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The mango seed weevil *Sternochetus mangiferae* (Fabricius) (Coleoptera: Curculionidae) is characterized by low genetic diversity and lack of genetic structure

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Abstract

1 The mango seed weevil *Sternochetus mangiferae* (Fabricius) is distributed across the major mango-producing areas of the world and causes significant economic losses of mango fruit. Despite its importance as a crop pest, we have only limited information on the population genetics of the mango seed weevil.
2 Here, we examined the genetic diversity of this important pest using specimens intercepted by Beijing Customs District P. R. in China from 41 countries and regions. We used segments of the mitochondrial gene cytochrome c oxidase subunit I and the nuclear gene elongation factor 1-alpha to examine population genetic structure in this species.
3 Our results showed that genetic diversity is low in *S. mangiferae*, with a mean genetic distance of 0.095–0.14%. Other population genetic parameters also indicated a low level of genetic diversity among samples from a large geographic range. Analysis of molecular variance revealed little population genetic structure, and mismatch distribution analyses provided evidence of a population expansion, although other demographic metrics of population expansion were nonsignificant.
4 We suggest that the observed low level of genetic diversity and population genetic structure in *S. mangiferae* supports the hypothesis that the population genetics of this species has been impacted by anthropogenic transportation of mangoes and weevils.

Keywords Demography, genetic diversity, mango seed weevil, population genetic structure.

Introduction

Mango, *Mangifera indica* L., is an important fresh fruit crop that is produced in more than 100 countries (Abdulla *et al.*, 2016; Siddiq *et al.*, 2017; Yadav & Singh, 2017). Palaeobotanical evidence suggests that mangoes originated in the Indo-Burma-Malay region and have been cultivated in India as for as long as 4000–6000 years. From the seventh century to the present, this crop was spread by humans to China, East Africa, the Philippines and other tropical and subtropical areas of the world (Yadav & Singh, 2017). Mangoes have several pests, including *Sternochetus* weevils (Coleoptera: Curculionidae), that inhabit mango fruits. Of these weevils, the mango seed weevil *Sternochetus mangiferae* (Fabricius) is the most widely distributed and is a serious pest (Reddy & Sreedevi, 2016). This species was believed to have originated in India alongside mango (Smith, 1996; CABI/EPPO, 2005), but now, *S. mangiferae* is distributed across the major mango-producing regions of the world (Braimah & van Emden, 2010), including Australasia, Oceania, Asia, Africa, Hawaii, the Caribbean and South America (Woodruff & Fasulo, 2018).

Sternochetus mangiferae is a strict specialist and only feeds on mango (Louw, 2013; Abdulla *et al.*, 2016; Woodruff &

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Fasulo, 2018). The mango seed weevil was listed as a 'dangerous quarantine pest' by many countries, and its presence in exported mangos can lead to the rejection of entire shipments to prevent the spread of this pest into mango-producing countries that remain pest-free (Yahia, 2006; Hossain *et al.*, 2011; Abdulla *et al.*, 2016). Because of its economic importance, the life history characteristics of *S. mangiferae* have been well studied (Balock & Kozuma, 1964; Hansen *et al.*, 1989; Follett, 2002; Braimah *et al.*, 2009), and various management approaches were developed (Hansen, 1993; Peña *et al.*, 1998; Verghese, 2000; Braimah & van Emden, 2010; Abdulla *et al.*, 2016; Dassou *et al.*, 2018). Despite the importance of *S. mangiferae* as a crop pest, we currently lack molecular population genetic data for this species. Given that adult *S. mangiferae* are weak fliers that usually remain near their natal host tree (Smith, 1996), we predicted that there should be strong genetic structuring of populations caused by the natural history of these insects. However, long-distance dispersal may occur through anthropogenic transportation of fruits and seeds that contain *S. mangiferae* (Jarvis, 1946; Griesbach, 2003; Braimah & van Emden, 2010; Woodruff & Fasulo, 2018). To help resolve these contrasting predictions, we explored the genetic diversity and population genetic structure to investigate the historical demography of the mango seed weevil. Understanding the population genetic structure of pest species such as *S. mangiferae* is a critical first step in their control as many genetic techniques used to suppress pest populations are impacted by their population genetics (Leftwich *et al.*, 2016).

