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Global phylogeography of the insect pest *Callosobruchus maculatus* (Coleoptera: Bruchinae) relates to the history of its main host, *Vigna unguiculata*

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Abstract

Aim: The seed beetle *Callosobruchus maculatus* is an important tropical and subtropical pest of legumes distributed world-wide. Archaeological evidence suggests an African origin with later world-wide invasion facilitated by the last centuries' legume trading and exchange. To date, no studies could identify the routes or timing of dispersal of the species. Here, we investigate the global phylogeography of this pest to shed light on the main inter-continental dispersal routes that led to it becoming a cosmopolitan pest.

Location: World-wide.

Methods: We sampled seed beetles over a large fraction of the species' range and sequenced one nuclear and three mitochondrial loci. Using this data, we estimated spatio-temporal phylogeographical reconstructions, and the demographic history of the species. We also used our dataset to evaluate the effect of panmixia on Bayesian demographic estimations.

Results: *Callosobruchus maculatus* exhibited regional and continental genetic structure, with the highest genetic diversity found in Africa. Our discrete Bayesian phylogeographical approach indicated that the species first dispersed to Asia and then colonized the pantropical belt. The three methods used for inferring the demographic history of *C. maculatus* indicated a recent demographic expansion in the world-wide dataset, as well as in the subset restricted to African samples. Such a signal was, however, not observed in the subset composed of Asian specimens. This demographic expansion occurred in the Holocene and is likely explained by the spread of cowpea and other host legumes across and out of Africa.

Main conclusions: The inferred dispersal routes support the idea that the evolutionary history of *C. maculatus* relates to the trade of its main host plant, *Vigna unguiculata*. Human-mediated processes appear to have shaped the global genetic structure of this pest. As a methodological implication, we demonstrate that coalescent-based demographic reconstructions can be erroneous if the dataset violates the assumption of panmixia.

KEYWORDS

Bruchinae, *Callosobruchus*, demographic history, dispersal routes, human-mediated dispersal, insect pest, world-wide distribution

1 | INTRODUCTION

Human-mediated dispersal greatly contributes to the global expansion of species (Blakeslee et al., 2012; Däumer, Greve, Hutterer, Misof, & Haase, 2012). The number of species that became invasive after a first human-mediated introduction is considerable (Rius, Pascual, & Turon, 2008; Brunel, 2009; Roche, Torchin, Leung, & Binning, 2009; Hussner, 2012). Many invasive species are insect pests of crop plants, and can be ecologically and economically devastating (Pimentel, Zuniga, & Morrison, 2005; Sax, Stachowicz, & Gaines, 2005). Moreover, because most of these insect pests are associated with traded fruits and seeds, their dispersion is tightly linked to human activities. In such cases, tracing the evolutionary and phylogeographical history of pest species is informative of the (human-mediated) dispersal events having shaped their current spatial genetic diversity.

The discipline of phylogeography uses molecular markers to identify genetic lineages and interpret their spatial history (Hickerson et al., 2010). Although studies initially focused on wild species (see Hewitt, 2001) it quickly became obvious that studying the phylogeography of pest species was not only interesting from an evolutionary point of view, but could also provide information useful for defining successful pest management programmes (Ochando, Reyes, Segura, & Callejas, 2011). Traditionally, phylogeographical studies have been performed using methods such as, for instance, nested clade phylogeographical analysis (Templeton, 2004, 2008), spatial expansion tests (Excoffier & Lischer, 2010) or the fully integrated analysis of genetic and geographical information (Lemmon & Lemmon, 2008). However, none of these methods incorporate models of demographic expansion or genealogical uncertainty. More recently, Lemey, Rambaut, Drummond, & Suchard (2009), Lemey, Rambaut, Welch, & Suchard (2010) proposed a Bayesian approach for spatio-temporal phylogeographical reconstruction that incorporates stochastic models, assessing uncertainties along ancestral state reconstructions and the underlying phylogeographical process. This approach can simultaneously analyse sequence evolution, demographic models and lineage diffusion in space and time (Bielejec, Rambaut, Suchard, & Lemey, 2011), and has been successfully applied to many organisms (Camargo, Werneck, Morando, Sites, & Avila, 2013; Perea & Doadrio, 2015; Salvi, Bisconti, & Canestrelli, 2015; Vargas, Rumeu, Heleno, Traveset, & Nogales, 2015; Werneck, Leite, Geurgas, Miguel, & Rodrigues, 2015).

In the last decade, phylogeographical investigations of several insect pest species have allowed identification of the number of successful introductions leading to the establishment of populations and further spread into non-native areas (Downie, 2002; Zepeda-Paulo et al., 2010; Cullingham, James, Cooke, & Coltman, 2012). For instance, a world-wide study of the locust, *Locusta migratoria*, showed strong regional and local structuring (Chapuis et al., 2008; Ma et al., 2012). In the olive fly, *Bactrocera oleae*, a world-wide study using molecular data suggested the existence of several allopatric genetic lineages, in particular in Palaeotropical and mediterranean regions, the latter having recently invaded North America (Nardi, Carapelli, Dallai, Roderick, & Frati, 2005). Although important crop pests, the afore-mentioned species are not intimately tied to the crop on which they develop, which greatly limits their spread through human trade. In contrast, bruchine beetles (Coleoptera: Chrysomelidae: Bruchinae) display an obligatory larval stage within legume seeds, a feature that greatly increases their invasive potential through seed trade. Despite their importance, the phylogeographies of agricultural pest bruchine beetles have not been extensively studied, and little is known about the genetic structure or the invasion paths used to reach their current cosmopolitan pest status. Today, only few studies have investigated the world-wide phylogeography of bruchine beetles (e.g. Morse & Farrell, 2005; Alvarez et al., 2005; Carvalho Oliveira, Corrêa, Souza, Guedes, & Oliveira, 2013). In addition, two studies have recently investigated the spatial genetic structure of *Callosobruchus maculatus* (Fabricius). Tuda, Kagoshima, Toquenaga, & Arnqvist (2014) evaluated global sequence variation, demonstrating pronounced genetic differentiation in *C. maculatus* both globally and within Africa, but not within Asia, as well as an overall isolation by distance pattern but an absence of isolation by distance when considering only samples found on the host-plant *Vigna unguiculata* L., the putative ancestral host of *C. maculatus* (see below). Kébé et al. (2016) found that the combination of biogeographical processes, isolation by distance and human-mediated dispersal events can explain the genetic structure of *C. maculatus* in Africa. To further clarify the spatial genetic structure of this pest species, in this study, we examine the spatio-temporal dispersal pattern of this pest across the world, and its drivers.

