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2 A first inference of the phylogeography of the worldwide invader 3 *Xylosandrus compactus*

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8 Abstract

9 Native to Southeastern Asia, the ambrosia beetle *Xylosandrus compactus* is invasive worldwide. Its invasion is favoured by
10 its cryptic lifestyle, symbiosis with a fungus that facilitates a broad range of host plants, and predominant sib-mating repro-
11 duction. *X. compactus* invaded Africa more than a century ago and the Americas and Pacific Islands in the middle of the
12 twentieth century. It was not detected in Europe before 2011, when it was first reported in Italy before quickly spreading to
13 France, Greece and Spain. Despite the negative environmental, agricultural and economic consequences of the invasion of
14 *X. compactus*, its invasion history and main pathways remain poorly documented. We used COI and RAD sequencing to (i)
15 characterise the worldwide genetic structure of the species, (ii) disentangle the origin(s) of the non-native populations on the
16 three invaded continents and (iii) analyse the genetic diversity and pathways within each invaded region. Three mitochondrial
17 lineages were identified in the native range. Populations invading Europe and the American-Pacific region originated from
18 the first lineage and were only slightly genetically differentiated at nuclear SNP markers, suggesting independent introduc-
19 tions from close sources in or near Shanghai, ca. 60 years apart. Populations invading Africa originated from the second
20 lineage, likely from India or Vietnam.

21 **Keywords** Bioinvasion · Invasion route · Black twig borer · COI · RAD sequencing · Ambrosia beetle

22 Key message

- 23 • *Xylosandrus compactus* is native to Asia and invasive 25
- 24 in Africa, the Americas, and the Pacific Islands, and it 26
- recently invaded Europe. 27
- 25 • We used COI and RAD sequencing to identify its source 28
- 26 populations and decipher its invasion history. 29
- 27 • Populations from Europe and the American-Pacific 30
- 28 region are closely related, show almost no genetic diver- 31
- 29 sity and presumably originated from independent intro- 32
- 30 ductions from Eastern China. 33
- 31 • The invasion in Africa likely originated from Southeast- 34
- 32 ern Asia, potentially from India or Vietnam. 35
- 33 • Invasions probably happened through the international 34
- 34 trade of living plants. 35

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36 **Introduction**

37 Biological invasions have been increasing dramatically
38 in the last decades, with no sign of plateauing, and are
39 now one of the main threats to biodiversity and ecosys-
40 tems health and services (Pejchar and Mooney 2009; See-
41 bens et al. 2017, 2020; Sardain et al. 2019). Invasions are
42 known to cause biodiversity loss (Dueñas et al. 2021), eco-
43 system disruption (Morales et al. 2017; Simberloff et al.
44 2013; Kenis et al. 2008), economic loss (Bradshaw et al.
45 2016) and human health problems (Schindler et al. 2015;
46 Jones 2017; Jones and McDermott 2017). International
47 trade plays a major role in insect biological invasions,
48 dispersing pest species between geographically isolated
49 ecosystems (Gippet et al. 2019). Invasion scenarios can
50 however be diverse, for example resulting from single or
51 multiple introductions from the species' native range, and
52 may or may not involve strong bottlenecks depending on
53 the number of dispersed propagules. One of the invaded
54 regions can also serve as a source for further introductions,
55 a phenomenon known as “bridgehead effect” (Lombaert
56 et al. 2010). Understanding the routes of invasions and
57 determining the source populations are thus critical in
58 developing management strategies to prevent further intro-
59 ductions. The most effective way to retrace invasive spe-
60 cies' invasion history is to study their worldwide genetic
61 structure (Estoup and Guillemaud 2010).

62 Bark and ambrosia beetles (Coleoptera: Curculioni-
63 dae: Scolytinae) are among the most successful invasive
64 species groups. They represent 0.2% of insect species but
65 more than 50% of insect interceptions in ports of entry
66 (Hulcr and Dunn 2011). Ambrosia beetles take their name
67 from their obligate association with symbiotic ambrosia
68 fungi. The females dig galleries into the xylem of their
69 host plant, where they inoculate spores of their fungal
70 symbiont, which will be used as the only food source by
71 both larvae and adults. This symbiosis allows them to
72 attack a broad range of host plant species and easily shift
73 to new hosts in invaded ranges, which is a major reason for
74 their success as invaders (Kirkendall et al. 2008). Because
75 they are tiny insects living inside galleries most of their
76 life, they can easily travel long distances unspotted, hid-
77 den in living plants or wood packaging material (Raffa
78 et al. 2015). While most ambrosia beetles are harmless in
79 their native range, attacking only dead or weakened trees,
80 some species can attack healthy trees and economically
81 important crops in the ecosystems they invade (Hulcr et al.
82 2017; Kühnholz et al. 2001; Ploetz et al. 2013). Ambrosia
83 beetles can also spread pathogenic fungi and diseases in
84 naive ecosystems (Hulcr and Dunn 2011). For instance,
85 the laurel wilt disease caused by the pathogenic fungus
86 *Raffaella* spread by the redbay ambrosia beetle (*Xyleborus*

glabratus) has killed hundreds of millions of trees in the
Lauraceae family since it was first detected in the USA in
2002 and is responsible for a \$356 million annual loss in
the avocado industry (Evans et al. 2010).

Xylosandrus is a particularly successful genus of invading
ambrosia beetles. Out of the 54 *Xylosandrus* species pres-
ently recognised, four are worldwide invaders causing major
losses in plant nurseries and cultivations, namely *X. crassi-*
usculus, *X. germanus*, *X. morigerus* and *X. compactus* (Gug-
liuzzo et al. 2021; Dole et al. 2010). Like other ambrosia
beetles, *Xylosandrus* species have biological and ecological
characteristics favouring invasion (Kirkendall and Odegaard
2007). They are haplodiploid (i.e. non-fertilised eggs give
haploid males, while fertilised eggs give diploid females)
and predominantly mate between siblings as females usu-
ally mate with their brothers in maternal galleries before
dispersing. More, as adults are relatively long-lived, a single
unmated *Xylosandrus* female is able to find a population by
mating with its haploid male offsprings (Jordal et al. 2001).
The combination of haplodiploidy and regular inbreeding
allows to lower inbreeding depression by purging deleterious
alleles (Peer and Taborsky 2005), which prevents detrimen-
tal effects of low population density typical for regularly
outcrossing diploid species, such as the mate-finding Allee
effect (Gascoigne et al. 2009). The invasive *Xylosandrus*
species were reported on hundreds of hosts species belong-
ing to dozens of plant families (Weber and McPherson 1983;
Browne 1961). This could be caused by generalist genotypes
able to live in multiple host plants rather than complexes
of multiple genotypes specialised on diverse plant families.
Indeed, Andersen et al. (2012) showed that deeply diverg-
ing genotypes of *X. morigerus* shared broad and completely
overlapping niches without any sign of host specialisation.