Materials and methods

Sampling

We obtained 175 specimens of *S. mangiferae* and 2 specimens of *Sternochetus olivieri* (Faust) from the Beijing Customs District P. R., China, that were transported between 2015 and 2018. The samples were obtained from mangoes brought by airplane passengers from 41 countries or regions (Table 1). The specimens were preserved in 100% ethanol and stored at −30 °C until DNA extraction. For our analyses, we treated the samples from each country or region as a 'population'.

DNA extraction, amplification and sequencing

We extracted genomic DNA using the TIANamp Genomic DNA Kit (Tiangen Biotech (Beijing) Co. Ltd., China). We used the nondestructive DNA extraction methods (Jurado-Rivera *et al.*, 2009) because it allowed us to retain the beetles as voucher specimens. Two gene regions were amplified: ∼640 bp of the 5′ end of the mitochondrial cytochrome c oxidase subunit I (COI) and a ∼740 bp fragment of the nuclear elongation factor 1-alpha gene (EF1-α). The amplification protocols followed that of a previous study (Xue *et al.*, 2011), and both the forward and reverse products were sequenced by Beijing Sunbiotech Co. Ltd. We aligned and edited the sequences using CodonCode Aligner 3.7.1 (CodonCode, Dedham, Massachusetts). We assessed the quality of our sequences by aligning them to closely related species of Curculionidae, verifying that there were no stop codons. EF1-α sequences from 34 individuals were heterozygous as judged by double peaks in chromatograms from both directions. Thirty-three of the individuals had only a single heterozygous site, and these haplotypes were scored manually. A single individual had two heterozygous sites (Ethiopia_232), and so, the gametic phase was defined in PHASE 2.1.2 (Stephens *et al.*, 2001). We did this by using 10 000 Markov chain Monte Carlo (MCMC) iterations, sampled every 10 iterations, and the first 1000 iterations were removed as burn-in. All the sequences were deposited into GenBank (COI: MT706457 – MT706633; EF1-α: MT747670 – MT747829).

Genetic diversity

We used a total of 181 COI sequences (175 newly sequenced and six from GenBank: HQ268806-HQ268809, KU871375 (from India), KM443510 (from Germany)) and 160 EF1-α sequences in the genetic diversity analysis. For the outgroups, we included four COI sequences from *S. olivieri* (two newly sequenced and two from GenBank: MG017439, MG017440) and one EF1-α sequence from *Sympiezoscelus spencei* (KP677857) and *Hylastes attenuatus* (KY805871).

Intra- and inter-specific sequence divergence of *S. mangiferae* and *S. olivieri* was calculated with MEGA 7.0 (Kumar *et al.*, 2016) using Kimura two-parameter distances. For each gene, we calculated the number of polymorphic sites (Np), the number of haplotypes (h), haplotypic diversity (Hd), the average number of nucleotide differences (K) and nucleotide diversity (π) using DNaSP 6.12.03 (Rozas *et al.*, 2017). We used TCS version 1.2.1 (Clement *et al.*, 2000) to create haplotype networks with a probability cut-off of 95% for both the COI and EF1-α datasets.

Phylogenetic reconstructions

Phylogenetic trees were constructed for each gene using neighbour joining (NJ) and maximum likelihood (ML) methods. NJ trees were inferred using MEGA 7.0 (Kumar *et al.*, 2016), and ML trees were obtained using RaxML 8.2.10 (Stamatakis, 2014). The trees were constructed using the CIPRES Science Gateway portal (https://www.phylo.org/) (Miller *et al.*, 2010). The best-fit models of nucleotide substitution were selected under the corrected Akaike Information Criterion with jModelTest 2.1.3 (Darriba *et al.*, 2012). For both NJ and ML trees, 1000 nonparametric bootstrap replicates were calculated.

Population structure and demography

To characterize the distribution of genetic variation among and within populations, we conducted a molecular analysis of variance (AMOVA) with 10 100 permutations using Arlequin 3.5.1.3 (Excoffier & Lischer, 2010). Populations with fewer than four samples were excluded from this analysis.