Callosobruchus maculatus is a multivoltine species (Tuda, 1996) that infests legume seeds both in the field and in storage. If uncontrolled, pest populations can grow exponentially, causing significant losses in seed weight, germination viability and marketability (Caswell, 1968; Southgate, 1979). Biogeographically, although the species occurs in all tropical and subtropical habitats, it is the most abundant in Africa and Asia (Beck & Blumer, 2011). Its biogeographical origin is uncertain, although it is suspected to be closely associated with that of its principal and possibly ancestral African host plant, the cowpea *V. unguiculata* (Tuda, Chou, Niyomdham, Buranapanichpan, & Tateishi, 2005). In this framework, understanding the phylogeography and the demographic history of the pest might allow obtaining valuable information to unravel the species' evolutionary history. Indeed, studying its phylogeography is of particular agronomic and food-security concerns, since identifying the native range of a species' lineages may guide the search for appropriate agents of biological control (Alvarez et al., 2005). Also, recognizing dispersal routes and the world-wide distribution of genetic pools and genetic diversity can help better predict the outcomes of pest control programs, as well as provide tools to understand the distribution of adaptive traits among populations.

In this study, we investigated the phylogeography and demographic history of *C. maculatus*. We used molecular markers, spatio-temporal phylogeographical reconstruction and inferences of the

species' demographic history on specimens from a large part of the species' range with the aims of (1) identifying the spatial genetic structure of *C. maculatus*, (2) investigating the main inter-continental dispersal routes of the species, and (3) inferring the temporal variation in effective population sizes of the species, both globally and at the continental scale. Our overall goal was to elucidate the events that shaped the species' recent demographic history.

2 | MATERIALS AND METHODS

2.1 | Sampling, DNA extraction, amplification and sequencing

To obtain the most complete representation of the genetic variation in *C. maculatus*, we sampled 105 individuals world-wide (Appendix S1). Genomic DNA was extracted from all specimens using the DNeasy 96 Blood & Tissue Kit (QIAGEN, Hilden, Germany). Four DNA regions [one nuclear—the internal transcribed spacer ITS1—and three mitochondrial regions—cytochrome oxydase b (Cytb), cytochrome oxydase I (COI) and cytochrome oxydase II (COII)] were amplified and sequenced. The primers used were CIL and CIU for ITS1 (Vogler & Desalle, 1994), CB1 and CB2 for Cytb (Simon et al., 1994), C1-N-2191 and C1-J-1751 for COI (Simon et al., 1994), and TL2-J-3037 and modC2-N-3661 for COII (Mardulyn, Milinkovitch, & Pasteels, 1997). PCR reactions were performed in a 30-μl volume containing 1 U *Taq*-polymerase, 0.1 mM dNTP, 1× PCR buffer (PROMEGA, Heidelberg, Germany) and 1.0 μM of each primer, and consisted of an initial denaturation at 93°C for 1 min 30 s, followed by 35–36 cycles of a 35-s denaturation phase at 93°, 1 min annealing (at 47°C for Cytb and COI, 53°C for COII and 57° for ITS1) and a 1-min extension, and ending with a final extension at 72°C for 10 min. PCR products were purified using a QIAquick PCR Purification Kit (QIAGEN, Hilden, Germany) according to the manufacturer's instructions. Finally, Sanger sequencing was performed at the Centre for Integrative Genomics (CIG), University of Lausanne, using the PCR primers.

2.2 | Sequence variation and genetic structure

We checked and edited all sequences using MEGA 5.1 (Tamura et al., 2011). We aligned them using the ClustalW algorithm (Thompson, Higgins, & Gibson, 1997) as implemented in BIOEDIT 7.0.5 (Hall, 2005), and further visually revised them. We searched for evidence of recombination in the ITS1 nuclear marker using the RECOMBINATION DETECTION PROGRAM (RDP) Beta 4.5 (Martin et al., 2010). We also checked the mtDNA reading frames using MEGA 5.1, which revealed no evidence of putative nuclear pseudogenes (NUMTS; Cristiano, Fernandes-Salomao, & Yotoko, 2012; Martins et al., 2007) in the dataset. The three mtDNA gene alignments were then concatenated to obtain a mitochondrial (mtDNA) supermatrix using the program SEQUENCE MATRIX 1.7.8 (Vaidya, Lohman, & Meier, 2011).

We calculated the number of unique haplotypes (alleles), haplotype (h) and nucleotide (π) diversities using DNASP 5.10.01 (Librado & Rozas, 2009). Values were calculated for the entire dataset, as well as for each sampled geographical region independently (Africa, America and Asia + Oceania).

We examined the population genetic structure using an analysis of molecular variance (AMOVA) based on pairwise F_{ST} values, as implemented in ARLEQUIN 3.5.1.2 (Excoffier & Lischer, 2010). AMOVAs were performed on the ITS1 and the mtDNA datasets separately. In this analysis, the group level corresponds to the continental level (Africa, America, Asia + Oceania) and the population level corresponds to sampled localities within continents. The statistical significance of values was obtained by performing 10,000 random permutations of the data.