The genetic structures of populations of these four spe-
cies have been studied in the last decade, but the worldwide
patterns of invasions were only addressed for *X. germanus*
(Dzurenko et al. 2020) and *X. crassiusculus* (Storer et al.
2017; Ito and Kajimura 2009; Landi et al. 2017). Despite
similar ecological characteristics, these two species were
proved to have drastically different invasion histories. In par-
ticular, all non-native populations of *X. germanus* proved
to originate from a single region in Japan, and invasion
in Europe and in North America occurred independently.
Results based on a mitochondrial and a nuclear gene fur-
ther suggested that only one introduction event occurred in
Europe, while several introductions were suggested in North
America. On the other hand, genetic structure and invasion
history of *X. crassiusculus* seem more complex. Cryptic
diversity was identified worldwide, and divergent lineages
were introduced in different regions of the world, with each
invasive population potentially resulting from numerous
introductions, or from a single genetically diverse introduc-
tion, or a mix of both.

140	Very little is known about <i>Xylosandrus compactus</i> genetic	193
141	structure and invasion history. The only genetic study focusing	194
142	on <i>X. compactus</i> so far was centred on India and based	195
143	on a single mitochondrial marker, showing a very low	
144	genetic diversity in spite of a sampling including almost	
145	200 specimens (Kiran et al. 2019). However, this work did	
146	not discuss <i>X. compactus</i> invasion history. Yet, <i>X. compac-</i>	
147	<i>tus</i> is a worldwide invader native to temperate and tropical	
148	regions of Asia. It is reported on more than 220 host species	
149	from more than 60 families (Ngoan et al. 1976; Beaver et al.	
150	2014), including several plants of economic importance,	
151	such as cacao, mango, avocado and coffee (Oliveira et al.	
152	2008). Solely in Uganda, <i>X. compactus</i> is responsible for	
153	\$40 million annual loss due to damages on coffee planta-	
154	tions (Egonyu et al. 2015). It is also known to spread poten-	
155	tially pathogenic fungi such as <i>Fusarium solani</i> (Bosso et al.	
156	2012). <i>X. compactus</i> is still expanding worldwide and colo-	
157	nisising new territories, notably in Europe where it spreads	
158	at an alarming rate. It has been present in Madagascar and	
159	Africa for more than a century, and it colonised North Amer-	
160	ica in the 1940s, Hawaii in 1964 and South America in the	
161	late 1970s. Colonisation of Europe is much more recent, as	
162	it was first detected in Italy in 2011 (Garonna et al. 2012), in	
163	France in 2014 (Roques et al. 2019), in Greece (Spanou et al.	
164	2019) and Mallorca (Balearic Islands) (Leza et al. 2020)	
165	in 2019, continental Spain in 2020 (Gallego et al. 2020)	
166	and Corsica in 2021 (A.R., pers. obs.). Species distribution	
167	modelling suggests that <i>X. compactus</i> could spread to most	
168	Mediterranean regions and along the Atlantic coast from	
169	Portugal to the United Kingdom. It could also establish in	
170	new countries such as Australia, New Zealand or Mexico,	
171	where environmental conditions are predicted to be suitable	
172	(Urvois et al. 2021).	
173	The aim of the present study was to characterise the	
174	global genetic structure and invasion history of <i>X. compac-</i>	
175	<i>tus</i> worldwide, with a focus on Europe where it was the most	
176	recently introduced. We used both mitochondrial and nuclear	
177	markers to test whether they bring consistent information,	
178	as these two types of markers can be differently affected by	
179	the species' demographic history and could show contrast-	
180	ing patterns (Toews and Brelford 2012). Moreover, we used	
181	genome-wide nuclear data based on Restriction-site Associ-	
182	ated DNA (RAD) sequencing (Davey and Blaxter 2010) to	
183	describe at high resolution the species' genetic structure.	
184	Our objectives were (i) to compare the worldwide genetic	
185	structure obtained with mitochondrial and nuclear markers,	
186	and to determine if the species consisted of differentiated	
187	lineages; (ii) to disentangle the origin(s) of the non-native	
188	populations on the three invaded continents (Africa, Amer-	
189	ica and Europe), testing if they were colonised independ-	
190	ently and if each continent was invaded once or several	
191	times; and (iii) to analyse the genetic diversity and pathways	
192	within each invaded region. Answering these questions is	
	timely to develop management strategies and propose plans	193
	for efficient epidemiological surveillance and early detection	194
	for this highly invasive pest.	195
	Material and methods	196
	Insect sampling	197
	We collected <i>Xylosandrus compactus</i> females from 29	198
	locations (Table 1). <i>X. compactus</i> is commonly described	199
	as native to Southeastern Asia. Still, the exact boundaries	200
	of its native range are unknown and it is not possible to	201
	know whether it should be considered invasive in the periph-	202
	ery of its Asian distribution, such as India. To simplify, we	203
	decided to consider all Asian localities as part of its native	204
	area. China was the only country sampled in the presump-	205
	tive native range of the species. Low sampling coverage in	206
	invasive species' native range is a common issue as they	207
	often cause less damage in their native area and are thus	208
	harder to find there. We collected specimens at 25 sites in the	209
	invaded range, in 6 countries distributed on three continents.	210
	The insects were obtained either directly from the host tree,	211
	from traps baited with ethanol or more specific attractants	212
	(Roques et al., in prep) or from collections. Whenever pos-	213
	sible, insects from each location were caught from different	214
	trees and traps, and at different dates, to minimise within-	215
	location inter-individuals relatedness. Individuals were	216
	stored in 96% ethanol and at -18 °C until DNA extraction.	217
	DNA extraction	218
	Mycangia were removed, and each specimen was washed	219
	with 70% alcohol and cleaned with a paintbrush to limit	220
	potential fungal contamination. DNA was then extracted	221
	from the whole insect using the Macherey–Nagel Nucleo-	222
	Spin Tissue kit following the manufacturer's instructions,	223
	with two successive elutions in 50 µL elution buffer BE to	224
	increase DNA yield, and stored at -18 °C.	225
	Mitochondrial DNA sequencing	226
	We sequenced between 1 and 8 insects per location for a	227
	total of 96 specimens. We amplified the barcode COI frag-	228
	ment via PCR using the primers HCO2198 (5' –TAAACT	229
	TCAGGGTGACCAAAAATCA – 3') and LCO1490 (5'	230
	– GGTCAACAAATCATAAAGATATTGG – 3') (Folmer	231
	et al. 1994) (Table 1). The PCR was performed as follows:	232
	denaturation for 5 min at 94 °C followed by 35 cycles of	233
	amplification of 45 s at 94 °C, 50 s at 47 °C and 90 s at 72 °C	234
	and finally 5 min at 72 °C. PCR products were cleaned using	235
	the NucleoSpin Gel and PCR Cleanup kit (Machery-Nagel)	236
	and sequenced in both directions using the ABI Prism	237

Table 1 Summary of the localities sampled and specimens used in the COI and RAD sequencing analyses. UFFE is short for University of Florida's Forest Entomology Laboratory and uffeID represents the sample's unique identifier in the UFFE collection database. PACA is short for the French region Provence-Alpes-Côtes d'Azur

