The Early Peopling of the Philippines based on mtDNA

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Despite the efforts made to reconstruct the history of modern humans, there are still poorly explored regions that are key for understanding the phylogeography of our species. One of them is the Philippines, which is crucial to unravel the colonization of Southeast Asia and Oceania but where little is known about when and how the first humans arrived. In order to shed light into this settlement, we collected samples from 157 individuals of the Philippines with the four grandparents belonging to the same region and mitochondrial variants older than 20,000 years. Next, we analyzed the hypervariable I mtDNA region by approximate Bayesian computation based on extensive spatially explicit computer simulations to select among several migration routes towards the Philippines and to estimate population genetic parameters of this colonization. We found that the colonization of the Philippines occurred more than 60,000 years ago, with long-distance dispersal and from both north and south migration routes. Our results also suggest an environmental scenario especially optimal for humans, with large carrying capacity and population growth, in comparison to other regions of Asia. In all, our study suggests a rapid expansion of modern humans towards the Philippines that could be associated with the establishment of maritime technologies and favorable environmental conditions.

Traditionally it is considered that the first humans who colonized Oceania departed from Southeast Asia (SEA) and reached the austral continent through Sumatra, Java and Timor1. According to this approach, the Philippine archipelago, constituted by more than 7,000 islands and located in a more northern region, would not be involved in the ancestral human migrations that colonized Oceania2. However, there are some studies that contradict this approach. The fossil record confirms that our modern humans were in the Philippines at least 40,000–50,000 years ago3–5, the genus Homo possibly 66,700 years ago6,7. Another finding is the presence in the archipelago of Negritos groups related to the first migrations of Homo sapiens outside Africa4,8,9. Indeed, several genetic studies detected an archaic substrate in current populations of the Philippines4,5,10–14. Hence, the human presence in the Philippines during the first stages of expansion of anatomically modern Homo sapiens is very likely. The recent finding of Homo luzonensis7 in the Philippines does not provide new information on the origin and expansion process of our species although it does demonstrate the importance of the archipelago to understand the past of our lineage. Consequently, the Philippines probably presented a relevant role in the out of Africa expansion of modern humans to colonize the SEA and Oceania.

Despite the relative certainty concerning the timing of the entry into the Philippines, only some studies investigated the population genetics and evolutionary processes occurring in the first expansion of modern humans towards this region. Alves, et al.15 and Pugach, et al.16 found that Paleolithic populations in Eurasia and Oceania, respectively, could have expanded with long-distance dispersal (LDD) events, rather than through a progressive expansion along the landscape. However, little is known about LDD and the migration routes used to reach the Philippines and about the Palaeolithic population dynamics in this region. The Philippines is an especially interesting region to test these population processes because its colonization required an expansion through large stretches of sea (bottlenecks), which could be done using boats or rafts as proposed for other regions of the world17,18.

In the present work, we investigated the timing of colonization, migration patterns and the population dynamics that occurred in the Philippine archipelago at the first stages of human expansion. Mitochondrial DNA

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(mtDNA) has been shown as a very informative genetic marker to study the genetic diversity and genetic relationships among populations of the Philippines19–23. In agreement with these previous works and in order to address the previously presented questions, we collected sequences from the D-Loop region of mtDNA of 157 individuals selected from native volunteer donors from different geographic regions of the archipelago. All of them carried mitochondrial variants older than 20,000 years. It is important to consider that mtDNA is inherited to the maternal line (but see24), hence here we mainly make focus on the female evolutionary history of the archipelago, which is unequivocally related to the global history25. Next we applied approximate Bayesian computation (ABC) based on extensive spatially explicit computer simulations to identify the scenario of migration towards the archipelago that fits better with the data. We also estimated a variety of population genetic parameters informative about this settlement such as the time of the onset of the expansion, carrying capacity (available resources), demographics (including ancestral population size and population growth rate), mutation rate, migration rate, and proportion of migration events with LDD.

