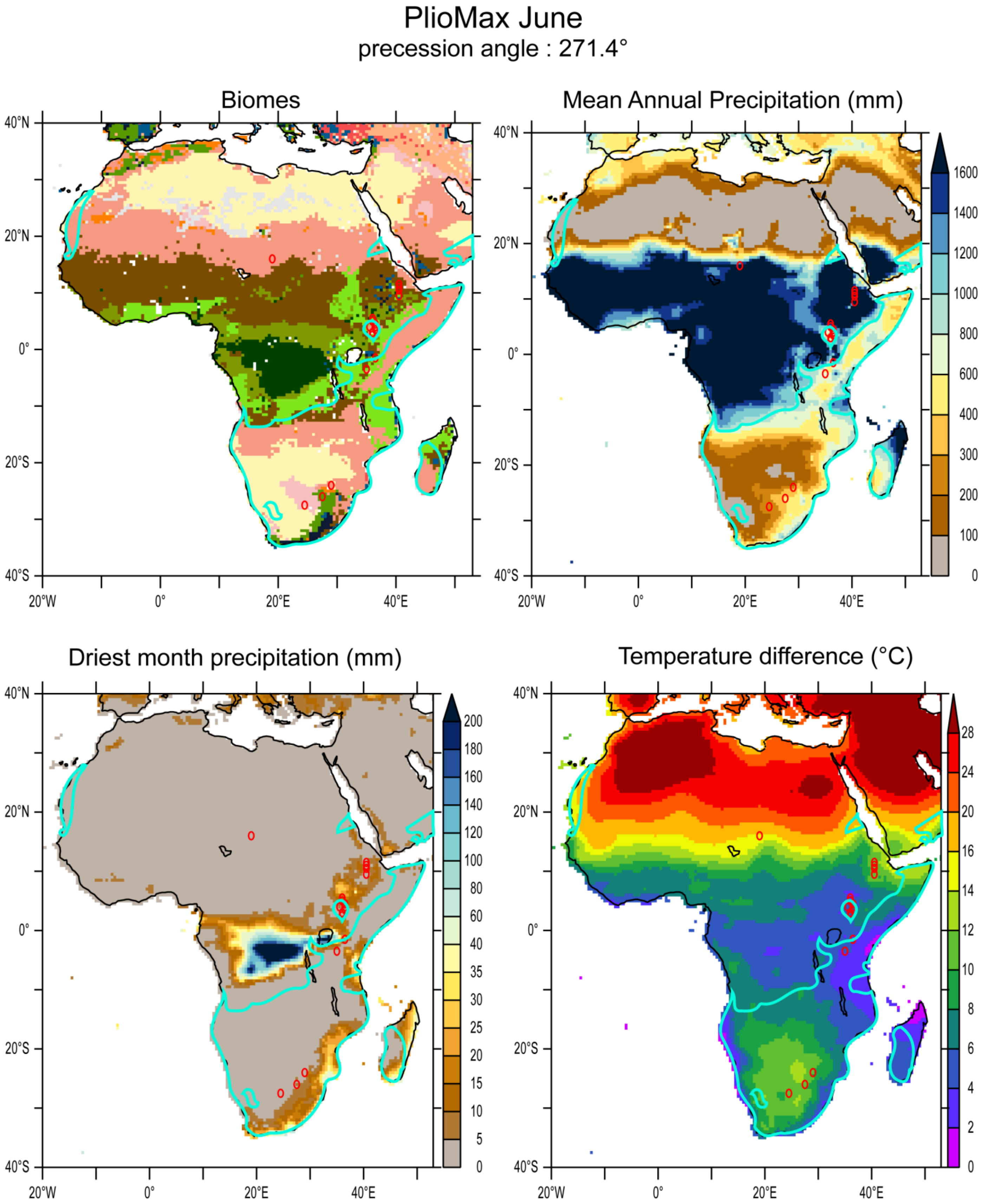
Driest month precipitation (mm)

Temperature difference (°C)