Range	Sender (Gen-Bank accession number/uffeID)	Country	State/Province/Region	Locality	Latitude	Longitude	No. in COI analysis (haplotype)	No. in RAD analysis (group)
Africa	GenBank (GU808707.1)	Ghana	Western Region	Ankasa	5.454129	-2.049559	1 (B2)	-
Africa	Fabrice Pinard	Uganda	Central Region	Bunjako Island	0.002465	32.133916	2 (B2)	7 (group 3)
Asia	UFFE (31,708)	China	Fujian	Shuyang	27.159615	119.685488	2 (A5)	2 (group 4)
Asia	UFFE (31,704)	China	Guizhou	Zunyi	27.702703	106.923687	2 (A4)	2 (group 4)
Asia	GenBank (MN620067.1)	China	Hong Kong	-	22.351683	114.167294	1 (C)	-
Asia	GenBank (MN620068.1)	China	Jiangsu	Nanjing	32.073142	118.608523	1 (A5)	-
Asia	UFFE (31,864)	China	Jiangxi	Xiangshan	27.554360	116.039123	1 (A6)	1 (group 4)
Asia	UFFE (33,225, 33,226)	China	Shanghai	Shanghai Botanical Garden	31.148935	121.441839	5 (A1)	10 (group 1)
Asia	GenBank (MT178811.1)	India	Karnataka	Cottabetta	13.729165	75.574106	1 (B1)	-
Asia	GenBank (KY172634.1, KY172635.1)	India	Karnataka	Mudigere	13.08	75.63	2 (B2)	-
Asia	GenBank (MN620069.1)	Japan	Okinawa	-	26.344871	127.801188	1 (A3)	-
Asia	GenBank (KU727031.1)	Vietnam	Phú Yên	Tuy Hoa	13.112984	109.277958	1 (B2)	-
Europe	INRAE team	France	Corsica	Cotti	41.772022	8.773401	2 (A1)	-
Europe	INRAE team	France	PACA	Cap d'Ail	43.728410	7.402091	1 (A1)	1 (group 1)
Europe	INRAE team	France	PACA	Cap Ferrat	43.676092	7.329719	4 (A1)	5 (group 1)
Europe	INRAE team	France	PACA	Château-Léoube	43.122588	6.275151	6 (A1)	7 (group 1)
Europe	INRAE team	France	PACA	Garoupe	43.563996	7.124504	2 (A1)	5 (group 1)
Europe	INRAE team	France	PACA	Le Lavandou	43.154	6.413	2 (A1)	-
Europe	INRAE team	France	PACA	Nice	43.695849	7.267888	4 (A1)	4 (group 1)
Europe	INRAE team	France	PACA	Sainte-Marguerite	43.519819	7.048594	2 (A1)	2 (group 1)
Europe	INRAE team	France	PACA	Saint-Tropez	43.261871	6.645200	1 (A1)	1 (group 1)
Europe	INRAE team	France	PACA	Villa Thuret	43.563996	7.124504	6 (A1)	5 (group 1)
Europe	Massimo Faccoli	Greece	Peloponnese	-	37.349380	22.352093	8 (A1)	8 (group 1)
Europe	INRAE team	Italy	Latina	Circeo Park	41.297216	13.046848	4 (A1)	11 (group 1)
Europe	Giovanna Tropea	Italy	Sicily	Donnafugata	36.881903	14.563506	2 (A1)	5 (group 1)
Europe	Giovanna Tropea	Italy	Sicily	Donnalucata	36.766307	14.636295	2 (A1)	5 (group 1)
Europe	Giovanna Tropea	Italy	Sicily	Marina di Ragusa	36.785731	14.548371	5 (A1)	5 (group 1)
Europe	Diego Gallego	Spain	Tarragonès	Vila-seca	41.11125	1.13381	4 (A1)	-
North America	UFFE (11,379)	USA	Florida	Austin Cary Forest	29.749605	-82.212870	5 (A2)	5 (group 2)
North America	UFFE (20,588, 20,595)	USA	Florida	Highlands Hammock Park	27.471267	-81.531776	6 (A2)	5 (group 2)
Pacific Island	GenBank (KX055191.1)	France	French Polynesia	Tefarerii	21.899523	-159.560966	1 (A2)	3 (group 2)
Pacific Island	Jared Bernard	USA	Hawaii	Kaua'i Coffee Cie	21.31564	-157.80398	5 (A2)	6 (group 2)

Table 1 (continued)

Range	Sender (Gen-Bank accession number/uffeID)	Country	State/Province/Region	Locality	Latitude	Longitude	No. in COI analysis (haplotype)	No. in RAD analysis (group)
Pacific Island	GenBank (KX818316.1 to KX818319.1)	USA	Hawaii	Kona Research Farm	22.198215	-159.334457	4 (A2)	-
Pacific Island	Jared Bernard	USA	Hawaii	Mānoa Valley	21.483681	-158.022090	5 (A2)	3 (group 2)
Pacific Island	Jared Bernard	USA	Hawaii	Moloa'a Coffee	-19.6359	-155.95	2 (A2)	-
Pacific Island	UFFE (27,780)	USA	Hawaii	O'ahu	-16.79	-150.962	1 (A2)	-
South America	GenBank (GU808706.1)	Brasil	Espirito Santo	-	-19.179798	-40.318079	1 (A2)	-
South America	UFFE (17,769)	France	French Guiana	Amazon Lodge	4.559321	-52.207490	4 (A2)	5 (group 2)
South America	UFFE (31,702)	France	French Guiana	Carrefour de Gallion	4.824021	-52.486669	1 (A2)	1 (group 2)

238 BigDye Terminator v3.1 Cycle Sequencing Kit on an ABI
 239 Prism 3500 Genetic Analyzer (Thermo Fisher Scientific).
 240 We used CodonCode (CodonCode Corporation) to check
 241 electropherograms, create contigs and trim all sequences to
 242 566 bp. DNA sequences were aligned using ClustalW in
 243 MEGA X (Kumar et al. 2018). We completed the align-
 244 ment with all the barcode COI sequences publicly available
 245 from Genbank and for which location information was avail-
 246 able. Thus, 14 sequences from 10 locations in 8 countries
 247 were added, including sequences from Mitchell and Mad-
 248 dox (2010) (KX818316, KX818319), Cognato et al. (2020)
 249 (MN620067, MN620068, MN620069), Dole et al. (2010)
 250 (GU808707), Stouthamer et al. (2017) (KU727031.1) and
 251 Kiran et al. (2019) (KY172634.1, KY172635.1). The final
 252 alignment hence included 110 individuals (Table 1).