Materials and Methods
Sample collection and ethical statements. A total of 157 samples were collected covering most of the geographical area of the archipelago (Figs. 1 and S1; Table S1). The samples were obtained from Filipinos currently living in Spain but with known geographic origin in the Philippines. Each participant was informed about the study and signed an informed consent document for study participation according to the Helsinki protocol for the use of these samples. Indeed, the protocol was approved by the bioethics Committee of the Complutense University of Madrid. Next, the participants completed a survey about their origins and predecessors (including ethno-linguistic groups; Table S2). The samples were only collected from participants presenting the four grandparents in the region and accounting for the geographical diversity of the Philippines by donors from the three major regions of the archipelago: Luzon (n = 84), Visayas (n = 59) and Mindanao (n = 14). Moreover, given that the first two regions include a large number of islands, intraregional samples were collected. In particular, Luzón was divided into five subregions –Bicol (n = 10), Calabarzon (n = 20), Ilocos (n = 13), Manila (n = 17) and a central region (n = 24) – and, Visayas was divided into three subregions –West (n = 30), Center (n = 15) and East (n = 14).

MtDNA amplification, sequencing and incorporation of additional sequences. Samples consisted of oral swabs (two per individual) that were kept dry in paper envelopes at 4 °C. Next, DNA was extracted by standard phenol-chloroform method including a final purification with AMICON filters following the
instructions of the manufacturer (Merck). The mtDNA D-loop (control region) was sequenced for all 157 individuals using the BigDye Terminator kit v1.1 (Applied Biosystems), in two or three fragments depending on the samples between positions 16,000 and 600. Amplified fragments were identified previously to the sequencing reaction in 4% agarose gel. Finally, the fragments were sequenced on Applied Biosystems ABI PRISM 3130 genetic analyzer. The genetic sequences were deposited at GenBank with accession numbers MH910797-MH910953. The identification of spatial genetic variation is more accurate by considering a well-distributed sampling over the landscape. Because of that, we included genetic samples from neighboring regions of the Philippines. Unfortunately, most of the studies involving humans from those regions only shared sequences of the hypervariable I mtDNA region (HVR-I) and therefore posterior analyses were based on this region. We obtained from the bibliography genetic sequences from regions surrounding the Philippines (with a relatively even geographic distribution, Figs. 1 and S1; Table S1) and where each sampling location included genetic data from at least 10 individuals. We only considered sequences belonging to haplogroups older than 20,000 years6 to avoid lineages with origin posterior to the Philippines settlement8. The haplogroup assignment was performed with HAPLOFIND29 and MitoTool80 (Table S2). All the sequences were aligned with MAFFT91. The final multiple sequence alignment (MSA) included a total of 720 individuals collected from 25 different locations, from which 157 individuals of 9 populations of the Philippines were chosen and sequenced for this study. Details about sample size (number of individuals), geographic location and source (present study or other studies) are shown in Table S1 and depicted on the map in Figs. 1 and S1. Despite the limitations of our data due to the need of incorporating genetic information from different geographic areas, we found that our final dataset was sufficient to yield accurate model selection and estimation of population genetics parameters (see Results).

Testing migration routes to the Philippines. Migration routes to the Philippines could affect the genetic diversity and population structure observed in this archipelago. Therefore, first, we investigated the fitting of diverse scenarios of migration towards the Philippines with the real data using ABC (details shown in following subsections).

Considering the geography of the Philippines, its neighboring regions and suggestions from previous studies14,32,33, we designed a total of 7 scenarios based on migration patterns and migration routes to the archipelago: (i) migration presenting LDD events (LDD, as suggested for Eurasia15; details about the LDD model are shown in the Supplementary Material) and, 6 scenarios of migration through different routes and without LDD proposed in the “Beyer’s Wave Migration Theory”32 and other studies14,33: (ii) a north route and three south routes (AllCorr), (iii) only a north route (North), (iv) only the three south routes (AllSouth), (v) only the southwest route (SW), (vi) only the south-central route (SC) and, (vii) only the southeast route (SE) (Figs. 1 and S2). Next, we evaluated non-nested scenarios by fitting with real data to identify the most likely scenario. In particular, in order to evaluate the influence of LDD, we evaluated: LDD vs AllCorr and, LDD vs AllSouth vs North. We also performed comparisons between other non-nested scenarios without LDD to explore the fitting of particular migration routes: AllSouth vs North (to explore migration from the north respect to migration from the south) and, SW vs SC vs SE (to explore the most likely migration route/s from the south).