We also estimated mismatch distributions in DnaSP 6.12.03. If populations have undergone sudden expansions, the mismatch distribution will be unimodal, whereas stable or contracting populations have multimodal mismatch distributions (Rogers & Harpending, 1992; Galbreath *et al.*, 2009). To test whether the mismatch distributions fit a uni- or multimodal distribution, we

Table 1 Sequences of the mango seed weevil *Sternochetus mangiferae* from the intercepted samples by Beijing Customs District P.R. China, and downloaded from National Center for Biotechnology Information (NCBI) (marked with *) used in the present study

		GenBank number	
Continent	Country/region	Cytochrome c oxidase subunit I	Elongation factor 1-alpha
Africa	Algeria	MT706458	
	Angola	MT706459- MT706475	MT747670-MT747688
	Burundi	MT706478	
	Chad	MT706480	MT747691
	Congo-Brazzaville		MT747782, MT747783
	Congo-Kinshasa	MT706481, MT706482	MT747692
	Cote Dlvoire	MT706483-MT706485	MT747693, MT747694
	Egypt	MT706486-MT706488	MT747695, MT747696
	Equatorial Guinea	MT706489, MT706490	MT747697, MT747698
	Ethiopia	MT706457, MT706491-MT706525	MT747699-MT747731
	Ghana	MT706526-MT706536	MT747732-MT747741
	Kenya	MT706541-MT706546	MT747748-MT747754
	Madagascar	MT706547	MT747755
	Mali	MT706548-MT706551	MT747756-MT747759
	Mozambique	MT706552-MT706553	MT747760, MT747761
	Niger	MT706556-MT706558	MT747762-MT747764
	Nigeria	MT706559-MT706567	MT747765-MT747776
	Senegal	MT706575, MT706576	
	South Africa	MT706579, MT706580	
	Sudan	MT706581, MT706582	MT747786
	Tanzania	MT706586-MT706587	MT747789, MT747790
	Togo	MT706592-MT706594	MT747793-MT747795
	Uganda	MT706598-MT706605	MT747800-MT747811
	Zambia	MT706624-MT706626	MT747822-MT747825
	Zimbabwe	MT706627-MT706631	MT747826-MT747829
Asia	Cambodia	MT706479	MT747690
	Hong Kong	MT706537-MT706539	MT747742-MT747745
	India	MT706540, HQ268806-HQ268809*, KU871375*	MT747746, MT747747
	Myanmar	MT706554-MT706555	
	Pakistan	MT706568	
	Philippines	MT706569-MT706571	MT747777-MT747779
	Qatar	MT706572, MT706573	MT747780, MT747781
	Singapore	MT706577, MT706578	MT747784, MT747785
	Taiwan	MT706585	MT747788
	Thailand	MT706588-MT706591	MT747791, MT747792
	Turkey	MT706595-MT7065977	MT747796-MT747799
	United Arab Emirates	MT706606-MT706617	MT747812-MT747819
	Vietnam	MT706619-MT706623	MT747821
Europe	Switzerland	MT706583, MT706584	MT747787
	Germany	KM443510*	
North America	United States	MT706616-MT706618	MT747820
South America	Brazil	MT706476, MT706477	MT747689
Total		181	160

used parametric bootstrapping to simulate the expected distributions in Arlequin 3.5.1.3 (Excoffier & Lischer, 2010). We bootstrapped both the sum of squared deviations (SSD) and Harpending's raggedness index (r) (Harpending, 1994) for this test.

To reconstruct the demographic changes of *S. mangiferae* over time, Bayesian skyline plot (BSP) analysis (Drummond *et al.*, 2005) was implemented in BEAST 2.4.8 (Bouckaert *et al.*, 2014). Independent MCMC analyses were run for 5×10^7 steps, sampling every 1000 generations and discarding the initial 10% as burn-in. Tracer 1.7.1 (Rambaut *et al.*, 2018) was used to visualize skyline plots. Because there was no sign of population expansion, we did not convert the estimates into real time.