253 Mitochondrial data statistical analysis

254 We calculated Kimura 2 Parameters (K2P) genetic distances
 255 between haplotypes using MEGA X (Kumar et al. 2018).
 256 Haplotype and nucleotide diversities were calculated using
 257 the pegas package (Paradis 2010) in the R Software (R Core
 258 Team 2018). We reconstructed a phylogeny between haplo-
 259 types using Maximum Likelihood and Bayesian inference,
 260 with *X. germanus* and *X. crassiusculus* as outgroups (acces-
 261 sion numbers NC036280.1 and MT230099.1, respectively).
 262 A Maximum Likelihood phylogeny was performed with
 263 MEGA X (Kumar et al. 2018) with 1000 bootstraps using
 264 K2P distances. A Bayesian inference of the haplotype phy-
 265 logeny was performed with MrBayes (Ronquist et al. 2012)
 266 with a GTR + I + Γ evolutionary model, and four chains run
 267 four times during 2,000,000 generations with a diagnostic
 268 every 100 generations. A median-joining network was real-
 269 ised with PopArt (Bandelt et al. 1999). Haplotype maps were
 270 performed using the R packages maps (Becker et al. 2018),

ggplot2 (Wickham 2016) and scatterpie (Guangchuang 271
 2020). 272

RAD sequencing 273

274 DNA quantity and quality were assessed using the Qubit
 275 dsDNA HS Assay Kit with a Qubit fluorometer. As the DNA
 276 amount obtained from each individual was too small for the
 277 construction of RAD libraries, we followed the protocol used
 278 by Cruaud et al. (2018) to perform a whole genome amplifi-
 279 cation of each individual DNA sample with the Genomiphi
 280 kit V3 following the manufacturer's procedure. Individual
 281 RAD libraries were then constructed following Baird et al.
 282 (2008) and Etter et al. (2011) with a few modifications listed
 283 hereafter. DNA was digested using 250 ng of DNA in 22
 284 μ L per sample and 0.5 μ L of the PstI-HF enzyme for a total
 285 volume of 25 μ L. The digested fragments from each speci-
 286 men were tagged with a unique 5- or 6- bp barcode and a P1
 287 adapter using 1.5 μ L of P1 adapter (100 nM) and 0.5 μ L of
 288 T4 Ligase (2,000,000 U/ml) for a total volume of 30.5 μ L.
 289 Specimens were then pooled 19 by 19 to create seven librari-
 290 es. Libraries were sonicated on a Covaris S220 (duty cycle
 291 10%, intensity 5, 200 cycles/burst, duration 75 s) to obtain
 292 300–600 bp fragments. Each library was then tagged with a
 293 5- or 6- nucleotide barcode and a P2 adapter using 1 μ L of
 294 P2 adapter (10 nM) and 0.5 μ L of Quick Ligase (2,000,000
 295 U/ml). The sizing and purification steps were realised using
 296 AMPure XP beads (Agencourt). We performed 5 PCR
 297 enrichment with 15 cycles (30 ng DNA input, NEB Phusion
 298 High-Fidelity PCR Master Mix) for each library to increase
 299 fragment diversity. After quality control using the Agilent
 300 2100 Bioanalyzer, the libraries were pooled altogether at an
 301 equimolar ratio and sent to MGX-Montpellier GenomiX for
 302 sequencing. The library was verified on a Fragment Analyser
 303 (Agilent, HS NGS fragment Kit), quantified by qPCR (Kapa
 304 Library quantification kit) and sequenced on a SP lane in

305 paired-end 2 × 150 nt mode on a Novaseq6000 (Illumina)
306 according to the manufacturer's instructions.

307 RAD sequence data processing

308 We used the RADIS pipeline (Cruaud et al. 2016) to (i)
309 demultiplex individuals using process_radtags (Catchen
310 et al. 2013), (ii) homogenise read length and remove a
311 few low-quality bases at the 3'-ends by trimming reads to
312 139 bp and (iii) remove PCR duplicates using clone_filter
313 (Catchen et al. 2013). The following steps were performed
314 using STACKS (Catchen et al. 2013; Rochette et al. 2019)
315 on the Genotoul Bioinformatics Platform (INRAE, Tou-
316 louse, France). We tested two values of the M parameter
317 from *ustacks* (i.e. the maximum distance allowed between
318 stacks) M=6 and M=8. We also tested two values of the
319 n parameter from *cstacks* (i.e. the number of mismatches
320 allowed between sample loci when building the catalogue)
321 n=4 and n=6. In order to remove potential fungal con-
322 taminations, we aligned the obtained loci on the *Ambro-*
323 *siella xylebori*'s (*X. compactus*' symbiotic fungus) refer-
324 ence genome (Vanderpool et al. 2018) (accession number:
325 ASM277803v1) using the BWA-MEM algorithm (Li and
326 Durbin 2009) to create a loci blacklist that we later used to
327 filter the fungus' reads in STACKS' *populations* module. In
328 STACKS' *populations* module, we used three filtering val-
329 ues for parameter r (the minimum percentage of individuals
330 required to process a locus, here with one population) r=0,
331 0.5 and 0.7. We compared the number of SNPs obtained for
332 each of the M, n and r Stacks parameters combinations. We
333 also performed Principal Component Analyses (PCAs) and
334 clustering with SNPrelate (Zheng et al. 2012) for the four
335 M and n combinations parameters for r=0.7. We excluded
336 loci with a mean read depth lower than 8 using VCFtools
337 (Danecek et al. 2011). We did not apply filtering based on
338 minor allele frequency (we kept all SNP with at least one
339 allelic variation) in order to avoid biasing subsequent statisti-
340 cal analyses (Linck and Battey 2019).

341 Lastly, we also wanted to determine the genetic structure
342 of the symbiotic fungus. We thus ran the STACKS' *popu-*
343 *lation* module using the loci mapping on the *Ambrosiella*
344 *xylebori* reference genome as a whitelist, using r=0.3 and
345 excluding loci with a mean depth lower than 4.

346 RAD SNP statistical analysis

347 We estimated the specimens' relative ancestry using
348 Admixture (Alexander et al. 2009), with a putative num-
349 ber of populations, K, ranging from 1 to 12 with a 100-fold
350 cross-validation to assess the best K. We then used the pong
351 1.4.9 software (Behr et al. 2016) to estimate the major mode
352 (using a greedy approach with 100 runs and a similarity
353 threshold value of 0.90) and plotted the results using the

package pophelper (Francis 2017) in the R Software (R Core
Team 2018). A Maximum Likelihood tree was generated
using RAxML 8.2.21 (Stamatakis 2014). We used the GTR
CAT approximation and allowed the program to automati-
cally halt bootstrapping using the bootstrap converge crite-
rion (Pattengale et al. 2010) through the autoMRE option.
The tree was visualised using FigTree V.1.4.4 ([https://
github.com/rambaut/figtree/releases](https://github.com/rambaut/figtree/releases)). Besides, a hierarchi-
cal clustering tree was built using SNPrelate (Zheng et al.
2012) on an individual dissimilarity matrix (Zheng 2013).
We also calculated the pairwise Fst (Weir and Cockerham
1984; Wright 1951) and Nei distances (Nei 1972) between
the different groups obtained with the methods mentioned
above using the StAMPP package (Pembleton et al. 2013).
We also estimated the relative ancestry of the symbiotic
fungi *Ambrosiella xylebori* and built a hierarchical cluster-
ing tree using the same procedure as for *X. compactus*.