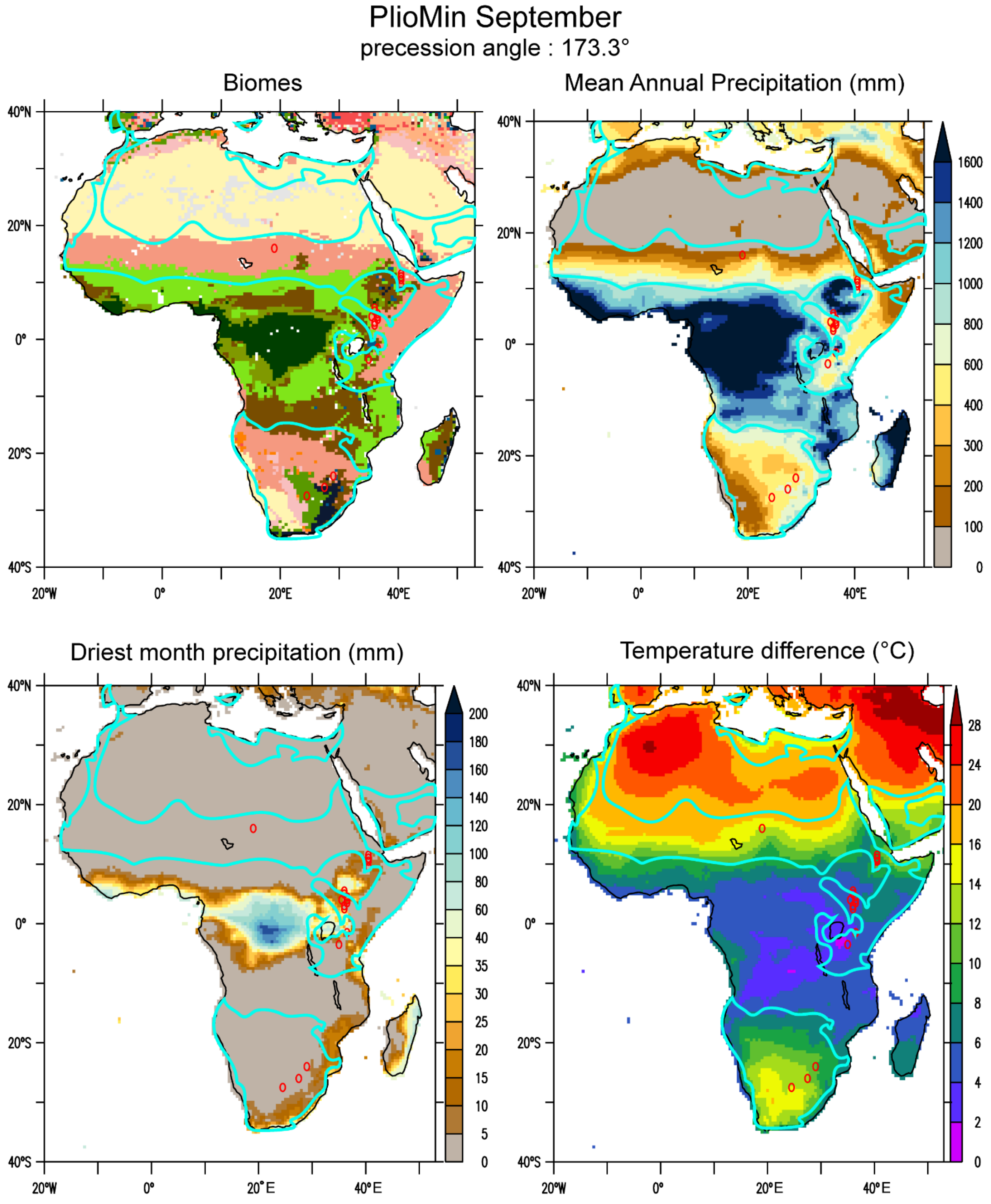
Supplementary Figure 3. Biomes, Mean annual precipitation (MAP), driest month precipitation (DMP), temperature difference between the coldest and warmest months (DT). Areas suitable for hominins from figure 4 PlioMin June final model are marked by contours.



Supplementary Figure 4. Biomes, Mean annual precipitation (MAP), driest month precipitation (DMP), temperature difference between the coldest and warmest months (DT). Areas suitable for hominins from figure 4 PlioMax September final model are marked by contours.