Three neutrality metrics, Tajima's *D* (Tajima, 1989), Fu's *Fs* (Fu, 1997) and R_2 (Ramos-Onsins & Rozas, 2002), were also calculated using DNaSP 6.12.03 (Rozas *et al.*, 2017) to test for evidence of past demographic expansions. Significance was evaluated *via* 10 000 coalescent simulations.

Results

The overall mean genetic distance within *S. mangiferae* was 0.14% (min 0, max 1.44%) for COI, whereas the mean genetic distance of the closely related species *S. olivieri* was 4.03%,

Table 2 Population genetic parameters of *Sternochetus mangiferae*

Locus	n	Np	h	k	Hd	π
Cytochrome c oxidase subunit I	181	11	7	0.899	0.592	0.00142
Elongation factor 1-alpha	160	5	7	0.702	0.588	0.00095

n, sample size; Np, number of polymorphic sites; h, number of haplotypes; k, average number of nucleotide differences; Hd, haplotype diversity; π, nucleotide diversity.

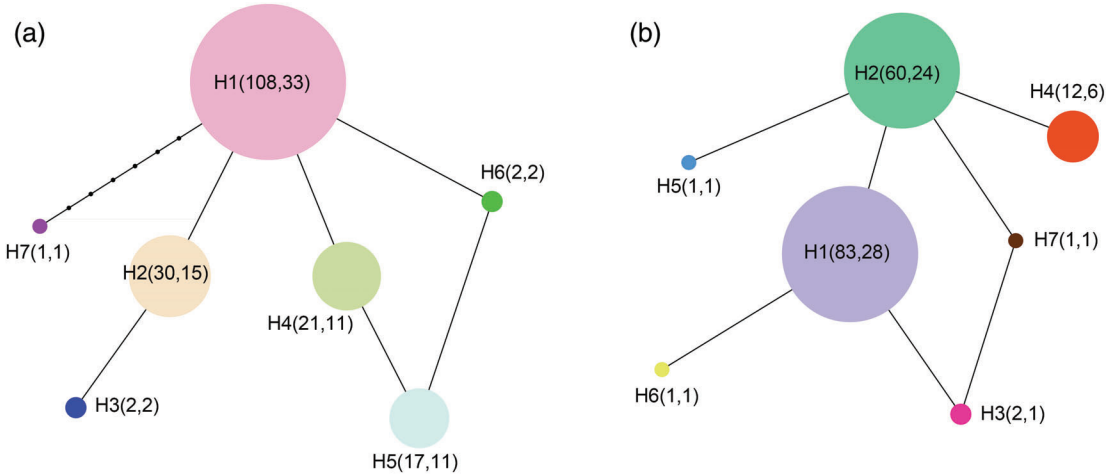

Figure 1 Maximum parsimony networks for cytochrome c oxidase subunit I (COI) and elongation factor 1-alpha (EF1-α) from *Sternochetus mangiferae*. The area of each circle is proportional to the number of individuals/alleles with that haplotype. Straight lines and small black dots reflect mutations and median vectors, respectively. The values in parentheses are the number of individuals/alleles and the number of source country/region, respectively. (a) Based on COI; (b) based on EF1-α. [Colour figure can be viewed at wileyonlinelibrary.com].

although this estimate is based on a small sample size and may be misleading (four individuals; min 0, max 6.09%). Similarly, the mean genetic distance as estimated by EF1-α was 0.095% (min 0, max 0.407%). Among the ingroup, there were 11 (1.7%) segregating sites in the COI dataset, of which 4 (0.6%) were parsimony informative and 7 (1.1%) were singletons. For EF1-α, there were five (0.68%) segregating sites, of which three (0.41%) were parsimony informative and two (0.27%) were singletons. The other population genetic parameters are shown in Table 2.