371 Results

372 Mitochondrial diversity and differentiation

373 We obtained nine haplotypes worldwide (Fig. 1a–c, Table 1),
374 with 70 variable sites out of 566 bp. Eight haplotypes were
375 found in *X. compactus*' native area, including 5 in China
376 (A1, A4, A5, A6 and C), 1 in Japan (A3), 1 common to
377 India and Vietnam (B2) and 1 only in India (B1). Only three
378 haplotypes were found in *X. compactus*' invaded range.
379 The haplotype B2 was found in the two African countries
380 studied, Uganda and Ghana. Only the haplotype A1 was
381 observed in the invaded sites of southern Europe, this hap-
382 lotype being also present in Shanghai but not in the site
383 of the close Jiangsu province (Nanjing) nor the other sam-
384 pled provinces. The haplotype A2 was found only in the
385 invaded range and was present in every locality sampled in
386 the Americas and the Pacific Islands. The K2P genetic dis-
387 tances suggested that the haplotypes could be divided into
388 three groups with distances within groups lower than 0.045
389 (mean 0.018) and between groups higher than 0.056 (mean
390 0.0648) (Table 2). The first group (lineage A) comprised
391 six haplotypes (A1 to A6) and was present in China, Japan,
392 Europe, the Americas, Hawaii and French Polynesia. The
393 haplotypes A1 and A2, the only haplotypes found in most of
394 the invaded range, differed only by one substitution (Fig. 1c).
395 The second group (lineage B) comprised two haplotypes
396 (B1 and B2) and was found in Vietnam, India, Uganda and
397 Ghana. The third group (lineage C) consisted of only one
398 haplotype found in Hong Kong, whose sequence was pub-
399 lished in a recent study by Cognato et al. (2020).

400 We found only one haplotype in each locality; thus,
401 haplotype and nucleotide diversities and their respective
402 standard deviations at the locality level all equalled zero.

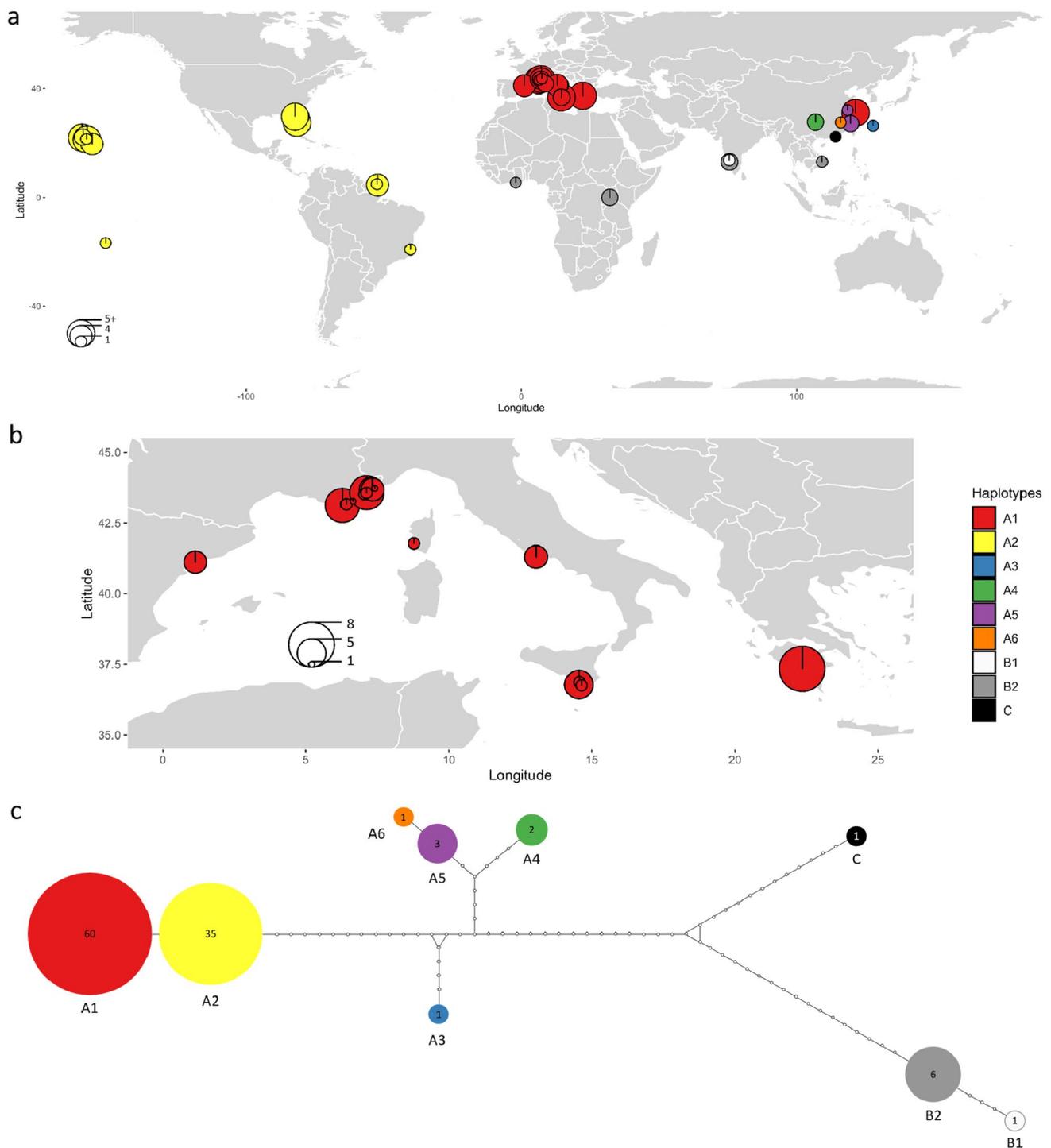


Fig. 1 *Xylosandrus compactus* haplotype maps (a and b) and median-joining network (c) based on COI sequences. The diagrams represent the sampling size and the proportion of each haplotype in each locality sampled a worldwide, and b focusing on Europe

403 The Maximum Likelihood tree reached high support values for every node and set the groups A and C in the same
 404 clade. The Bayesian inference tree had a lower resolution but
 405 placed groups B and C in the same clade with a significant
 406 posterior probability (Supplementary Figure S1).
 407

Genetic structure at nuclear SNPs obtained from RAD sequencing

We obtained a total of 563,419,874 reads, with an average of 2,324,174 (445,028 SD) reads per specimen after

408
409

410
411

Table 2 Genetic distances between COI haplotypes based on the Kimura 2-parameter model

	A1	A2	A3	A4	A5	A6	B1	B2
A1								
A2	0.002							
A3	0.033	0.031						
A4	0.044	0.042	0.027					
A5	0.042	0.040	0.025	0.013				
A6	0.040	0.038	0.023	0.011	0.002			
B1	0.086	0.084	0.068	0.070	0.071	0.070		
B2	0.082	0.080	0.064	0.066	0.067	0.066	0.007	
C	0.073	0.071	0.065	0.063	0.065	0.063	0.063	0.056

demultiplexing, and of 1,382,550 (252,282 SD) after removing low-quality reads and PCR duplicates. Depending on the combinations of the parameters M and n , 1.65 to 1.69% of the sequences mapped on the *Ambrosiella xylebori*'s genome and were blacklisted. The combination used of the parameters M and n had limited effects on our results. Indeed, each parameter combination of M , n and r yielded very similar numbers of loci, variant sites, and observed homozygosity (Supplementary Table 1). This was expected given the relatively low heterozygosity of the genome of species with regular inbreeding (Kirkendall et al. 2015). The Principal Component Analyses and the clustering analyses also gave similar results for the different parameter combinations (Supplementary Figure S2, Supplementary Figure S3). We decided to focus exclusively on the results obtained with $M=6$ and $n=4$, excluding loci with a mean depth lower than 8 or shared by less than 70% of the specimens ($r=0.7$). This M and n parameter set corresponds to the parameters used by Storer et al. (2017), adjusted for the read length. With these selected parameters values, we kept 27,583 SNPs.