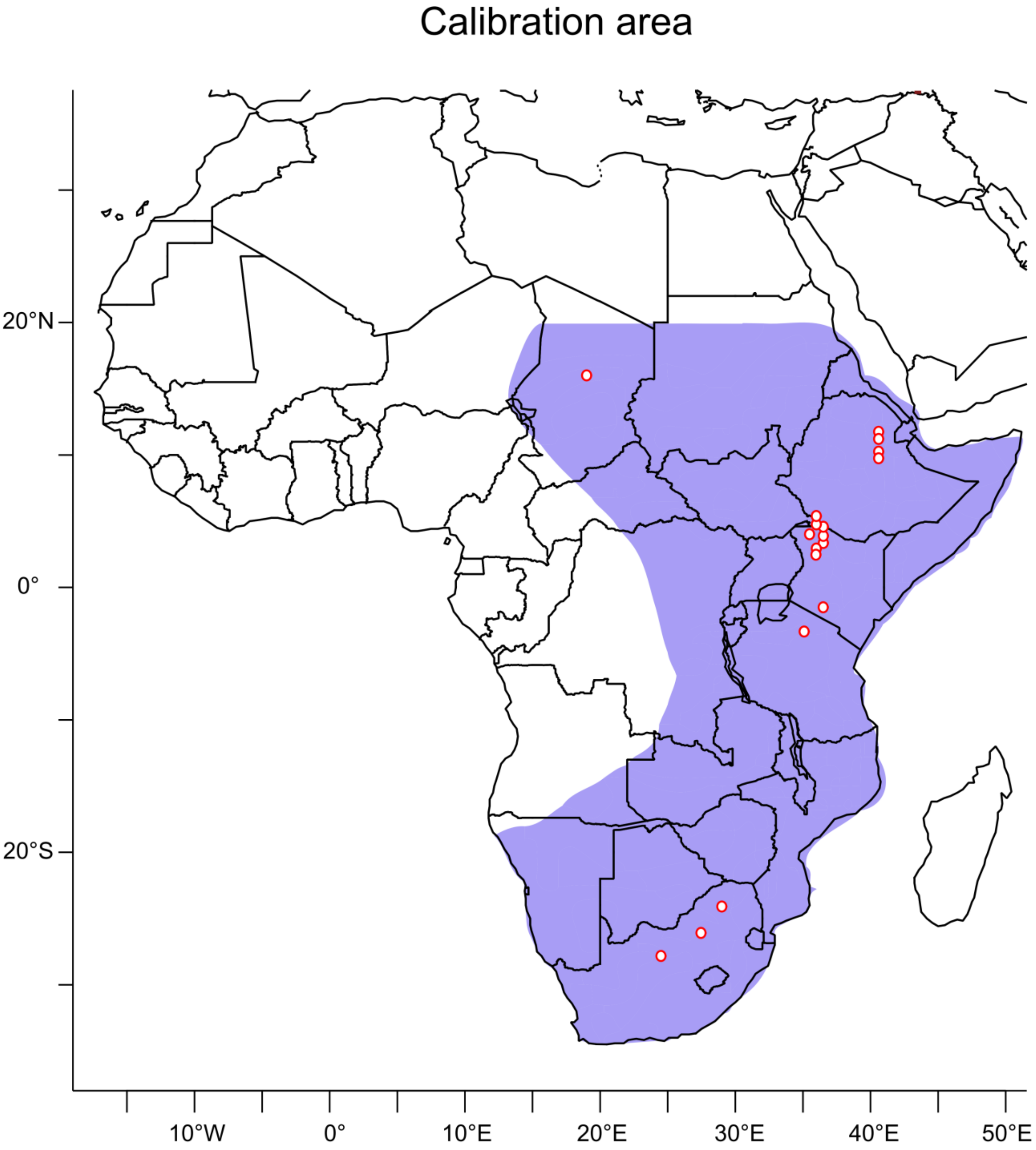


Supplementary Figure 5. Biomes, Mean annual precipitation (MAP), driest month precipitation (DMP), temperature difference between the coldest and warmest months (DT). Areas suitable for hominins from figure 4 PlioMax June final model are marked by contours.



Supplementary Figure 6. Biomes, Mean annual precipitation (MAP), driest month precipitation (DMP), temperature difference between the coldest and warmest months (DT). Areas suitable for hominins from figure 4 PlioMin September final model are marked by contours.

Supplementary Figure 7. Orbital eccentricity, June solstice and September equinox insolation at 30°N from 3 to 4 Ma (Laskar 2004). Red lines represent the values used for the Pliocene 'mean' climate (present-day values). Red stars indicate values chosen for orbital climate simulations.



Supplementary Figure 8. Calibration area. The purple area is used to compute KUENM-Maxent model, the probability distribution associated with occurrences is compared with background points randomly sampled in the environment within calibration area. It should encompass all occurrences points, but should not be too large to avoid model overfitting.

Supplementary Table 1. Model-data comparison at hominin sites.

Site	Modeled biome	Data-inferred paleovegetation	Water resource
Koro-Toro	Tropical xerophytic shrubland	Gallery forest, wooded savannah, open grassland (Fara et al. 2005, Novello et al. 2017)	Freshwater lake (Schuster et al. 2009, Novello et al. 2017)
Woranso-Mille	Tropical xerophytic shrubland	Swamp, open woodland, grassland (Behrensmeyer & Reed 2013), riparian forest (Saylor et al., 2019)	River, springs (Haile-Selassie et al. 2007, Barboni et al. 2019), lake (Saylor et al., 2019)
Hadar & Dikika	Tropical xerophytic shrubland	Tropical xerophytic shrubland (Bonnefille et al., 2004), open grassland (Behrensmeyer & Reed 2013)	River, lake (Taieb et al., 1975)
Middle Awash	Tropical xerophytic shrubland	Grassy woodland-bushland (Behrensmeyer & Reed 2013)	
Galili	Tropical xerophytic shrubland	Woodland to bushland with some open grassland (Behrensmeyer & Reed 2013, Kullmer 2008)	
Usno	Tropical savanna	Ecotonal environment at the edge of woodland and grassland (Bobe 2011)	River (Bobe 2011)
Shungura	Tropical xerophytic shrubland	Same as Usno	Same as Usno
Fejej	Tropical xerophytic shrubland	unknown	
Koobi Fora	Tropical xerophytic shrubland	Tropical savannah (Salzmann et al. 2008)	Floodplain (Behrensmeyer & Reed 2013)
Allia Bay	Tropical xerophytic shrubland	Seasonal, mosaic of woodland-grassland (Behrensmeyer & Reed 2013)	
Lomekwi	Tropical xerophytic shrubland	Tropical deciduous woodland (Salzmann et al. 2008)	Fluvio-lacustrine (Boyd et al. 2018)
Lothagam	Tropical xerophytic shrubland	Dry and seasonally open (Behrensmeyer & Reed 2013)	
Kanapoi	Tropical xerophytic shrubland	Grassy woodland (Quinn & Lepre 2018), shrub savannah (Head & Muller 2018)	Lake, river margin (Head & Muller 2018)
Kantis	Tropical deciduous woodland	Mosaic of woodland, shrubland, grassland (Mbua et al. 2016)	
Laetoli	Tropical savanna	mosaic of woodland, bushland, shrubland, grassland (Su & Croft 2018)	River margin (Su & Croft 2018), probable springs (Barboni et al. 2019)
Makapansgat	Tropical xerophytic shrubland	Mosaic of riparian woodland, bushland, edaphic grassland (Reed 1997)	River or spring (Behrensmeyer & Reed 2013)
Sterkfontein	Warm mixed forest	Temperate sclerophyll woodland (Salzmann et al. 2008), riparian forest, bushland (Behrensmeyer & Reed 2013)	
Taung	Temperate sclerophyll woodland	Dense woodland (Behrensmeyer & Reed 2013)	Spring (McKee & Kuykendall, 2016, review in Barboni et al., 2019)