2.3 | Phylogenetic analyses

We inferred phylogenetic relationships applying a Bayesian Markov chain Monte Carlo (MCMC) phylogenetic search using BEAST 1.6.2 (Drummond & Rambaut, 2007). Because a preliminary phylogenetic analysis showed that the ITS1 region was not informative, the analyses were done on the mtDNA dataset only. It is important to note here that our results thus represent the history of this maternally inherited marker, and should be further explored in future studies using other nuclear markers or high-throughput sequencing methods.

We partitioned data by locus, and identified the best fit model of molecular evolution for each partition using the Akaike information criteria (AIC, Akaike, 1973), as implemented in MRMODELTEST 2.3 (Nylander, 2004). A general time reversible (GTR) model was selected for the COII locus, and a Hasegawa–Kishino–Yano (HKY) (Hasegawa, Kishino, & Yano, 1985) model for COI and Cytb. The COI and COII DNA regions were subject to a gamma distribution, while the Cytb presented invariable sites. We set the substitution rates to different values for each gene: COI (1.72% ± 0.8%), COII (0.52% ± 0.3%), CytB (0.34% ± 0.2%). These were obtained from Borer et al. (2010) and Pons, Ribera, Bertranpetit, & Balke (2010); and were used with an uncorrelated relaxed clock model assuming a lognormal distribution of rates (Drummond, Ho, Phillips, & Rambaut, 2006). Six independent MCMC analyses were run for 100,000,000 generations, sampling one tree every 1,000 generations. After confirming stationarity using TRACER 1.6 (Rambaut, Suchard, Xie, & Drummond, 2014), we discarded the first 10% of trees (i.e. the burn-in phase) and we constructed a maximum credibility tree using TREEANNOTATOR 1.4.5 (Drummond & Rambaut, 2007).

We built statistical parsimony networks for the mtDNA dataset with TCS 1.21 (Clement, Posada, & Crandall, 2000). Here, parsimony probability was set to 95%.

2.4 | Demographic history

To investigate the demographic history of *C. maculatus*, we used the mtDNA data and considered three different datasets: (1) all samples (complete dataset), (2) all African samples, and (3) all Asian + Oceania samples. We used three methods to test the demographic history of *C. maculatus*. First, we used DNASP 5.10.01 to calculate Tajima's

D (Tajima, 1989), Fu's *Fs* (Fu, 1997) and *R*2 (Ramos-Onsins & Rozas, 2002) and thus assess population expansion. We evaluated their significance with 10,000 coalescent simulations. In this test, significant negative values of Tajima's *D* and Fu's *Fs* indicate a recent population expansion.

Second, we performed a mismatch distribution analysis using ARLEQUIN. This analysis evaluates the distribution of the number of nucleotide mismatches between all pairs of DNA sequences from a population. Here, populations having experienced rapid demographic growth in the recent past exhibit unimodal distributions, while populations at the demographic equilibrium have multimodal distributions (Rogers & Harpending, 1992). We statistically tested the validity of the expansion model with a bootstrap approach, followed by a calculation of the sum of square deviations (SSD) between the observed and the expected distribution (Schneider, Roessli, & Excoffier, 2000). We also computed a Harpending's raggedness index (Rg), which estimates the fluctuation in the frequency of pairwise differences (Harpending, Sherry, Rogers, & Stoneking, 1993).

Third, we used the extended Bayesian skyline plot (EBSP; Heled & Drummond, 2008) method, as implemented in BEAST. This method considers the coalescent history of each gene and simultaneously characterizes the effective population size through time using a MCMC sampling. We performed two independent runs for 100,000,000 generations, sampling one tree every 10,000 generations. Because more complex models (see phylogenetic analysis section) could not reach convergence, we applied a unique model of evolution (HKY) and an identical strict substitution rate to all partitions (0.862%/Myr; mean substitution rate value; see above). Once the two runs reached convergence, we combined the results using LOGCOMBINER 1.5.3 (Drummond & Rambaut, 2007) and calculated the population sizes over time in BEAST.

2.5 | The effect of population structure and departure from panmixia on EBSP results

The EBSP method has strong assumptions regarding the demographic characteristics of the population(s) being analysed (Heled & Drummond, 2008). One of these assumptions is panmixia, which is often violated in phylogeographical analyses. Because our results show that *C. maculatus* presents a spatial genetic structure that is associated with reduced among-demes genetic exchanges (see below), we performed supplementary analyses to explore how departure from panmixia might affect our results. So far, to our knowledge, only two studies (Pannell, 2003 and Chikhi, Sousa, Luisi, Goossens, & Beaumont, 2010) have investigated the consequences of population structure on the characterization of effective population size through time, but none of those approached the topic from a phylogeographical perspective. More recently, Heller, Chikhi, & Siegismund (2013) demonstrated how Bayesian skyline plot results can be affected by population structure. Because of this, in this study, we decided to evaluate the consistency of the demographic results obtained when different reduced datasets were considered, using a bootstrapping approach. We thus performed the same EBSP analysis for five sets of 10 bootstrapped datasets. We randomly selected one sample per population ("one sample per population" datasets) for (1) all populations ("one sample per population, full" dataset), (2) all African populations ("one sample per population, Africa" dataset), (3) all Asian + Oceania populations ("one sample per population, Asia" dataset), while we randomly selected 30 samples ("random" datasets) from (4) all populations ("random, full" dataset) and (5) all African populations ("random, Africa" dataset). Subsampling could not be done on Asian + Oceania samples, because they led to a dataset identical to the original one (i.e. our global dataset comprises 30 Asian specimens). We should be able to identify an effect of the lack of panmixia (indicated by spatial genetic structure) on the EBSP results by comparing results from "random" to those from "one sample per population" datasets. Specifically, while in the "random" datasets we might be able to track the effect of panmixia since we allow choosing many representatives from the same population, we can expect this effect to be less strong or absent when sampling in the "one sample per population" datasets.