The average homozygosity was 0.99 (0.002 SD), and the average inbreeding coefficient was 0.899 (0.02 SD). Using Admixture to explore the worldwide genetic structure of *X. compactus*, the cross-validation values reached a plateau for $K=4$ (Supplementary Figure S4). Increasing K above 4 increased the model's complexity at the cost of the geographical signal (Supplementary Figure S5); we thus selected $K=4$ as the most parsimonious number of genetic groups. With a similarity threshold of 0.90, the 100 Admixture runs yielded 24 different modes, the major mode representing 77 of them, with a pairwise similarity of 0.999. In all 233 runs of the major mode, all specimens were assigned to one of the four groups with a score higher than 0.95, and most of them scored more than 0.999 (Fig. 2). All specimens from Shanghai and Europe were assigned to group 1. The specimens from the Americas and Hawaii clustered together in group 2. The two remaining groups corresponded to the individuals from Uganda, Africa (group 3) and the other Chinese localities (group 4). Groups 1 and 2 were the closest, with a genetic distance of 0.03 (Table 3), while

the genetic distances between group 4 and groups 1 and 2 were seven times larger. Group 3 was the most distant, with a genetic distance over 1 when compared with any of the three other groups. Despite the small number of specimens in group 4, the third-best mode split it into two groups. The RAxML analysis stopped after 400 bootstraps with a best tree scoring a GAMMA-score of -91,723.68 and depicting a genetic structure consistent with the Admixture results. Indeed, the Maximum Likelihood tree clearly divided the same four groups, respectively, Uganda, Europe and Shanghai, the Americas and Hawaii and the remaining localities in China. This analysis also showed a higher genetic differentiation between individuals from the different locations in Asia compared to between individuals within each of the three other clusters. The hierarchical clustering tree on the individual dissimilarity matrix yielded a similar genetic structure between samples (Supplementary Fig. 3).

Using the blacklisted reads as a whitelist to focus on the symbiotic fungus, we obtained only 95 SNPs after filtering with $r=0.3$ and excluding loci with a mean depth lower than 4. As for *X. compactus*, the cross-validation values reached a plateau for $K=4$ (Supplementary Material S6). With a similarity threshold of 0.90, the 300 Admixture runs yielded 83 different modes, the major mode representing 191 of them, with a pairwise similarity of 0.949. The analyses distinguished the same four groups as for the insect symbiont. However, in some runs, a few samples from group 1 were assigned to group 2 and, reciprocally, most probably resulting from restricted power due to the limited number of loci (Supplementary Table S6).

Discussion

Invasion history of *X. compactus* and plausible scenarios

In spite of a limited sampling obtained in the native range, our results suggest the existence of genetic diversity and differentiation among *X. compactus* populations in Asia, with

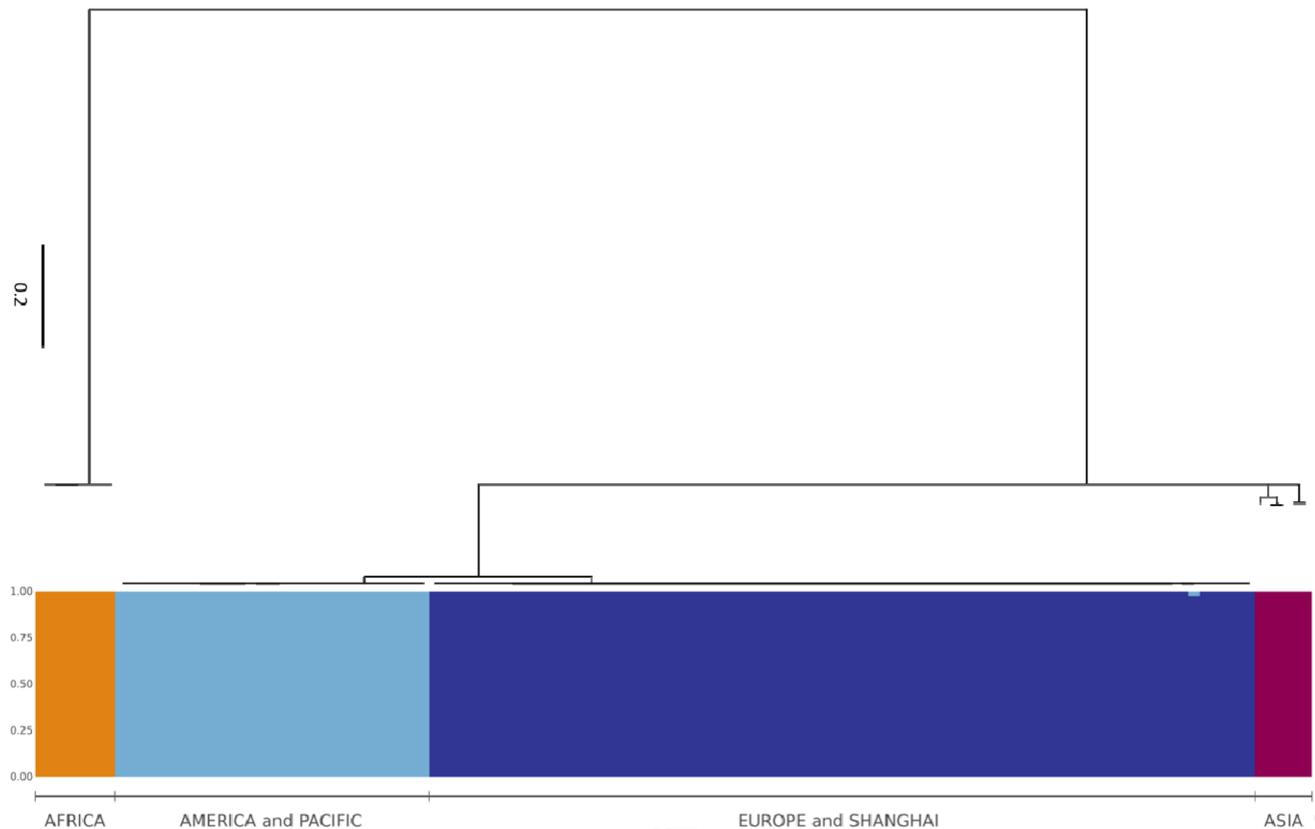


Fig. 2 Maximum likelihood tree performed with RAxML 8.2.1 and admixture plot for $K=4$ calculated on RAD sequencing data. Specimens are divided according to their geographical origin