Koro-Toro site, Chad

Fara et al., (2005) conclude that *"paleoenvironments were heterogeneous"*, with *"lakeside environments surrounded by a patchwork of gallery forest, wooded savannah and open grassland"*. Diatom data indicate freshwater lake, and phytolith data confirm the heterogeneous pattern and abundance of C_4 grasses (Novello et al. 2017). The model simulates tropical xerophytic shrubland, here dominated by tropical raingreen trees and C_4 grasses, with some woody desert plants, corresponding to the vegetation reconstructions. There is also evidence of lacustrine conditions (Schuster et al., 2009) at Koro-Toro site. A lake large enough would have locally impacted surrounding vegetation, even to a larger extent than gallery forest, especially on its eastern side, where the hominin site is located and where precipitation could have been increased by the presence of the lake (Contoux et al., 2013).

Awash Basin, Ethiopia

For the Awash sites, the model simulates tropical xerophytic shrubland for which the LAI of tropical raingreen trees is between 2.51 and 3.13, i.e. values typical of open woodlands. Data describe mosaic environments mixed C_3-C_4, grassy woodlands and bushlands (Behrensmeyer and Reed, 2013) likely to correspond to tropical savanna or to tropical xerophytic shrubland. In the model, tropical savannah (for which LAI must be superior to 4 in the model) is simulated on the grid cells located just to the west of each Afar site (Fig. 1), in agreement with plausible greater humidity and cooler temperature on the escarpments, which even today sustains a slightly more wooded and green vegetation compared to the lowlands.

Turkana Basin

At Usno the model simulates tropical savannah. For all the other sites in the Turkana basin, the model simulates tropical xerophytic shrubland. The data suggest, similarly to the Awash basin, a mosaic of woodland and grassland, more wooded at Usno and Shungura than in the rest of the basin, in agreement with the presence of the large and permanent Omo River fluvial complex (fluvio-deltaic context at Shungura, floodplain at Koobi-Fora, fluvio-lacustrine environments at Lomekwi, Behrensmeyer and Reed 2013).

Kantis, Kenya

Mbua et al., (2016) indicate a mosaic of woodland, shrubland, grassland with more C_4 than other *Au. afarensis* sites. Here the model simulates more mesic environments than those of the Awash and of the Turkana basins, with the same mix of PFTs (tropical raingreen trees, C_4 grass and woody desert plants). All PFTs are more productive, leading to the tropical deciduous woodland biome.

Laetoli, Tanzania

Via a combination of faunal and floral analyses, Su and Croft (2018) find that vegetation at Laetoli was a *"mosaic of woodland, bushland, shrubland, grassland with riverine woodland in a relatively arid and seasonal environment"*. The review of Barboni (2014) also indicates a mosaic of dry and moist woodlands and grassland, and few components of Afromontane forest. In our study, the simulated biome at Laetoli for the Pliocene mean climate is tropical savannah, with dominant tropical raingreen trees, the presence of conifer forest, C_4 grass and woody desert plants. Thus, our simulated biome at Laetoli is consistent with the reconstructions.

South Africa

Makapansgat

The biome simulated at Makapansgat is tropical xerophytic shrubland, dominated by tropical raingreen trees, with the presence of temperate broad-leaved evergreen trees, conifer forest, C_4 grass and woody desert plants, suggesting a strong heterogeneity of the landscape. This could correspond to the habitat mosaic recognized by Reed (1997).

Sterkfontein

Salzmann et al. (2008) interpret data from Reed (1997) and Bamford (1999) as being representative of temperate sclerophyl woodland, while Reed (1997) suggests that Sterkfontein is more open than Makapansgat. Our model however simulates warm mixed forest, i.e. a landscape dominated by temperate broadleaved evergreen trees, with tropical raingreen trees, conifer forest, C_4 grass and woody desert plants. This can hardly be reconciled with the reconstructions.

Taung

Fauna suggest relatively dense woodland (Behrensmeyer and Reed, 2013) while the model simulates temperate sclerophyll woodland, i.e. a rather open landscape composed of mainly temperature broadleaved evergreen trees, conifer forest, grass and woody desert plants.