Spatially explicit computer simulations. We performed spatially explicit computer simulations with the evolutionary framework SPLATCHES36. Information about the applied evolutionary models and landscape is presented in the Supplementary Material. The computer simulations were based on prior distributions for population genetic parameters following previous studies (Table S3). We assumed a range expansion with origin posterior to the Philippines settlement8. The haplogroup assignment was performed with HAPLOFIND29 and MitoTool80 (Table S2). All the sequences were aligned with MAFFT91. The final multiple sequence alignment (MSA) included a total of 720 individuals collected from 25 different locations, from which 157 individuals of 9 populations of the Philippines were chosen and sequenced for this study. Details about sample size (number of individuals), geographic location and source (present study or other studies) are shown in Table S1 and depicted on the map in Figs. 1 and S1. Despite the limitations of our data due to the need of incorporating genetic information from different geographic areas, we found that our final dataset was sufficient to yield accurate model selection and estimation of population genetics parameters (see Results).

Approximate Bayesian computation for selection among evolutionary scenarios and parameters estimation. The real data was analyzed with the ABC approach40, which basically applies extensive computer simulations to estimate posterior probabilities of alternative scenarios and parameters by a statistical fitting between simulated and real data. Next, we describe the steps of our ABC method.

Computer simulations. For each of the seven evolutionary scenarios previously described, we performed a total of 100,000 spatially explicit computer simulations according to the prior distributions presented in Table S3. For each scenario, we also performed 100 additional and independent simulations (hereafter, test datasets) to evaluate the power of selection among evolutionary scenarios and parameters estimation (details shown later).

Summary statistics. Summary statistics (SS) from real and simulated datasets were obtained with ARLEQUIN ver.3.54. To perform this task, the 25 populations were classified into five geographic groups (Fig. S1) that allowed the estimation of diverse group-based SS. Group 1 included samples from the north of the continent; group 2 included samples from the south of the continent; group 3 included samples from the Philippines; groups 4 and 5
included the remaining samples separated according to the Wallace line (Fig. S1). We considered that this general grouping was properly since the ABC performance reduces quickly as the number of statistics grows40. We applied a total of 18 SS with biological meaning: (i) genetic diversity in every group and in all groups together (pairwise differences, \(\pi\); including standard deviation) and, (ii) genetic differentiation (\(F_{ST}\)) between every two groups and all groups together. We found that this set of SS was informative for the ABC inferences (see validations in Results section). We did not apply partial least square (PLS) components to reduce the number of SS because our selected SS were informative enough and because PLS components can generate SS without biological meaning, being difficult to interpret and leading to biases when comparing components that are calculated separately42.

Selection among evolutionary scenarios. As indicated above, we generated 100,000 simulated datasets for each of the seven migration scenarios. In addition, we simulated 100 test datasets for each scenario to evaluate the accuracy of the estimation method. We applied three ABC approaches to perform the selection of the best-fitting evolutionary scenario with the real data: The rejection approach developed by Pritchard et al.43 (Pr) and, the rejection approach implemented in the abc package of R44 (Rrej) and the neuralnet (Rnn; nonlinear heteroscedastic regression45) approach also implemented in the abc package of R. Following the authors recommendation we retained 1% of simulations with SS closer to the SS of the real data44.

For the evaluation of the selection among alternative scenarios, we applied the 100 test datasets (considering them as true data) and also for Rnn the leave-one-out cross-validation method implemented in the abc library of R (cv4postpr function) that accounts for non-linearity adjustment based on 100 permutations and again with a tolerance of 144. The neuralnet method required more computational costs but, according to Csilléry et al.44, it could provide more accurate inferences.

Although traditionally the goodness of fit analysis is only applied to the preferred scenario, we performed goodness of fit analyses (based on principal component analysis (PCA) and a comparison among the null distributions from the selected SS44) to all the evolutionary scenarios designed in the study. In addition, for these analyses of goodness of fit we included the position of the real dataset on the simulated parameters landscape for every comparison of scenarios, providing a preliminary view of the fitting of every scenario with the real data. Finally, we selected the scenario that better fits with the real data applying the ABC approaches previously described (Pr, Rrej and Rnn).