The parsimony network identified seven COI haplotypes among 181 individuals, and there were two dominant haplotypes that were observed in 108 and 30 weevils (Fig. 1a). Similar to the COI data, seven unique EF1-α sequences were identified, with the two dominant sequences being observed in 83 and 60 weevils(Fig. 1b). Phylogenetic analysis of the mtDNA sequences showed a single well-supported clade containing 32 individuals (haplotypes 2 and 3 of COI; Fig. 1a); furthermore, these individuals were obtained from widely dispersed populations (Fig. S1). The EF1-α phylogeny had one clade containing 12 alleles (haplotype 4; Fig. 1b) that was well supported (Fig. S2). AMOVA revealed that the majority of the genetic variance occurred within, rather than between, populations. Both fixation indices were small and nonsignificant (Table 3).

The mismatch distribution analyses showed that both the COI and EFI-α data have unimodal peaks (Fig. 2). Statistical tests of the mismatch distribution also showed nonsignificant values of the SSD and Harpending's raggedness indices (Table 4). Based on the COI data, Bayesian skyline plots supported the view that *S. mangiferae* populations have remained at a stable population size. In contrast, a slight population expansion was supported based on EF1-α data (Fig. 3). The neutrality tests showed negative values of Tajima's *D* and Fu's *Fs* and small positive values of R_2 (Table 4).

Discussion

The overall mean genetic distance within *S. mangiferae* indicated that intraspecific genetic diversity is quite low. Other population genetic parameters also indicated that *S. mangiferae* has low haplotype and nucleotide diversity (Table 2). For instance, the mtDNA nucleotide and haplotype diversity values observed in *S. mangiferae* are similar to that of a number of other species (Brusentsov *et al.*, 2013; Garcia-Cisneros *et al.*, 2016; Cao *et al.*, 2017; Nakano *et al.*, 2017; Kohli *et al.*, 2018; Audusseau *et al.*, 2020), which were also implicated as possessing low genetic diversity.

Despite its worldwide distribution and opportunity for divergence, we observed little genetic structure among *S. mangiferae* populations. There was only a modest number of nucleotide differences between any two haplotypes, ranging from one to four substitutions, except in haplotype 7, which had seven nucleotide differences and was found in only one individual from India (Fig. 1a). From the presumed native range of mango and the weevils in India, six COI sequences were observed (including five from databases), and among them, four were haplotype 1, one was haplotype 6, and the last was haplotype 7. The results of

Table 3 Analysis of molecular variance for cytochrome c oxidase subunit I (COI) and elongation factor 1-alpha (EF1-α) among different populations of *Sternochetus mangiferae*

Loci	Source of variation	Sum of squares	Variance components	Percentage of variation	Fixation index (F_{ST})	*P*-value
COI	Among populations	6.377	0.01390	3.00	0.03003	0.140
	Within populations	48.925	0.44885	97.00		
EF1-α	Among populations	0.022	−0.00073	−8.91	−0.08906	1.000
	Within populations	0.971	0.00891	108.91		

Populations with sample size less than 4 were excluded in the analyses.