2.6 | Discrete phylogeographical analyses

To reconstruct the global spatial diffusion process for *C. maculatus*, we applied a Bayesian discrete phylogeographical approach (Lemey et al., 2009) using BEAST and the COI sequences. In addition to the 105 sequences, 118 already published COI sequences (Tuda et al., 2014) were integrated in our dataset, resulting in a total of 223 sequences (Appendix S1). Because of computational restrictions, we ran the analysis using a subsample of the full COI dataset (92 samples), by randomly selecting for each locality only one sample per haplotype. We used default settings, applied the same model of molecular evolution as presented above, and used an uncorrelated relaxed clock model assuming lognormal rate distribution (Drummond et al., 2006). We assigned each sequence to one of the 48 localities, and the exchange process of locations throughout the entire phylogeny was modelled using a symmetric substitution model with the Bayesian stochastic variable selection model (BSSVS). This procedure uses Bayes Factor (BF) to identify the most likely colonization process. The MCMC was run for 200,000,000 generations, sampling one tree every 20,000 generations. After confirming stationarity of parameter estimates using TRACER v1.6, the first 10% of trees (i.e. the burn-in period) were discarded and a maximum credibility tree was built using TREEANNOTATOR v1.4.5. The tree with the estimated ancestral locations through time was converted to a keyhole markup language (kml) file using SPREAD (Bielejec et al., 2011).

3 | RESULTS

3.1 | DNA sequence variation and genetic structure

No insertions, deletions or stop codons were present in any of the mitochondrial sequences, indicating that the retrieved sequences are not nuclear pseudogenes. We could not detect recombination in the nuclear dataset. We found 64 haplotypes and 27 alleles in the

mitochondrial (1536 bp) and nuclear genes (757 bp) respectively (Table 1). Haplotype (*h*) and nucleotide (π) diversities were, respectively, 0.98 and 0.010 for the mitochondrial genes, and 0.89 and 0.00047 for the ITS1 dataset.

AMOVAs (Table 2) showed that the among-continents grouping significantly explained 12.7% of the mtDNA genetic variance, while the values were not significant for the nuclear dataset. Among-population differences significantly explained 48.7% and 49.0% of the genetic variance for the mitochondrial and nuclear datasets, respectively, while 38.6% and 53.8% of the variation was significantly explained by within-population differences in the mitochondrial and nuclear datasets respectively.

TABLE 2 Analysis of molecular variance (AMOVA) for the mitochondrial and nuclear regions analysed in *Callosobruchus maculatus*

	Source of variation	*df*	Variance (%)	Fixation indices	*p*-value
mtDNA	Among continents	2	12.7	F_{CT} = 0.13	.004
	Among population within groups	22	48.68	F_{ST} = 0.61	<.0001
	Within populations	77	38.62	F_{SC} = 0.56	<.0001
ITS1	Among continents	2	−2.87	F_{CT} = −0.03	.61
	Among population within groups	22	49.03	F_{ST} = 0.46	<.0001
	Within populations	77	53.83	F_{SC} = 0.48	<.0001

3.2 | Phylogenetic analyses

The mtDNA phylogeny (Figure 1) showed that the monophyly of *C. maculatus* was strongly supported, and seven well-supported and two less well-supported clades were retrieved. Clade I was composed of samples from Asia and Brazil. Clade II and clade VII comprised samples from western Africa. Clade IV included individuals from Africa and California. With the exception of one individual from Madagascar, clade V was composed of individuals from Asia. Clade VI comprised samples from western Africa and one specimen from Syria. Clade VIII was composed of individuals from Africa and Asia. Finally, clades III and IX were composed of samples from Congo and Uganda respectively. The mtDNA parsimony network (Appendix S2) showed the same relationships as the Bayesian phylogenetic tree.

3.3 | Historical demography

The neutrality tests of Tajima's *D* (p = 0.033) and Fu's *Fs* (p = 0.002) showed significant negative values when considering the complete sampling, suggesting a past demographic expansion. Ramos-Onsins and Rozas' *R*2 was significant (p = 0.035) and reached results similar to the other tests. Both *D* and *Fs* were negative in African and Asian populations, but only *Fs* was significant in African populations (p = 0.021). *R*2 values were not significant in any of the continents (Table 3).

The frequencies of pairwise differences in the mismatch distribution analysis within the full and the African datasets were consistent with an expansion model (Figure 2). The SSD and Rg statistics derived from the mismatch distribution were not significant and thus, the null hypothesis of recent population expansion could not be rejected. These results contrast with the analysis of Asian populations, for which the Rg was significant, indicating a less important demographic expansion in that region.

The EBSP estimation for the full dataset (Figure 3a) indicated an initial phase of constant effective population size that ended about 13,000 years ago (ya), followed by an increase in the effective population size. This growth continued until reaching a peak at about 230 ya, after what the EBSP identified a strong decrease in the effective population size. This decrease is unexpected, since we know that, particularly during the last two centuries, this species should have seen its population size grow strongly as a result of increased world-wide commercial seed exchanges. This general pattern was also identified in the African and Asian datasets. It is worth mentioning that although the general demographic pattern is similar across continents, the population size values differ, that is, ca. 170,000 for the complete dataset, ca. 128,000 for the African dataset and ca. 32,000 for the Asian one.