In summary, hominin sites are mostly mosaic environments of tropical trees, grasses and shrubs. Because data reconstructions are mostly qualitative, it is difficult to compare to model results, which also represents a larger spatial scale which smoothes heterogeneity, notably because it does not include water sources. Nonetheless, the model simulates a mix of trees, grasses and shrubs at all the hominin sites, in broad agreement with reconstructions. Thus the simulated large-scale vegetation is coherent with local-scale vegetation reconstructions at hominin localities, except for Sterkfontein and Taung localities (2 sites over 18). We are therefore confident that our model’s climatic variables can be used to reconstruct the *Australopithecus* climatic envelope at a broad geographic scale.

Appendix 2

R scripts for KUENM and Maxent analysis

Example script for Pliocene 'mean' climate

Computed with Rmarkdown

Environmental layers

Import of the simulated climatic layers from files beforehand cropped with calibration area (see Annexe 1) and preparation of the 2210 KUENM variables sets. "Plio_vars_noncor/var/m3_clipped" is the folder where non-correlated cropped layers are stored, "Plio_vars_noncor/FullVar" is the folder where non-cropped (all Africa) layers are stored.

```
library(kuenm)
library(raster)
library(rgeos)

setwd("yourKUENMfolder")

## preparing M variables (cropped layers for model computation)
kuenm_varcomb(var.dir = "Plio_vars_noncor/var/m3_clipped", out.dir = "M_variables", mi
n.number = 2, in.format = "ascii", out.format = "ascii")

## preparing G variables (non-cropped layers for projection of the model)
kuenm_varcomb(var.dir = "Plio_vars_noncor/FullVar", out.dir = "G_variables", min.numbe
r = 2, in.format = "ascii", out.format = "ascii")
```

Occurrences of Pliocene hominids

Import of the occurrences of Pliocene hominids living in Africa between 4 and 3 Ma, see Table 1 for references and coordinates. The 18 occurrences are then splitted in training and testing datasets to conduct model calibration. For jackknife, leave-one out approach, 18 datasets are constructed by removing one occurrence point. The models used to evaluate the impact of orbital configuration are based on the full (18) dataset.

```
## Import from .csv files
hom <- read.csv("allOccurrence.csv", sep = ";")

## Splitting in training and testing datasets
kuenm_occsplit(occ = hom, train.proportion = 0.75, method = "random", save = TRUE, nam
e = "occ")
```

Candidate models, evaluation and selection

In this step, 2210 candidate models are produced and their performance are evaluated to select the best Maxent parameterization.

```
## Parameters for model calibration

# names for directory and files
occ_joint <- "occ_joint.csv"
occ_tra <- "occ_train.csv"
M_var_dir <- "M_variables"
batch_cal <- "Candidate_models"
out_dir <- "Candidate_Models"
# regression parameters
reg_mult <- c(seq(0.1, 1, 0.1), seq(2, 6, 1), 8, 10)
f_clas <- c("q", "lq", "lp", "qp", "lqp")
args <- NULL
```

```
maxent_path <- "C:/Maxent"
wait <- FALSE

run <- TRUE
occ_test <- "occ_test.csv"
out_eval <- "Calibration_results"
threshold <- 5
rand_percent <- 50
iterations <- 100
kept <- TRUE
selection <- "OR_AICc"
paral_proc <- FALSE

## Computation of the candidate models
kuenm_cal(occ.joint = occ_joint, occ.tra = occ_tra, M.var.dir = M_var_dir, batch = batch_cal, out.dir = out_dir, reg.mult = reg_mult, f.clas = f_clas, args = args, maxent.path = maxent_path, wait = wait, run = run)

## Computation of model evaluation and selection
cal_eval <- kuenm_ceval(path = out_dir, occ.joint = occ_joint, occ.tra = occ_tra, occ.test = occ_test, batch = batch_cal, out.eval = out_eval, threshold = threshold, rand.percent = rand_percent, iterations = iterations, kept = kept, selection = selection, parallel.proc = paral_proc)
```

Final models

Computation of the final models and projection on G_variables (i.e. the entire Africa)

```
batch_fin <- "Final_models"
mod_dir <- "Final_Models"
rep_n <- 10
rep_type <- "Bootstrap"
jackknife <- FALSE
out_format <- "logistic"
project <- TRUE
G_var_dir <- "G_variables"
ext_type <- "all"
write_mess <- FALSE
write_clamp <- FALSE
wait1 <- FALSE
run1 <- TRUE
args <- NULL

kuenm_mod(occ.joint = occ_joint, M.var.dir = M_var_dir, out.eval = out_eval, batch = batch_fin, rep.type = rep_type, jackknife = jackknife, out.dir = mod_dir, out.format = out_format, project = project, G.var.dir = G_var_dir, ext.type = ext_type, write.mess = write_mess, write.clamp = write_clamp, maxent.path = maxent_path, args = args, wait = wait1, run = run1)
```

