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1 **Extensive human-mediated jump dispersal within and across the native and introduced**
2 **ranges of the invasive termite *Reticulitermes flavipes***

3
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26 **Abstract**

27 As native ranges are often geographically structured, invasive species originating from a single
28 source population only carry a fraction of the genetic diversity present in their native range. The
29 invasion process is thus often associated with a drastic loss of genetic diversity resulting from a
30 founder event. However, the fraction of diversity brought to the invasive range may vary under
31 different invasion histories, increasing with the size of the propagule, the number of re-introduction
32 events, and/or the total genetic diversity represented by the various source populations in a
33 multiple-introduction scenario. In this study, we generated a SNP dataset for the invasive termite
34 *Reticulitermes flavipes* from 23 native populations in the eastern United States and six introduced
35 populations throughout the world. Using population genetic analyses and approximate Bayesian
36 computation Random Forest, we investigated its worldwide invasion history. We found a complex
37 invasion pathway with multiple events out of the native range and bridgehead introductions from
38 the introduced population in France. Our data suggest that extensive long-distance jump dispersal
39 appears common in both the native and introduced ranges of this species, likely through human
40 transportation. Overall, our results show that similar to multiple introduction events into the
41 invasive range, admixture in the native range prior to invasion can potentially favor invasion
42 success by increasing the genetic diversity that is later transferred to the introduced range.

43

44 1 | INTRODUCTION

45 The transport of species beyond their native ranges by human activity is breaking down
46 biogeographical barriers and causing global reorganization of biota (Capinha et al. 2015; van
47 Kleunen et al. 2015), with the ensuing invasions posing a serious threat to biodiversity, agriculture
48 and human health (Simberloff et al. 2013). Successful invaders must disperse into a
49 geographically distant area, establish a viable and fertile population, and spread throughout this
50 new environment, where the biotic and abiotic pressures may differ from those they faced in their
51 native range (Kolar and Lodge 2001). Biological invasions have long been seen as paradoxical,
52 as the invasion process was thought to occur in spite of the reduction of genetic diversity that
53 typically follows introductions of invasive species (Sax and Brown 2000). However, data from a
54 growing number of studies suggest that biological invasions are not always associated with a loss
55 of genetic diversity, and that a loss of genetic diversity is not always accompanied with inbreeding
56 costs and a loss of adaptive potential (Facon et al. 2006, Roman & Darling 2007, Estoup et al.
57 2016, Eyer et al. 2018a, Blumenfeld et al. 2021). In addition, the ecological dominance of invaders
58 in their novel environments is not necessarily the result of superior competitive ability compared
59 to native species, but may simply involve the filling of vacant niches (Dlugosh and Parker 2008,
60 Dlugosch et al. 2015, Bates et al. 2020).

61 Several life-history traits may enhance the invasive success of some species (Eyer &
62 Vargo 2021). Specific breeding systems, modes of dispersal or physiological characteristics may
63 influence the ability of species to spread and to become established. Investigating the
64 mechanisms underlying the invasion process requires determining whether these traits differ
65 between introduced and native populations. Such differences may arise after the introduction due
66 to new ecological pressures occurring in the invaded area (Wares et al. 2005; Keller and Taylor
67 2008), or they may already be present within native populations, thereby pre-adapting the source
68 population for invasion success. Therefore, determining the source population of invasive species
69 is critical to conduct comparative studies of life-history traits between introduced and native

70 ranges to understand how they evolved under distinct biotic and abiotic pressures (Barker et al.
71 2017).

72 Investigating invasion mechanisms also requires knowledge of the invasion history, in
73 which a series of demographic events may influence the invasion process and patterns of genetic
74 diversity. The introduced range may consist of a single invasive population. This introduced
75 population may have originated from a single introduction out of the native range, or from multiple
76 introductions out of the native range, either from the same or different source populations. In
77 contrast, the introduced range may comprise multiple invasive populations, which may originate
78 from separate introduction events from one source population, or from different source
79 populations out of the native range (Oficialdegui et al. 2019; Acevedo-Limón et al. 2020). Finally,
80 an established invasive population itself may become a source for subsequent invasions, a
81 phenomenon coined the '*bridgehead effect*' (Lombaert et al. 2010; Bertelsmeier and Keller 2018).
82 Therefore, reconstructing invasion histories is important for explaining the global distribution of
83 genetic diversity and understanding adaptive evolution in new environments (Cristescu 2015, van
84 Boheemen and Hodgins 2020).