Parameters estimation. We performed the parameters estimation under the evolutionary scenario with LDD, which was the scenario that fitted best with the real data (see Results). The parameters estimation was performed with the multiple regression adjustment implemented in the program ABCtoolBox46. Following the software documentation, we retained the best 5,000 simulations (with SS closer to the SS of the real data) and also because they provided robust parameters estimation (see Results). The robustness of the parameter estimation was assessed with the 100 test datasets simulated under the LDD scenario, considering them as true data. For each test dataset and parameter we computed the distance between the true value and the estimated value (median, mean and mode).

Results

We first describe the selection between alternative evolutionary scenarios of migration to the Philippines. After that, we present the parameters estimation under the best fitting evolutionary scenario.

Migration to the Philippines occurred with long-distance dispersal and through all north and south migration routes. The power to select among the designed scenarios of migration to the Philippines varied depending on the scenarios that are evaluated. We obtained high posterior probabilities to identify the correct scenario under the different ABC methods when comparing (i) LDD vs AllCorr (probabilities around 1, Table S4A), (ii) LDD vs AllSouth vs North (probabilities generally above 0.8, Table S4B) and, (iii) AllSouth vs North (probabilities around 1, Table S4C). However, we obtained a lower accuracy when comparing the three scenarios with only migration routes from the south, SW vs SC vs SE (probabilities above 0.4, Table S4D). This result was expected because both SW and SC routes come from the same island (Borneo). In order to further explore this finding, we also evaluated the scenarios SW vs SE and there we found probabilities generally above 0.9 (Table S4E). Note that we performed comparisons among non-nested scenarios. If nested scenarios are analyzed together (i.e., comparing all the scenarios) the performance of the method will be poor because nested scenarios under certain evolutionary circumstances can lead to similar genetic signatures (i.e., AllCorr vs AllSouth could be similar in cases where under AllCorr the migration rate from the north is very small by chance sampling from the prior distribution).

Real data clearly fitted better with the scenario of LDD, with posterior probabilities above 0.9 under any ABC method (Table 1). Indeed, the analyses of goodness of fit also supported this finding (Fig. S4).

Even considering that LDD was the best fitting evolutionary scenario, we explored the fitting of the different migration routes (without LDD) with the real data. We found that the migration to the Philippines through the south routes was generally more likely than the migration through the north route (Taiwan), but the north route could also be used (Table 1). When comparing the routes from the south, we found that all the routes were likely to be used, although the routes from Borneo (SW and SC) presented the highest probabilities. Note that the selection between SW and SC routes presented a poor performance (Table S4D), and therefore we cannot distinguish between SW and SC when fitting with the real data. The results slightly varied among ABC approaches.

The settlement of the Philippines was rapid and caused by a rapidly increasing population. The estimation of the population genetic parameters was performed under the best-fitting evolutionary scenario (LDD). Concerning the validation of the parameters estimation, the method presented a performance
of 25 years. Estimated migration rate (≈ 500 and near 7,000) and the estimated population growth rate in Eurasia varied between 0.4 and 0.9 (15,51). The estimated in other studies (i.e., in Europe and north of Africa the estimated carrying capacity varied between 0.82) were higher than expected, although they fell within the range of population growth rate per generation (≈ 3,000) and population sizes (near 40,000 individuals) in the region. Indeed, the estimated carrying capacity (≈ 0.04) was in agreement with previous findings (15,49). The estimated ancestral size (above 30,000 individuals and probably near 50,000) was larger than we expected. However, some previous works (e.g.,50,) also suggested large ancestral populations with overall small estimation errors that always fell within the 50% HPDI with respect to the true value (Table S5). The estimated population genetic parameters for the real data are shown in Table 2. The precision was low for the estimation of some parameters, in particular for the time and population size at the onset of the expansion and the carrying capacity. This was expected because the estimation of these parameters requires considerable genetic signatures of ancestral processes, also found in other studies (e.g.,15,47). However, we accounted for this uncertainty instead of fixing parameter values, since previous studies often disagree concerning these estimates (48). We considered acceptable the precision of the estimation of the remaining parameters, presenting in general more narrow posterior distributions (Table 2).