Computation of extrapolation risk analysis

As with any model fitting exercise, interpretation of model predictions outside the range of the independent variables on which models were calibrated is perilous. To estimate the extrapolation risk we use Mobility-Oriented Parity (MOP) analysis (Owen et al. 2013)

```
sets_var <- c("Set_8") #these are the variable combo sets used in Final models
out_mop <- "MOP_results"
percent <- 10
swd <- FALSE
paral <- FALSE
```

```
kuenm_mmop(G.var.dir = G_var_dir, M.var.dir = M_var_dir, is.swd = swd, sets.var = sets
_var, out.mop = out_mop, percent = percent, parallel = paral)

# MOP summary
dir.create("MOP_summary")

mops <- stack(list.files(out_mop, pattern = ".tif$", full.names = TRUE, recursive = TR
UE))

meam <- calc(mops, mean)
minm <- calc(mops, min)

writeRaster(meam, filename = "MOP_summary/Mean_MOP.tif", format = "GTiff")
writeRaster(minm, filename = "MOP_summary/Min_MOP.tif", format = "GTiff")
```

Computation of final model statistics

Last step of the KUENM analysis, caution incorrect sp_name and scenarios variables can prevent the analysis from running. The final model can be projected on multiples environmental layers by adding their names in “scenarios” variable (e.g. “Africa”, “PlioMin June”, “PlioMin September”) and the respective layers in G_variables.

```
# Model statistics: The final models to be analyzed will be found in the Final_Model_S
tats folder.
format <- "asc"
project <- TRUE
stats <- c("med", "range", "avg")
rep <- TRUE
# the type of extrapolation can be selected according to user requirements
ext_type <- c("E", "EC", "NE")
out_dir <- "Final_Model_Stats"

# Select names of taxa name in occurrence file and G_variable name (i.e. Africa)
sp_name <- "Hominin"
scenarios <- c("Africa")

kuenm_modstats(sp.name = sp_name, fmod.dir = mod_dir, format = format, project = proje
ct,
               statistics = stats, replicated = rep, proj.scenarios = scenarios,
               ext.type = ext_type, out.dir = out_dir)
```