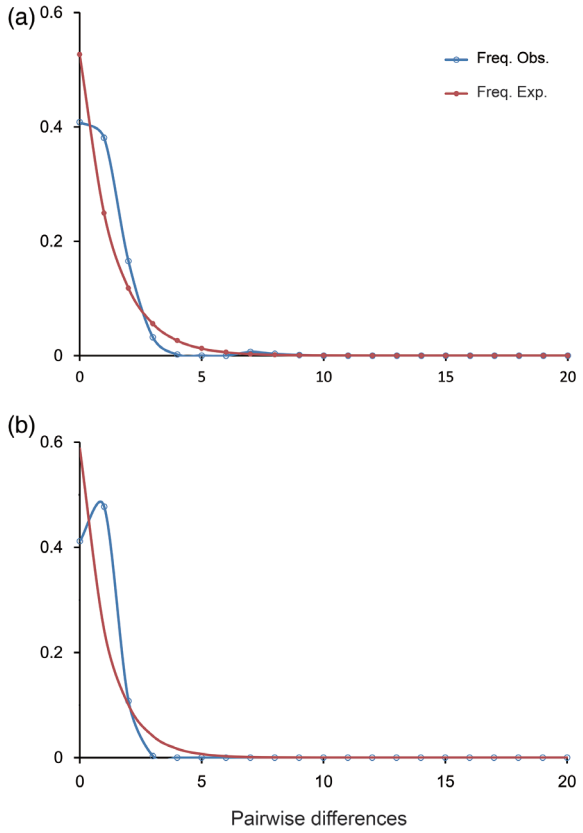

Figure 2 Mismatch distributions for all samples of *Sternochetus mangiferae* inferred from cytochrome c oxidase subunit I (COI) and elongation factor 1-alpha (EF1-α). Blue lines indicate the observed frequency of pairwise nucleotide differences between sequences, and red lines represent the expected distribution based on a model of sudden population expansion. (a) Based on COI; (b) based on EF1-α. [Colour figure can be viewed at wileyonlinelibrary.com].

the AMOVA also indicated that *S. mangiferae* populations lack significant genetic structure. One possible explanation for the apparent absence of genetic structure is that the global spread of these weevils originated from a small population in India, coupled with frequent anthropogenic movement between populations and regions.

The low genetic structure observed among populations suggests that *S. mangiferae* may have recently undergone a population expansion. Indeed, the mismatch distribution analyses showed that both the COI and EFI-α data have unimodal peaks (Fig. 2), indicative of a recent population expansion or a range expansion that includes high levels of gene flow between populations (Ray *et al.*, 2003; Excoffier, 2004). The nonsignificant values of the SSD and Harpending's raggedness indices (Table 4) also point to a sudden expansion. Although we observed negative values of Tajima's *D* and Fu's *F*s and small positive values of R_2 (Table 4), indicative of population growth (Aris-Brosous & Excoffier, 1996); these estimators were nonsignificant, suggesting that we may not have had enough samples to assess significance. Based on COI data, Bayesian skyline plots supported the view that *S. mangiferae* populations have remained at a stable population size. In contrast, a slight population expansion was supported based on EF1-α data (Fig. 3). Because mismatch distributions have less power (Ramos-Onsins & Rozas, 2002; Duran *et al.*, 2004) compared with neutrality tests (Ramos-Onsins & Rozas, 2002), we conservatively interpret these results to suggest that *S. mangiferae* has likely experienced a modest population expansion. This interpretation is consistent with the range expansion of mangoes by humans and the concomitant spread of weevils globally.

Adults of *S. mangiferae* are poor fliers that rarely fly and usually remain near the natal tree (Smith, 1996). These weevils overwinter under loose bark, in the forks of branches, in leaf litter beneath the mango tree or in the mango seed itself (Woodruff & Fasulo, 2018). Long-distance dispersal mainly depends on anthropogenic transportation of fruits and seeds that contain the weevil larvae, pupae or adults (Jarvis, 1946; Griesbach, 2003; Braimah & van Emden, 2010; Woodruff & Fasulo, 2018). Frequent transportation would cause range expansion and increase gene flow among populations, thereby lowering population differentiation. Alternatively, the low genetic diversity observed among weevil populations may also be explained if the weevils originated from one or a few populations in India, one of the original sites of cultivation.

Although the observed low level of genetic diversity in *S. mangiferae* provides evidence to support the hypothesis that the recent history of this species may have been strongly impacted by anthropogenic transportation, there are several caveats that warrant caution in the interpretation of these data. One caveat of this study centres on the source of the samples. All of the samples used in the present study were intercepted from airplane passengers, and thus, the points of origin of the passengers were known. Yet, departure localities may not accurately reflect the true location of the origin of the mangoes and weevils. Even so, our study was based on specimens from a wide range of sources that included 41 countries and regions, and we would have expected to observe some geographic structure if it were present. In addition, our sampling was necessarily imbalanced among regions (e.g., samples from Angola, Ethiopia

Table 4 Statistical tests of neutrality and mismatch distribution of the *Sternochetus mangiferae* populations

Locus	*D*	*Fs*	R_2	SSD	r
Cytochrome c oxidase subunit I	−1.27499 (0.075)	−1.028 (0.346)	0.0602 (0.317)	0.00059 (0.597)	0.06369 (0.403)
Elongation factor 1-alpha	−0.40946 (0.394)	−2.005 (0.189)	0.0713 (0.404)	0.00000003 (0.062)	0.95078 (0.957)

D, Tajima's D; *Fs*, Fu's Fs statistic; R_2, Ramos-Onsins and Rozas's R_2; SSD, sum of squared deviation; r, Harpending's raggedness index. *P*-values are in parentheses.