Our estimated date for the onset of the expansion of Anatomically Modern Humans (AMH) from Bangladesh (≈60 kya) fitted with previous studies (49). The estimated ancestral size (above 30,000 individuals and probably near 50,000) was larger than we expected. However, some previous works (e.g.,50,) also suggested large ancestral population sizes (near 40,000 individuals) in the region. Indeed, the estimated carrying capacity (≈3,000) and population growth rate per generation (≈0.82) were higher than expected, although they fell within the range estimated in other studies (i.e., in Europe and north of Africa the estimated carrying capacity varied between 500 and near 7,000) and the estimated population growth rate in Eurasia varied between 0.4 and 0.9 (15,51). The estimated migration rate (≈0.27) was high but fell within estimates in Eurasia (15). The proportion of LDD events (≈0.04) was in agreement with previous findings (49). Although the estimated mutation rate (≈1.3E-08) fitted with other studies (49), this parameter usually varies among studies, especially when they are obtained from different genetic markers (e.g.,36,56).

Discussion

Despite the efforts made to understand human phylogeography, there are still relevant regions of the world where the population genetics processes and migration patterns occurring in first colonizations have not been resolved. An especially interesting example is the Philippine archipelago. There is a clear evidence of an early settlement of the Philippines (4,8,10,11), however little is known about the population genetics, migration routes and migration patterns that occurred in this settlement. Concerning its geography, the Philippines is a particularly relevant region to test the influence of the geography on human migration and to understand the causes of the currently observed population structure and genetic diversity.

Addressing the early settlement of the Philippines by the study of current genetic variants is complex given that its current composition is the result of a superposition of migratory waves distant in time (49). Despite this complexity, here we investigated the fitting of diverse evolutionary scenarios of migration with real genetic data from
a large number of individuals from the Philippines and neighboring regions in order to provide clues about the population genetics of the settlement and migration routes that could have occurred in this archipelago. Note that the Philippine archipelago, given its geographic location, could be colonized by two major routes: from the north (through Taiwan) and from the south (which could contemplate different routes from Borneo or from northern Sulawesi). Indeed, diverse combinations of potential migration routes could have occurred. Moreover, this migration could also present LDD events. Here, we developed and applied an ABC method based on extensive spatially explicit computer simulations to determine whether the migration to the Philippines occurred with LDD or by progressive (gradual) migration from neighboring regions through particular migration routes. Finally, we estimated demographic and evolutionary parameters under the best fitting evolutionary scenario.

We found that the evolutionary scenario fitting best with the real data was the one that presents migration with LDD. This finding supports a previous study on the Palaeolithic expansion on Eurasia. Indeed, this result could be expected because the colonization of the archipelago implies displacements from island to island, which can lead to LDD events. The finding is also in agreement with some previous studies on the arrival of modern humans to Australia, which occurred crossing water barriers with watercrafts such as boats and rafts. Next, we explored the fitting of particular migration routes with the real data to identify possible migratory pathways towards the Philippines. Our results showed that migration routes from both the north and the south were used to colonize the Philippines, although the probability was slightly higher for the colonization from the south. Moreover, within migration from the south, all the proposed routes were likely to occur. Altogether, we found that the most likely migratory scenario involving the early colonization of the Philippine archipelago by modern humans implied LDD events and migration through routes from both the north and the south. In theory, the southern route could be more used given the low sea level during the Last Glacial Maximum (LGM) period that led to the emergence of the continental mass of Sunda, connecting the islands at the west of the Wallace line. A northern route favored by the LGM seems more difficult since this would require the use of advanced navigation techniques to connect distant islands. However, for many authors navigation technologies were already developed by *Homo erectus* and with respect to our species, the presence of archaic fossil remains confirm that our ancestors must have navigated, more or less frequently, more than 60,000 years ago. In this concern, our findings present genetic signatures of migration through LDD, which could fit with the use of techniques of navigation in the expansions of modern humans.