3.4 | The effect of population structure and departure from panmixia on EBSP results

The analysis of the EBSP performed on the bootstrapped datasets identified possible effects of the departure from panmixia, consequent to the strong genetic structure present in our dataset. While in all "random" datasets we retrieved the same unexpected pattern of a demographic reduction during the last centuries (Figure 3b,c), the effect was not perceptible in the "one sample per population"

TABLE 1 Total genetic diversity of *Callosobruchus maculatus* and genetic diversity within each of the three (Africa, America and Asia + Oceania) continents for the mitochondrial and nuclear regions. *N*, sample size; *H*, number of haplotypes; *h*, haplotype diversity; π, nucleotide diversity estimates

	Mitochondrial DNA (cytb/COI/COII)				Nuclear DNA (ITS1)			
Groups	*N*	*H*	*h*	π	*N*	*H*	*h*	π
Total	105	64	0.98 ± 0.006	0.0100 ± 0.0003	105	27	0.89 ± 0.016	0.00047 ± 0.0001
Africa	60	38	0.97 ± 0.009	0.0102 ± 0.0004	60	16	0.86 ± 0.025	0.0010 ± 0.0001
America	13	5	0.81 ± 0.066	0.0050 ± 0.0007	13	9	0.94 ± 0.058	0.0004 ± 0.0002
Asia + Oceania	32	22	0.96 ± 0.020	0.0101 ± 0.0006	32	12	0.89 ± 0.033	0.0006 ± 0.0003

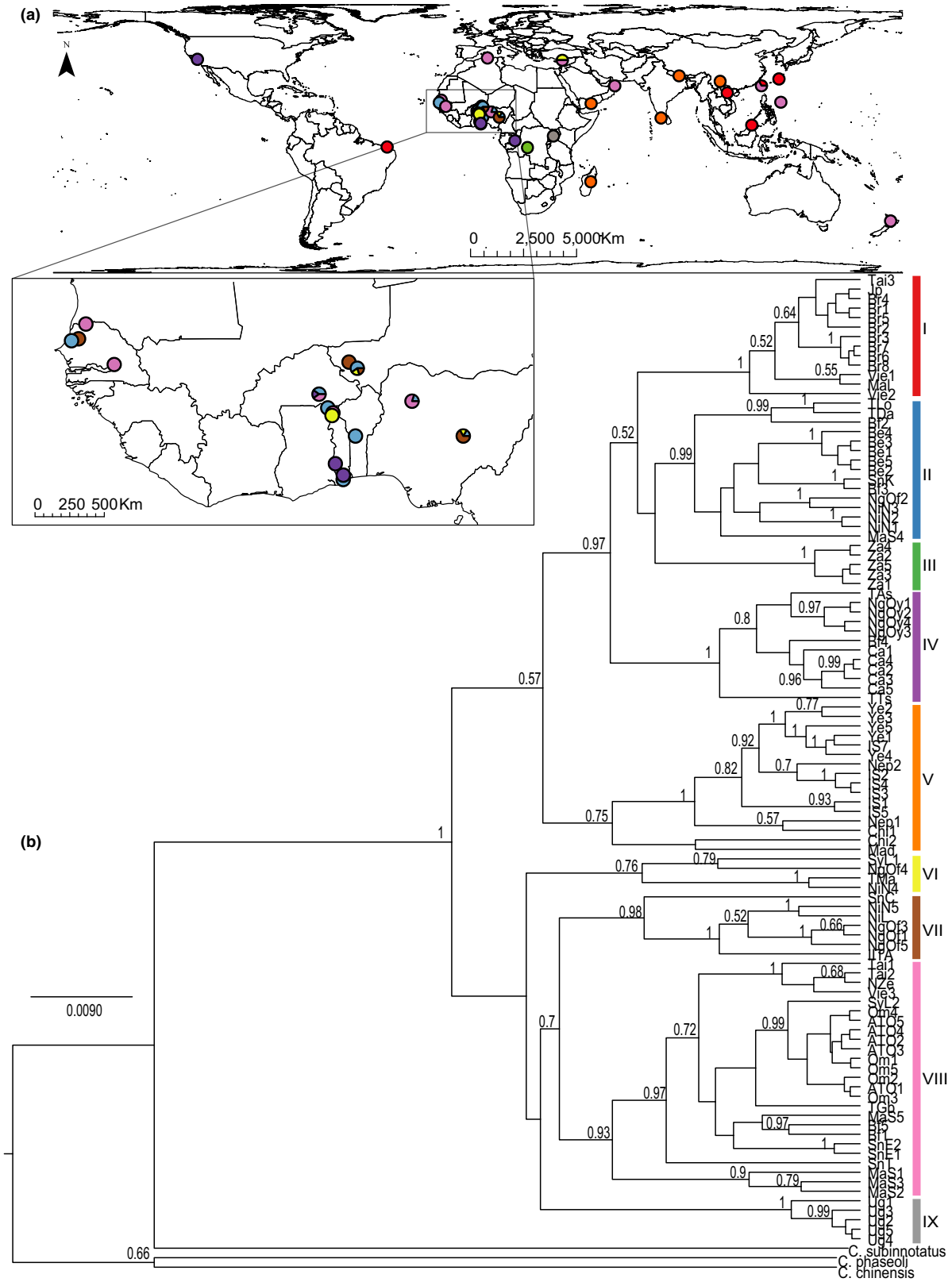

FIGURE 1 (a) Spatial distribution of clades with pie-chart proportions corresponding to the frequency of clades in each population. (b) Bayesian maximum credibility tree of the mitochondrial dataset of *Callosobruchus maculatus* obtained from BEAST. Bayesian posterior probabilities higher than 0.5 are shown on nodes

TABLE 3 Tajima's *D*, Fu' *Fs*, Ramons-Onsins and Rozas *R2*, sum of square deviation (SSD) and raggedness index (Rg) for the studied populations of *Callosobruchus maculatus*. *, $p < .05$