Figure 1

Biomes simulated with Pliocene mean climate

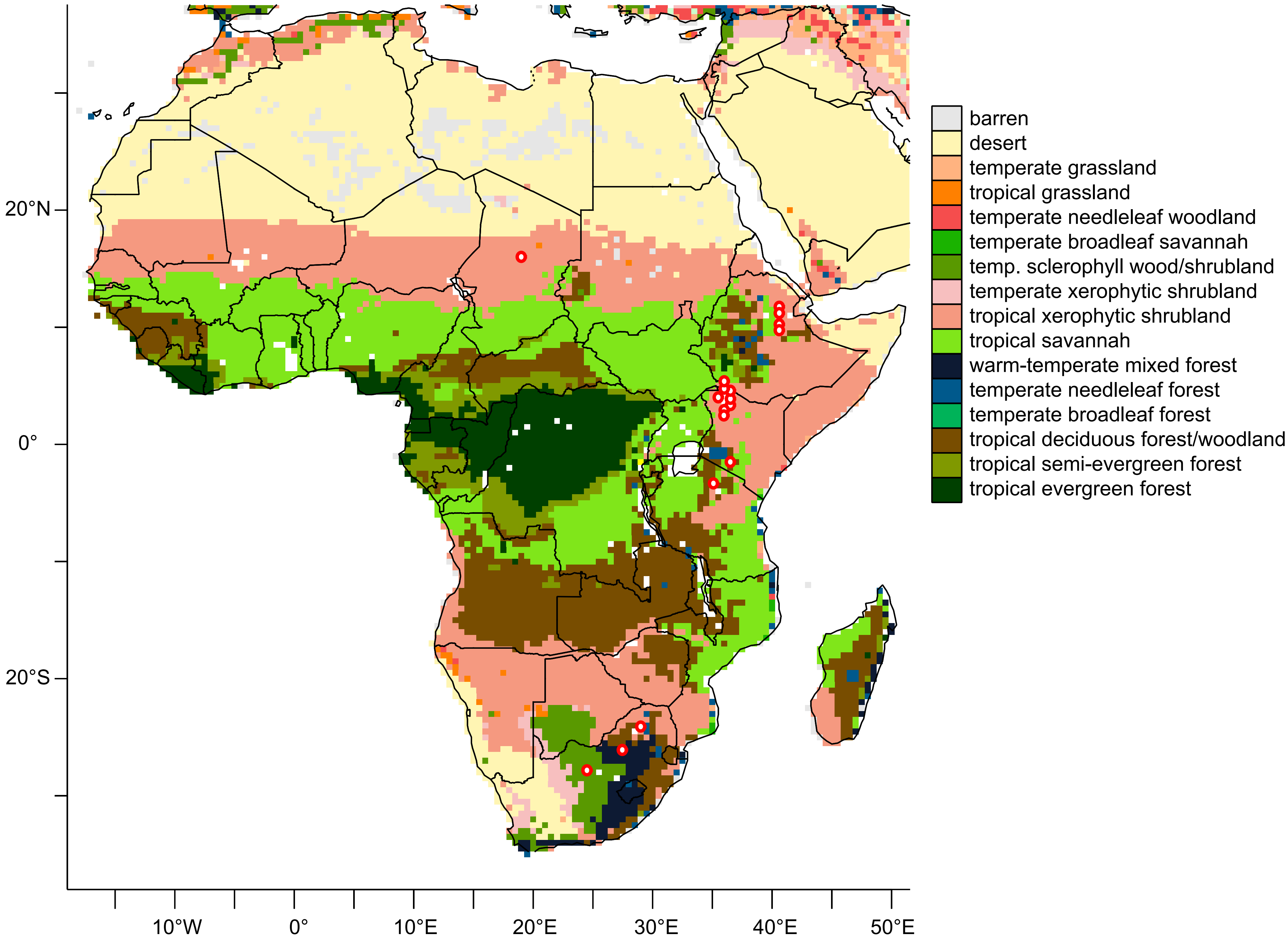
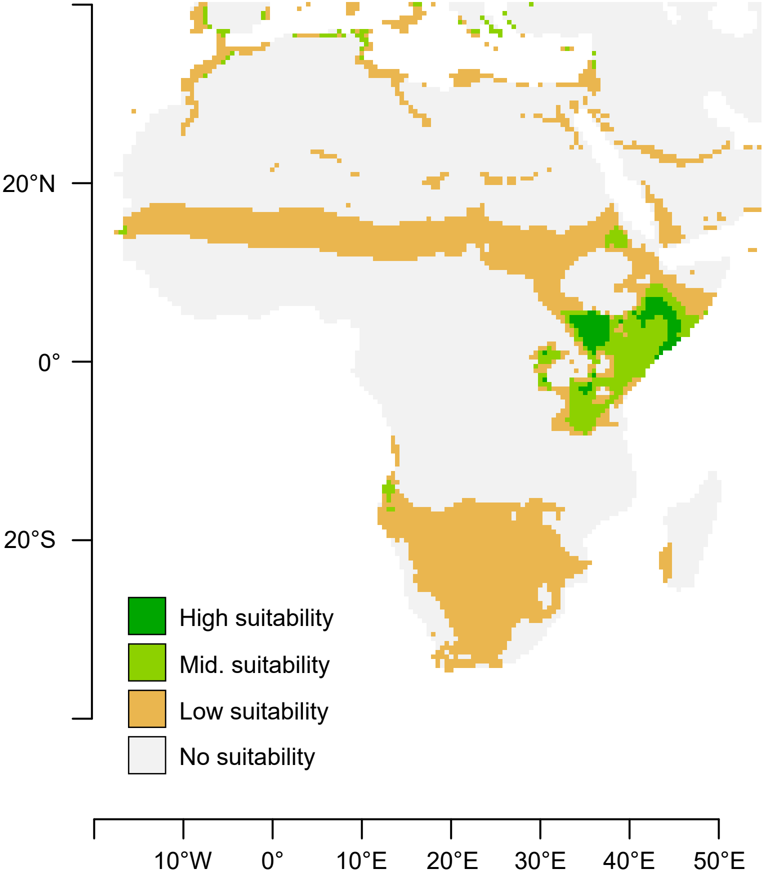
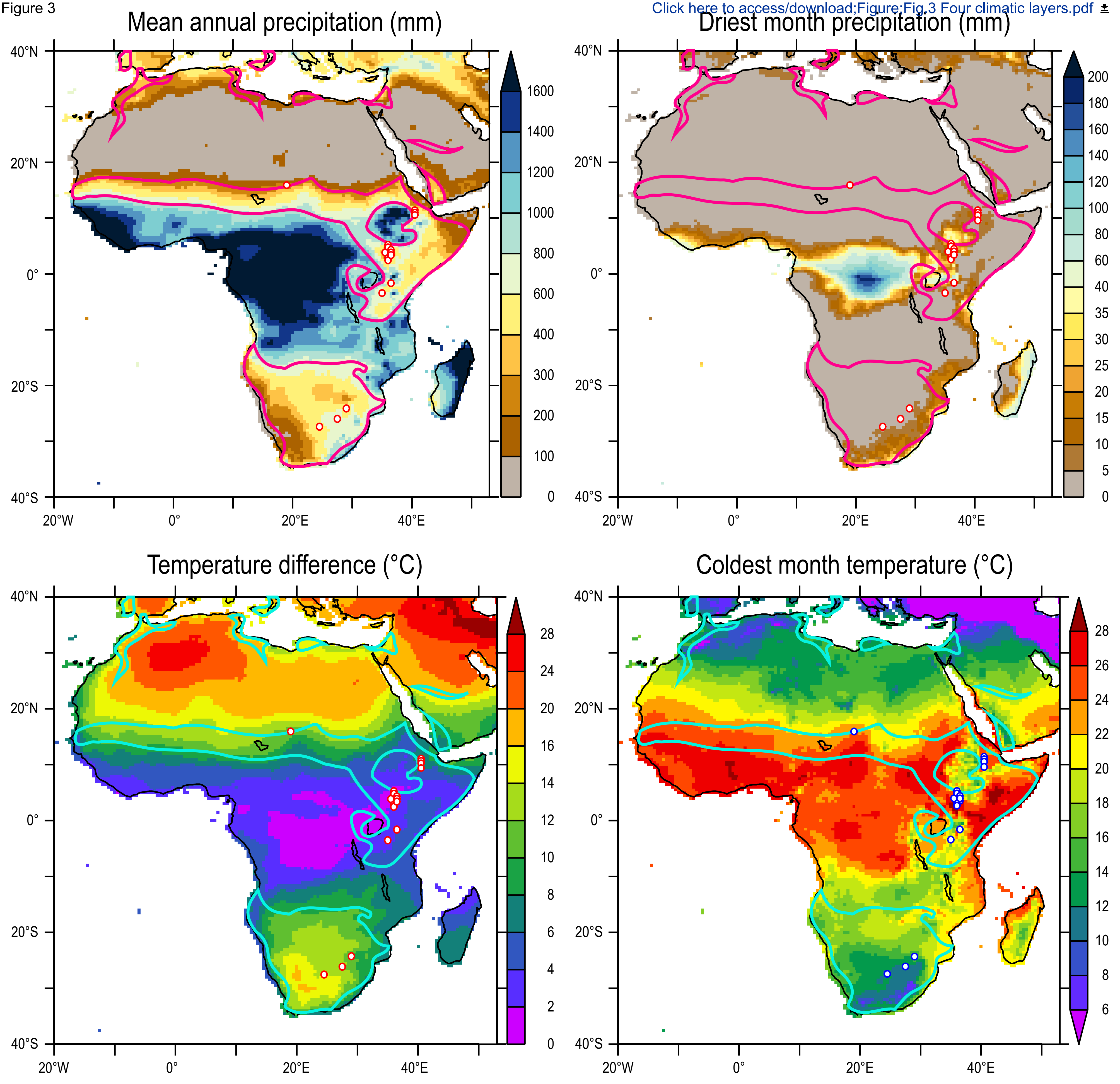