Table 3 Pairwise F_{st} (lower part) and Nei distances (upper part) calculated on RAD sequencing data between the four groups identified by Admixture

	Americas and Pacific	Africa	Europe and Shanghai	Asia
Americas and Pacific	0	1.315	0.028	0.195
Africa	0.994	0	1.315	1.109
Europe and Shanghai	0.797	0.994	0	0.196
Asia	0.938	0.975	0.954	0

at least three mitochondrial lineages. The geographical distributions of these genetic groups within the native range will need to be characterised, as well as the putative existence of unsampled additional lineages. We showed that two of these genetic groups were the sources of all the invasive populations. Lineage A independently colonised the Americas and the Pacific Islands in the 1960s and Europe in the 2010s, and lineage B colonised Madagascar and Africa in the early twentieth century. The regions invaded by mitochondrial lineage A (Europe, the Americas and the Pacific islands) were characterised by very low genetic diversity despite the use of mitochondrial and pangenomic markers

and extensive sampling coverage of their large geographical extent. Our results showed only one mitochondrial haplotype and almost no genomic diversity within each invasive group. This contrasts with other invasive ambrosia beetles, such as *X. crassiusculus*, whose populations in the invaded range were genetically diverse (Storer et al. 2017). However, it is similar to *X. germanus*, in which a single COI lineage was responsible for the European and the American invasions, although it showed higher haplotypic diversity in both continents than *X. compactus* (Dzurenko et al. 2020). According to the genetic invasion paradox (Sax and Brown 2000), we should expect invasive populations that experienced founder effects or bottlenecks to suffer from reduced fitness and evolutionary potential. *X. compactus*' populations, however, might not fulfil the conditions to be called paradoxical (Estoup et al. 2016) as they presumably do not experience inbreeding depression thanks to the purge of the genetic load through repeated inbreeding (Schrieber and Lachmuth 2017). Indeed, a previous experimental study using *X. germanus* showed signs of outcrossing depression but not of inbreeding depression in this species (Peer and Taborsky 2005). Andersen et al. (2012) showed that *X. morigerus* follows the general-purpose-genotype model

(Baker 1965), with generalist rather than specialised lineages with different ecological niches. *X. compactus* invaded Europe, the Americas and the Pacific Islands with almost no genetic diversity, suggesting that it also follows the general-purpose-genotype model and comprises generalist lineages occurring in various environmental conditions.

The absence of mitochondrial and genomic diversity both in Europe and in America and the Pacific is striking and suggests a single introduction in each continent followed by stepping-stone extension and within-continent human-aided dispersion, possibly through national and international live plant trade or timber and wood packaging material transportation. Indeed, further expansions involved long-distance dispersal that the insect's natural dispersal capacities cannot explain. Still, the absence of mitochondrial and genomic diversity could also result from repeated introductions from a single primary source in Europe and the American-Pacific region. As closely related but distinct mitochondrial haplotypes and RAD genetic groups occur in each region, we suppose that both continents were colonised independently from a very similar source. However, the very low genetic diversity found prevented us from inferring *X. compactus*' invasion history after its first entry, and we can only propose hypotheses based on historical data and dates of first detections. Concerning Europe, *X. compactus* was first detected in Italy in 2011 (Garonna et al. 2012), three years before France (Roques et al. 2019), which suggests that Italy might be the origin of the first step of the European invasion. However, we cannot infer the exact movements of the pest that caused the subsequent invasions in Greece, Mallorca, continental Spain and more recently Corsica. The same is true for the American-Pacific invasion, where a single colonisation event from the native range probably occurred. *X. compactus* was first detected in North America in 1941 (Ngoan et al. 1976), in Hawaii in 1964 (Hara and Beardsley Jr 1979) and South America in 1979 (Wood 1980). Thus, the populations from North America could have acted as a source for invasions in Pacific Islands or South America. *X. compactus* can disperse more than 8 km between two flying seasons (Gugliuzzo et al. 2019), which would be enough to disperse actively between close sites (e.g. between sampling sites in Hawaii, for example). Between remote places, however, its spread was probably human-mediated through international trade.

The analyses revealed a relatively low genetic differentiation at nuclear loci between populations in Europe versus in America and the Pacific, in addition to a single mutational step difference between their mitochondrial haplotypes. This suggests a recent divergence and potentially similar or geographically close origins but no recent gene flow between both. We did not find native specimens that would group with the specimens from the Americas and Pacific Islands, probably due to poor coverage of the *X. compactus*' native range. On the contrary, the analyses

consistently grouped the specimens from Europe with those sampled in Shanghai. Shanghai is one of the most economically important cities in China and the busiest port globally, from which quantities of goods, including ornamental plants, are exported worldwide (UNCTAD 2020). We thus hypothesise that Shanghai could be the donor area of the European and the American-Pacific invasions, presumably through international plant trade, but the origin may be larger since the samplings were limited in Eastern China. *X. compactus* is one of the most frequent pests in Shanghai's urban forests (Liu et al. 2021; Gao et al. 2017), and it is unknown whether it is native to Shanghai or not. Therefore, it cannot be excluded that the specimens we analysed originated from other parts of China through the trade of ornamentals within the country. Indeed, Shanghai imported various tree species from other Chinese regions to increase its plant diversity (Wang et al. 2020). Thus, Shanghai could have simply acted as a bridgehead by exporting plants infested by *X. compactus* from Shanghai, or already infested plants produced elsewhere as it has been reported by Bras et al. (2019) for the invasive box tree moth, *Cydalima perspectalis*. Another hypothesis would be that Europe was invaded by specimens from the American-Pacific regions. However, this is less parsimonious as we did not find the haplotype A2 in Europe, nor the haplotype A1 in the American-Pacific. Plus, the haplotype A2 is the only one sequenced in a large region, suggesting that it was stable over the last decades during the invasion of the Americas and the Pacific Islands. Thus, it is unlikely that it mutated before reaching Europe and Shanghai, or that the only mutation between A1 and A2 appeared both in the American-Pacific and Shanghai.

Ghana and Uganda were invaded by the same mitochondrial haplotype belonging to the lineage B, presumably more than a century ago (Egonyu et al. 2015). The haplotype B2, which occurs in Africa, was observed within the native range in a locality in Vietnam and a locality in India, where Kiran et al. (2019) sequenced around 200 specimens and found the haplotype B2 exclusively. These two localities are more than 3500 km apart, and a more thorough sampling throughout Asia might have revealed the haplotype B2 in other localities, potentially along the Bay of Bengal. Unfortunately, Vietnam, India, and Ghana were not included in the RAD sequencing experiment (Table 1), which could have helped propose hypotheses about Africa's invasion history. Although not much is known about the first steps of *X. compactus* invasion in Africa, we hypothesise that *X. compactus* might have been introduced to Africa from Southeastern Asia, maybe from India or Vietnam. Extensive sampling and genetic characterisation of *X. compactus* are needed to assess the number of lineages present in Madagascar and Africa and test whether genetic diversity is also almost non-existent in this continent.