Concerning the demographic and environmental conditions under which the colonization of the archipelago was carried out, we found that the expansion from Bangladesh occurred at 60,000 years ago or earlier (HPDI around 60,000–68,000), a date consistent with findings from other disciplines regarding the human presence in the SEA and Australia (e.g.) and previous studies proposing the presence of our species in Australia at 65,000 years ago. These dates agree with other studies (e.g.,) and are slightly earlier than the dating of the remains of Callao Cave in Luzon (67,000 years old) although such remains have been considered as another species (*Homo luzonensis*). In any case it should be noted that for some authors these remains are fragmentary and taxonomically ambiguous.

Our results described a rapid Palaeolithic expansion towards the Philippine archipelago. If that dispersal pattern is maintained for the posterior Neolithic expansion from current China, which could be likely considering the technological and cultural innovations developed by Neolithic populations but still to be demonstrated in the study area, our results would support the variant of the *Out of Taiwan* theory (e.g.), known as the *Express Train to Polynesia*, that defends a rapid migration of Polynesian ancestors from the Southeast Pacific (e.g.).

The estimated effective population size at the onset of the expansion varied between 25,000 and 50,000 individuals, with a higher probability for a large size. This large population size agrees with previous studies for the SEA. Indeed, our estimates are based on mtDNA and thus they may represent only the female component of the population. For some authors the female demographic component can be about eight times higher than the male component, although this was found for post-Neolithic periods characterized by patrilocal patterns. Studies focused on periods before the Neolithic, as in the present study, found a balanced sex-bias (e.g.,) considering cultural, historical and geographical singularities of the study regions. We believe that this large population size would favor the rapid spread of modern humans throughout the archipelago, in agreement with Jinam, et al. The estimated population growth rate and carrying capacity, directly related to *Annual Net Primary Production (ANPP)*, fit with previously found population demographic patterns, especially in hunter-gatherer societies. The average value obtained for the population growth rate was 0.82 per generation (but ranging between 0.59 and 1.0). This result agrees with previous estimates that presented values between 0.3 and 0.9 (e.g.,). On the other hand, the estimated carrying capacity (around 3,000) was higher than previous estimates in Eurasia (around 1,000 but with an upper estimate around 2,000) but lower than estimates for Neolithic populations (above 5,000). This suggests that Palaeolithic populations of the SEA could be favoured by an environment rich in natural resources, facilitating demographic growth. Actually, the paleoclimatic reconstructions of the SEA describe an ecological environment very similar to current sub-Saharan Africa and the presence of forests, which could be beneficial for the living-style of Palaeolithic humans. Note that the SEA is one of the most important geographical spaces in our evolutionary history from where movements to Europe, America and Australia started.

A possible consequence of the rapid demographic growth could be a rapid expansion throughout the islands of the Philippine archipelago. This affirmation is supported by the estimated high migration rates (around 27%) that reflect important human contingents movement, higher than those (23–25%) estimated for other groups of hunter-gatherers in Europe and north of Africa. In addition, the estimated proportion of individuals migrating with LDD events was approximately 4%, similar to that obtained for Palaeolithic populations in Eurasia, which again supports the rapid expansion of hunter-gatherers along Asia and expanding to Indonesia and Philippines.
The Philippines constitutes an important geographic region in the expansion of modern humans despite it was frequently ignored in human evolutionary analyses of the SEA and Oceania. Here we explored the expansion of modern humans towards the Philippines and we found that this expansion was rapid, presenting LDD events, and following diverse migration routes that geography and existing technology could allow. We believe that the rapid expansion an explosive population growth could be favored by optimal environmental conditions present in the region at the time of the expansion.

Data availability
The genetic sequences were deposited at GenBank with accession numbers MH910797-MH910953.

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Author contributions
M.A. and A.G.M. conceived and designed the study. A.G., E.C., H.R.V. and A.G.M. collected the data and obtained the sequences. M.A., J.M.B. and C.B. carried out the evolutionary analyses. All authors wrote and approved the final version submitted for publication.

Competing interests
The authors declare no competing interests.

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