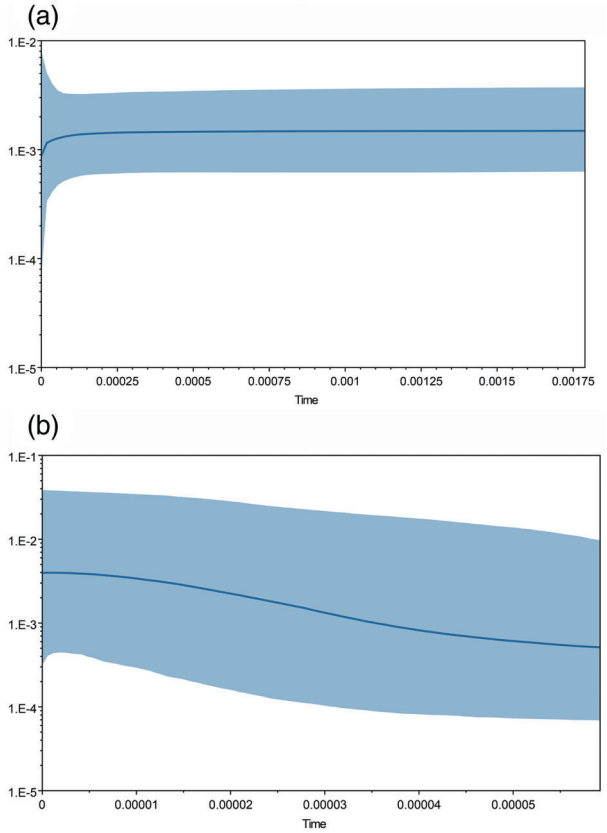

Figure 3 Bayesian skyline plots depicting the demographic history of *Sternochetus mangiferae*. The light blue shading indicates the upper and lower 95% confidence intervals of the Highest Posterior Density (HPD) analysis. (a) cytochrome c oxidase subunit I; (b) elongation factor 1-alpha. [Colour figure can be viewed at wileyonlinelibrary.com].

United Arab Emirates and Ghana represent about 40% of all samples), and this imbalance may lead to biased inference of the population genetic structure (Chikhi *et al.*, 2010; Radespiel & Bruford, 2014; Meirmans, 2019). Consequently, these results should be cautiously interpreted. Although the analysis indicated low genetic diversity for the global assemblage of the weevil, we identified one divergent haplotype (haplotype 7) present in a single individual from India, the presumed centre of origin of the weevil (Fig. 1a). Our sample size from this region is relatively low; thus, additional sampling in India and adjacent regions may detect greater levels of haplotype diversity that can help to resolve the patterns of genetic structure. Furthermore, we also used sequencing data from only two loci; thus, the results will reflect the evolutionary history of those genes and may differ if we had sampled the genome more broadly.

Together, the results suggest that the natural history of the mango seed weevil coupled with long-term cultivation of mango by humans may have shaped its population genetic structure. For instance, current transportation of these weevils mainly occurs though anthropogenic movement of infested mangos. Although a number of uncertainties remain, from the point of view of pest management, understanding the population genetic structure of pest species such as *S. mangiferae* can help in their control using genetic techniques (Leftwich *et al.*, 2016). To this end, the knowledge that there seems to be genetic homogeneity across the geographic range of *S. mangiferae* could benefit regional control strategies (Kébé *et al.*, 2016).

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Author Contributions

HJX and LJZ designed the research; BHX, LJZ, YW, CSZ, JGL and HJX performed the research; HJX and KAS were responsible for the writing, review and editing of this study. All authors have read and agreed to the published version of the manuscript.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1: Maximum-likelihood phylogenetic tree inferred from COI. Node support values lower than 50 are not shown.

Figure S2: Maximum-likelihood phylogenetic tree inferred from EF1-α. Node support values lower than 50 are not shown.

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