Group	*D*	*Fs*	*R2*	SSD	Rg
Total	−1.53*	−21.99*	0.05*	0.0022	0.0048
Africa	−1.40*	−9.11*	0.06	0.0063	0.0075
Asia	−0.25	−2.93	0.11	0.0130	0.0345*

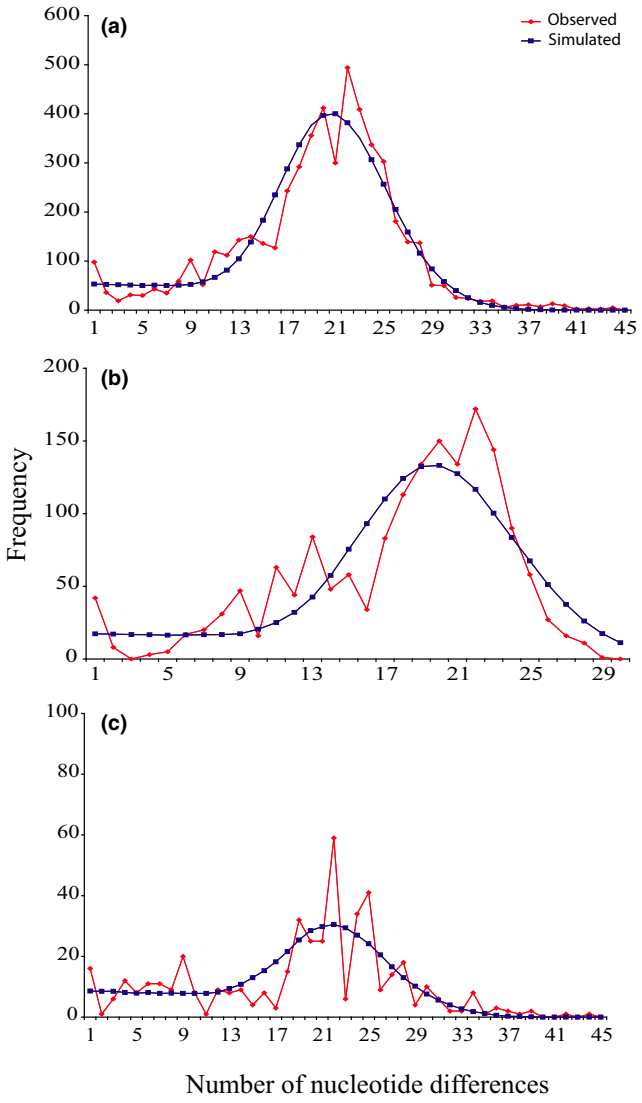

FIGURE 2 Sequence-pairwise mismatch distribution of *Callosobruchus maculatus*. X indicates the number of nucleotide differences; Y indicates frequencies. (a) All populations. (b) African populations. (c) Asian + Oceanian populations

datasets (Figure 3d–f). It appears that when the genetic structure (or departure from panmixia) is stronger, as it is the case in our "random" datasets, the analysis inaccurately estimated the demographic history, a bias that disappears when the dataset becomes less genetically structured (or more panmictic), as in the "one sample per population" cases.

It should be pointed that all "one sample per population" results were also highly congruent with the suspected timing of the species' world-wide expansion. The timing of population expansions observed for the full and African datasets started ca. 11,000 and ca. 9,400 ya, respectively, whereas for the Asian dataset, the expansion was more recent, starting ca. 800 ya.

3.5 | Discrete phylogeographical analyses

The maximum clade credibility (MCC) tree based on the DPAs showed considerable uncertainty for the area of origin of *C. maculatus* (results not shown). However, using a BF cut-off of four, we identified 23 global dispersal routes (Figure 4), with those between India and Yemen having the highest support with a BF of 11.15 (Appendix S3). Three connections between Africa and Asia were supported, with the route between Nigeria and India having the highest support (BF = 5.44). Five routes between Asia and Oceania were supported, the later having no connection with Africa, while no connection was supported between America (North and South) and the rest of the world.

4 | DISCUSSION

In this study, we aimed to unravel the phylogeographical history of *C. maculatus*, a cosmopolitan insect pest tightly associated with its host plant. Building on the works of Tuda et al. (2014) and Kébé et al. (2016), we combine biogeography and population genetics analyses to infer the spatial and temporal patterns of evolution of this insect pest at the scale of its whole distribution. Based on mtDNA, we found spatially structured genetic variation and significant signal for demographic expansion. Below, we discuss our results in further detail.

4.1 | Overall patterns of genetic structure

Most of the mtDNA genetic differences were present among and within populations, with little differentiation among continents (Table 2). This indicates the presence of high local genetic structure and high inter-population differentiation.

From a phylogenetic perspective, we retrieved nine clades, eight included African samples, and four were exclusively African (Figure 1). In Africa, we observed a strong genetic differentiation between western, eastern, northern and central populations, a pattern also previously identified in this pest and in other species. For instance, the geographical divergence observed between West Africa and the Democratic Republic of the Congo, as well as between West Africa and Uganda is identical to that found by Kébé et al. (2016) for the same species, and for *Busseola fusca* (Sezonlin et al., 2006). However, in contrast to that study, in which the divergence time was estimated to the early Pleistocene, the intraspecific differentiation in *C. maculatus* appears to be more recent and is probably explained by the recent introduction of cowpea in some of these