Figure 2



Final habitat suitability model for hominins

Figure 3


Mean annual precipitation (mm)
Driest month precipitation (mm)
Temperature difference (°C)
Coldest month temperature (°C)
40°N
20°N
0°
20°S
40°S
20°W
0°
20°E
40°E
0
100
200
300
400
600
800
1000
1200
1400
1600
0
5
10
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140
160
180
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28

Figure 4

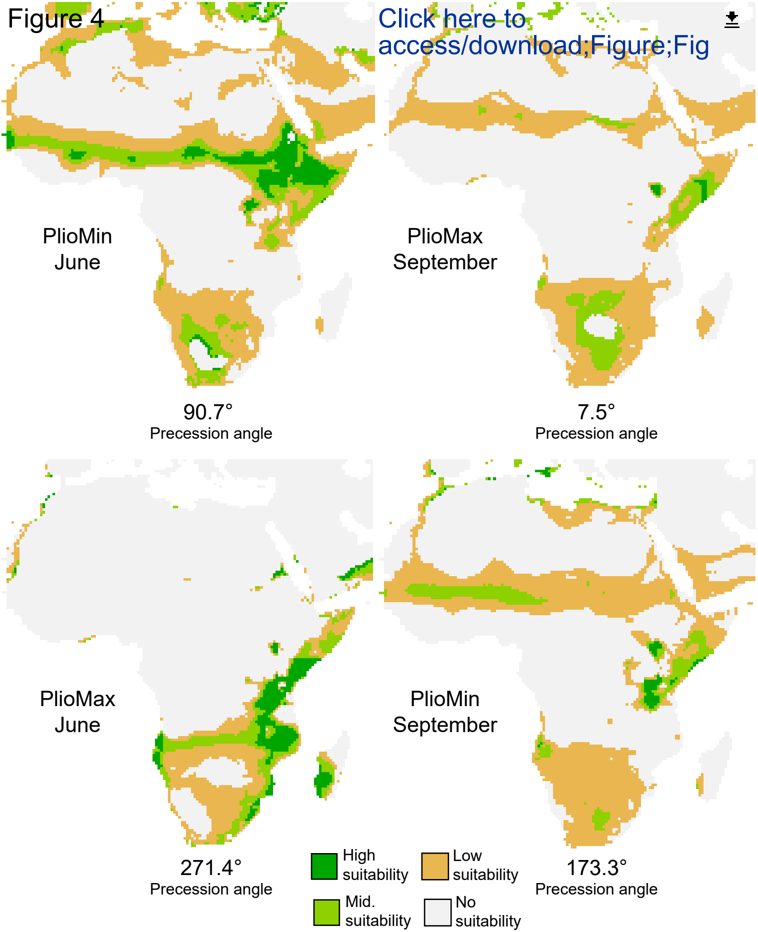
PlioMin
June
90.7°
Precession angle
PlioMax
September
7.5°
Precession angle
PlioMax
June
271.4°
Precession angle
PlioMin
September
173.3°
Precession angle
High suitability
Low suitability
Mid. suitability
No suitability

Figure 5

Consensus map of the four orbital precession projections and Pliocene ‘mean’ climate model