629 Despite a very limited sampling of the native range,
 630 we found that populations from the native range carried a
 631 higher genetic diversity than in the numerous populations
 632 sampled in the invasive range. We can hypothesise that,
 633 similarly to *X. crassiusculus* and *X. germanus*, genetic
 634 diversity in native populations of *X. compactus* is rela-
 635 tively high, and further genetic structure may be identified
 636 with a more extensive sampling there. A comprehensive
 637 study of *X. compactus* genetic structure in its native range
 638 is needed to better describe its genetic diversity, to map
 639 the distribution of the different mitochondrial lineages and
 640 increase our understanding of *X. compactus*' evolutionary
 641 history and colonisation pathways. This would also allow
 642 to formally test whether the genetic diversity is almost
 643 non-existent at the local scale. Specimens from Shang-
 644 hai excluded, Admixture assigned all Asian specimens
 645 to the group 4, despite larger differences between them
 646 than between specimens from the groups 1 and 2 (Fig. 2).
 647 This is most likely due to the difference of sample size
 648 between the larger groups 1 and 2, and group 4 (Table 1),
 649 and a study including more specimens from *X. compactus*'
 650 native range would presumably reach a higher number of
 651 clusters and notably split the group 3 in several groups,
 652 again arguing for a more extensive sampling of popula-
 653 tions in the native range.

654 Our analysis revealed low individual's heterozygosity and
 655 high *F_{st}* between genetic groups. This must be interpreted
 656 with caution, as restricted dispersal and hence low gene flow
 657 between populations, sib-mating and haplodiploidy contrib-
 658 ute to very low heterozygosity and to a predominant effect of
 659 drift on differentiation between lineages. Hence, these met-
 660 rics are expected to show particularly extreme values com-
 661 pared to organisms having higher dispersal and reproductive
 662 strategies implicating more random mating between local
 663 individuals and to diploid organisms. Nevertheless, such low
 664 heterozygosity and high differentiation are observed among
 665 a wide diversity of organisms, including insects (e.g. Eyer
 666 et al. 2018; Andreev et al. 1998). In the context of assess-
 667 ing invasion routes and identifying source locations of the
 668 invading lineages, such high *F_{st}* between lineages have one
 669 major advantage and one major inconvenient. The advantage
 670 is that given the depleted diversity and genetic stability of
 671 sib-mating populations, the several invading lineages can
 672 be deciphered efficiently and traced along their way. The
 673 disadvantage is that, as the potential source populations are
 674 highly differentiated, one has to genotype virtually almost all
 675 the source populations to be able to assign invading lineages
 676 to their source. This task would be much easier if popula-
 677 tions were less differentiated and with a smoother pattern of
 678 isolation by distance (e.g. Wasser et al. 2004). Less variable
 679 DNA markers (i.e. mitochondrial or nuclear ultra-conserved
 680 elements) may be more suitable to attain such objective in
 681 the context of highly structured populations.

682 The analyses performed on the symbiotic fungus lacked
 683 power, probably because of the relatively small number of
 684 loci available (95 compared to 27,583 for *X. compactus*).
 685 Yet, they showed results consistent with those for *X. com-*
 686 *pactus*, with four different groups emerging from Admixture
 687 and the clustering tree, which suggests a parallel genetic
 688 structure, gene flow, and invasion history of the pest insect
 689 and its symbiotic fungus. As the genome of *Ambrosiella*
 690 *xylebori* is available, it would be interesting in future studies
 691 to extract DNA of both the insect and the symbiotic fungus
 692 separately, to obtain more markers from the fungus and con-
 693 firm the parallel histories of both partners.

694 Management implications

695 The objective of invasive pest management is to lower the
 696 damage resulting from the invasion. This can be accom-
 697 plished by preventing the invasion, eradicating an incipient
 698 invasion, or adapting the management of nurseries, orchards,
 699 and forests to the new pest.

700 In terms of prevention of *X. compactus* invasion, it is no
 701 longer possible for the Americas, Europe and many islands.
 702 Once established, the eradication of *X. compactus* is likely
 703 impossible. Indeed, given in the absence of the Allee effect
 704 in the population dynamics of inbreeding ambrosia beetles,
 705 eradication would require the elimination of all individuals.
 706 Invasion eradication has succeeded in the case of *Xylosan-*
 707 *drus crassiusculus* in Oregon, but only while its distribution
 708 was restricted to one small area (LaBonte 2010).

709 *X. compactus* is not yet established in the entirety of the
 710 suitable area and could presumably colonise new countries
 711 such as Australia or New Zealand and pursue its expansion
 712 in its invaded range, notably in the Mediterranean (Urvois
 713 et al. 2021). The results we presented here showed that
 714 both mitochondrial and nuclear markers revealed the same
 715 invasion history without discrepancy and could be used to
 716 monitor and screen for the pest invasion in regions where
 717 it did not occur yet. Although RAD sequencing could be
 718 helpful to understand the finer genetic structure in *X. com-*
 719 *pactus*' native range, its development is demanding, and it
 720 is not necessary for detection and monitoring tools given
 721 the low diversity in the invaded ranges. We advise to use
 722 mitochondrial DNA sequencing to survey *X. compactus*
 723 in the invasive range, as it is faster, less expensive and
 724 requires less equipment. As our results point to a single
 725 source for both colonisations of Europe and the Americas,
 726 we suggest a more thorough screening of imports origi-
 727 nating from the region of Shanghai, mainly live plants
 728 or wood packaging, as it may be the source of the inva-
 729 sion of *X. compactus* in most of the world. Rizzo et al.
 730 (2021) developed a protocol allowing the identification
 731 of *Xylosandrus compactus*, *X. germanus* and *X. crassi-*
 732 *usculus* from a segment of gallery or frass. This could be

of great help to identify the species after the specimens have dispersed from the galleries. We also advise border protection agencies to deploy traps with attractive lures (a combination of UHR Ethanol, α -pinene, α -copaene and quercivorol, Roques et al., in prep) in ports of entry and to routinely sequence the specimens' mitochondrial DNA to characterise their lineage and haplotype to identify their origin. In already invaded areas, this could help detect additional invasions from new sources, which is a valuable information as populations from different origins could display different behaviours or have different ecological preferences, ultimately affecting management success. Identifying the source of the invasion would also help target the best agent in the case of classical biological control.

In countries where the species is established, there are only limited options for direct control of the pests. Fortunately, as with other *Xylosandrus*, *X. compactus* also attacks stressed trees more than healthy trees (Ranger et al. 2015). Therefore, improving tree health and ecosystem health is an effective management approach, particularly in terms of irrigation (Gugliuzzo et al. 2021).

Author's contribution statement

C.K., A.R. and M.A.A.R. designed the study. L.S., C.C. and T.U. completed the molecular biology work. T.U. and C.P. performed the bioinformatics, the statistical analyses and made the figures. Y. L., A.J.J. and J. H. organised the field work. T.U. wrote the original draft of the manuscript. All authors reviewed, edited and approved the final version of the manuscript.

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Availability of data and material The sequences were deposited in GenBank with the accession numbers XXX.

Declarations

Conflict of interest The authors declare no conflict of interests. Specimens sampled did not involve endangered nor protected species.

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