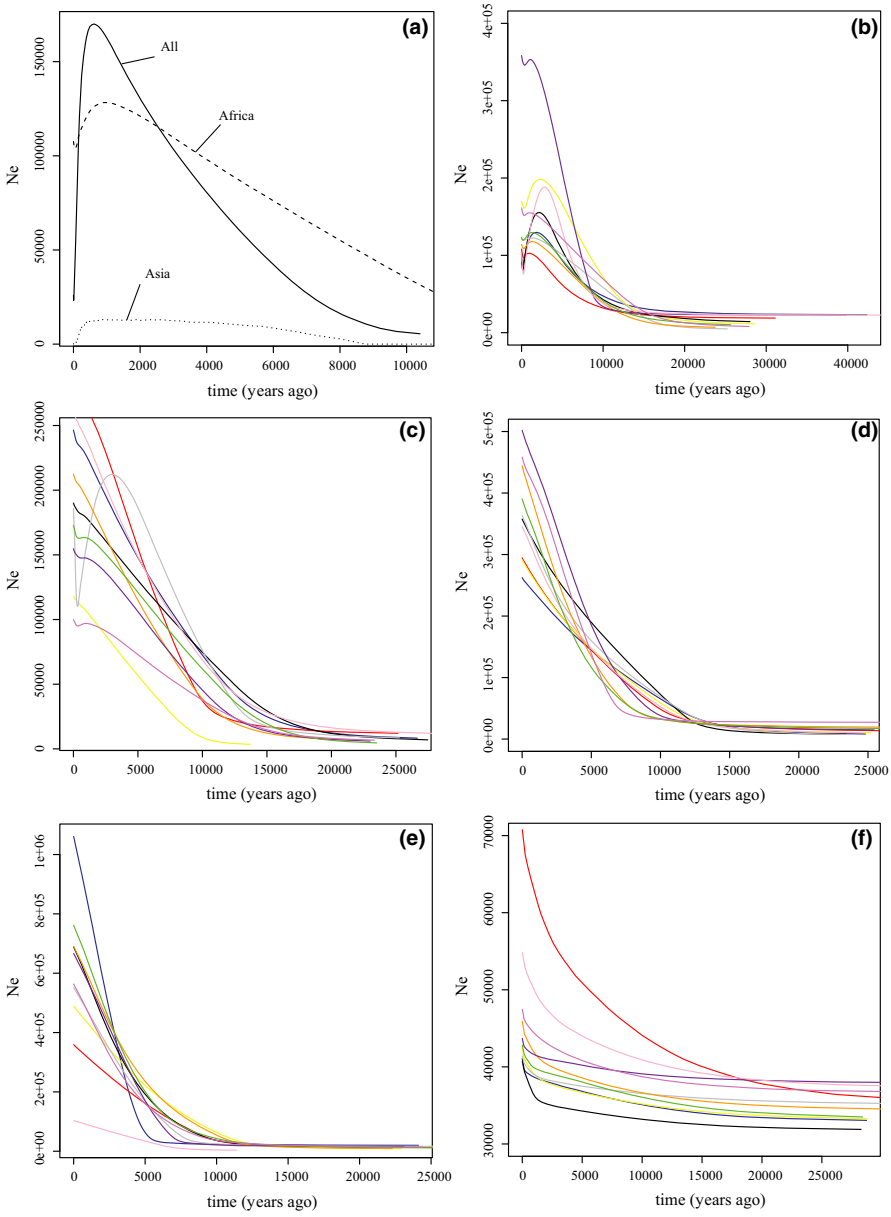

FIGURE 3 Demographic history of *Callosobruchus maculatus* performed with mitochondrial genes of (a) All, African and Asian datasets and inferred from the subsampled datasets (b, c, d, e and f) using the EBSP approach. X shows time in years; Y indicates effective population size (Ne). Colours indicate each subsampled dataset. (b) "random, full" dataset. (c) "random, Africa" dataset. (d) "one sample per population, full" dataset. (e) "one sample per population, Africa" dataset. (f) "one sample per population, Asia" dataset

regions. Asian specimens clustered mainly in three clades, with one of them containing only specimens from southeastern Asia. Specimens from North America grouped with West African samples, while specimens from Brazil clustered with Asian populations. These observations suggest that dispersal into the Americas may have happened from West Africa and Asia, a very likely scenario when considering intensive global trading.

4.2 | Historical demography of *C. maculatus*

Our demographic analyses (i.e. neutrality tests, mismatch distributions and EBSP) converged on indicating a recent population size expansion in the whole dataset, as well as in the African subset alone. These results agree with the observations of Tuda et al. (2014) and Kébé et al. (2016). However, the analysis shows weak support for such an expansion in Asia (Figure 3). The pattern retrieved from the EBSP on the full and "random" bootstrapped datasets showed a first demographic expansion about 13,000 ya, followed by a strong population contraction about 230 ya (Figure 3a–c).

While the first demographic expansion agrees with historical events, as it corresponds to the warming climate, preceding the beginning of the Holocene, the population size contraction at 230 ya is unexpected. Indeed, we could not identify any historical event able to explain a pattern of decrease in effective population size two centuries ago, and would have rather favoured a scenario of recent population size growth as a result of increased world-wide commercial seed exchanges. However, as mentioned above, the EBSP analysis assumes panmixia (Ho & Shapiro, 2011), which is largely violated in our spatially structured and locally diverse dataset (Table 2). This is confirmed by the results obtained from the

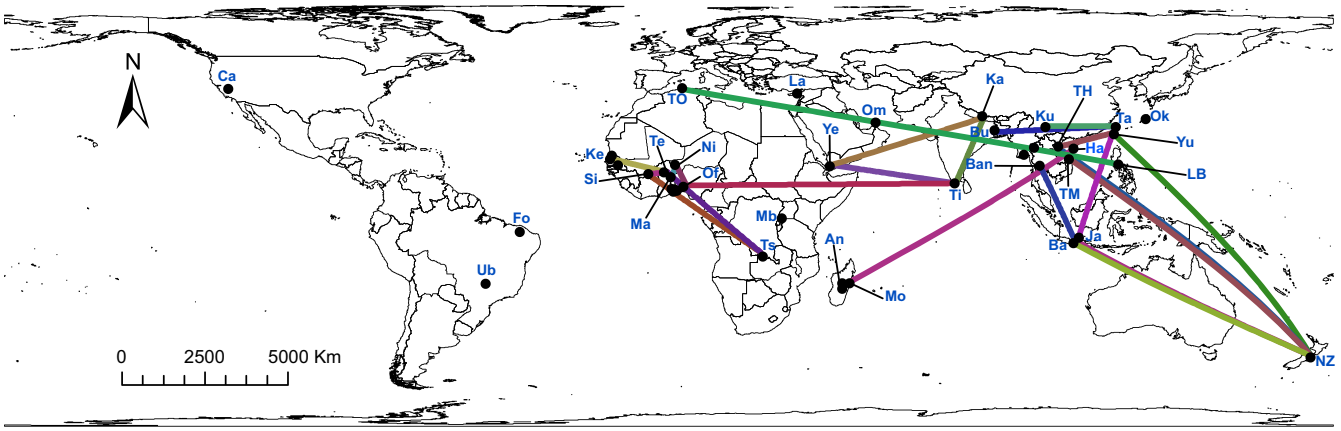

FIGURE 4 Map of supported colonization routes (BF > 4) of *Callosobruchus maculatus* inferred using Bayesian stochastic search variable test (BSSVS). Lines connecting localities indicate historical dispersal events and their colouring indicates the connections that were statistically supported in the inferred phylogeny. An, Antananarivo; Ba, Bali; Ban, Bangkok; Bu, Burdwan; Ca, California; Fo, Fortaleza; Ha, Hainan; Ja, Java; Ka, Kathmandu; Ke, Kebemer; Ku, Kunming; La, Lattakia; LB, Los Banos; Ma, Mango; Mb, Mbarara; Mo, Moramanga; Ni, Niamey; NZ, New Zealand; Of, Offa; Ok, Okinawa; Om, Oman; Si, Sikasso; Ta, Taipei; Te, Tenkodogo; TH, Thanh Hoa; Ti, Tirunelveli; TM, Tam Ky; TO, Tizi Ouzou; Ts, Tshopo; Ub, Uberlandia; Ye, Yemen; Yu, Yungkang

subsampling strategy (Figure 3d–f), where the decrease in population size was not perceptible in any of the "one sample per population" (reduced local structure) datasets. Moreover, this hypothesis is also in agreement with the results obtained in a study on the world-wide phylogeography of another invasive insect species (*Locusta migratoria*, Ma et al., 2012), in which such incongruent EBSP inferences were also obtained. Thus, these results warn on the interpretation of such analyses when applied to the study of spatially structured and/or isolated populations.

The EBSP inferences from the "one sample per population" datasets indicate a population growth just before or during the early Holocene, both for the whole dataset (around 12,000 ya) and for the African subset alone (around 8,000 ya). The latter pre-dates the more modest and younger expansion in Asian populations (around 800 ya, Figure 3f). The recent moderate expansion in Asia still suggests an introduction into the area more ancient than initially thought, which agrees with the high genetic diversity levels observed in the region (Table 1). The EBSP also indicated a slow and more recent increase in the population size of the Asian dataset, what could be associated with a time-lag related to a host-plant switch. Indeed, cowpea is less cultivated in Asia than in Africa, and it is possible that the bean beetle required some time to adapt and/or expand into other legumes more widespread in the Asian continent (e.g. *Cicer arietinum*).

4.3 | Historical dispersal routes of *C. maculatus*

Evidence and hypotheses (Anton, Halperin, & Calderon, 1997) suggest that Africa is the region of origin of *C. maculatus*. Previous phylogenetic studies (Tuda, Rönn, Buranapanichpan, Wasano, & Arnqvist, 2006) showed that the species belongs to a clade almost exclusively Afrotropical. Several results in the present study also suggest an African origin for the species. First, we identified a high number of unique haplotypes in African populations (data not shown). Second, our EBSP inferences recover the oldest historical events in the African dataset. Further, the DPA analysis of COI identified significant dispersal routes (BF > 4) between Africa and Asia, and between Asia and New Zealand, but not between the Americas and the other continents. This suggests a relatively recent presence of *C. maculatus* in both the Americas and Oceania, and suggests initial dispersal events from Africa and Asia. On this, the route identified between Offa (Africa) and Tirunelveli (Asia) is interesting and informative. Indeed, Friedman & Rowlands (1977) emphasized the existence of long-distance exchanges since 5,000 ya between some regions of Africa and Asia. According to Allen (1983), cowpea was introduced from Africa to the Indian subcontinent approximately 2,000 to 3,500 ya; a period that could correspond to the introduction of *C. maculatus* to Asia, and which is supported by the connection we observed between Nigeria and India.

5 | CONCLUSIONS

Our results suggest that the world-wide colonization of *C. maculatus* likely occurred at the beginning of the Holocene, following human-mediated dispersal of domesticated crops such as *V. unguiculata*. In addition, our results reveal a strong signal of long-distance dispersal. We propose that *C. maculatus* dispersed first into Asia, mainly through human-mediated activities and once trade was established between the two areas. The relatively old age of these inter-continental contacts could explain the high levels of genetic diversity encountered in Asia. Dispersal events towards other regions of the world seem to be, based on our results, more recent, and may have happened from both Africa and Asia.

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DATA ACCESSIBILITY

New sequences are available in GenBank under accession numbers KY995204-KY995246 (COI), KY995247-KY995284 (Cytb) and KY995285-KY995321 (COII).

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BIOSKETCH

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SUPPORTING INFORMATION

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