85 A bottleneck event following an introduction usually results in a loss of genetic diversity in
86 the introduced population (Dlugosch and Parker 2008), but the amount of genetic diversity lost
87 may vary under different invasion scenarios. The degree to which genetic diversity is reduced
88 may be limited when the initial colonizing force is large, when the introduced population is
89 subsequently re-invaded by additional individuals during multiple introduction events, and/or
90 when the introduced population is invaded by individuals from several genetically distinct source
91 populations (Facon et al. 2006). Sometimes, when there are several introductions from different
92 source populations and these interbreed within an invasive population, genetic diversity may even
93 be higher within this population than its native source population(s) (Facon et al. 2008). In
94 contrast, the bridgehead effect may result in a severe loss of diversity, as subsequent
95 introductions arise from an already depauperate introduced population. The bridgehead effect

96 has been suggested to promote the spread of phenotypic traits enhancing invasion success in
97 secondary invasive populations, as these traits are already selected for and widespread in the
98 initial introduced population, although there is limited support for such a phenomenon
99 (Bertelsmeier and Keller 2018). Investigating patterns of genetic diversity in native and introduced
100 populations can therefore provide insights into the introduction history of invasive species (e.g.,
101 Winkler et al. 2019, Geburzi et al. 2020, Hirsch et al. 2021, Resh et al. 2021, Wesse et al. 2021).

102 *Reticulitermes flavipes* is a subterranean termite species native in the eastern USA, where
103 it ranges from Texas to Massachusetts. The termite has become invasive in localities both near
104 to and distant from the eastern USA. In both its native and introduced ranges, this termite species
105 is responsible for large amounts of damage to human structures (Evans et al. 2013, Shults et al.
106 2021). This includes the western USA (Austin et al. 2005; McKern et al. 2006), the Province of
107 Ontario in Canada (Kirby 1965), the Bahamas (Scheffrahn et al. 1999), Chile (Clément et al. 2001)
108 and Uruguay in South America (Austin et al. 2005; Su et al. 2006) and France, Germany, Austria
109 and Italy in Western Europe, where it was first reported in 1837 (Kollar 1837; Weidner 1937;
110 Clément et al. 2001; Ghesini et al. 2010). This species has also been reported (GBIF) from Mexico
111 and the outermost regions of Spain (Canary Island; Hernández-Teixidor et al. 2019) and Portugal
112 (Azores; Austin et al. 2012).

113 The native and invasive populations of *R. flavipes* have been the focus of numerous
114 studies investigating its breeding system. In the French invasive range, colonies are large, readily
115 fuse together and contain several hundred neotenic (worker or nymph-derived reproductives that
116 replace the primary or alate-derived reproductives who found new colonies) (Dronnet et al. 2005;
117 Vargo and Husseneder 2009; Perdereau et al. 2010a). Although substantial variability in breeding
118 structure is present among the native USA populations of *R. flavipes*, colonies from most native
119 populations are spatially less expansive, fuse only occasionally and are headed by a
120 monogamous pair of primary reproductives or a few neotenic (Vargo and Husseneder 2009;
121 Vargo et al. 2013; Agüero et al. 2020). Interestingly, colonies in a population from Louisiana share

122 some of the same traits as those in France (Perdereau et al. 2010a; Perdereau et al. 2010c;
123 Perdereau et al. 2015).

124 Previous genetic analyses based on microsatellite markers and mtDNA haplotypes have
125 shown that the introduced French population of *R. flavipes* exhibits an average decrease in
126 genetic diversity of 60-80% compared to native USA populations (Perdereau et al. 2013). The
127 analysis also revealed the occurrence of three main genetic clusters within the native USA range
128 – the ‘Eastern cluster’ (West Virginia, Virginia, Delaware, North and South Carolina), the ‘Gulf
129 Coast cluster’ (Florida and Eastern Mississippi–Louisiana) and the ‘Southern Louisiana cluster’
130 (the New Orleans and Baton Rouge regions in Louisiana) (Perdereau et al. 2013). Notably, some
131 microsatellite and mtDNA haplotypes found in France were unique to the Southern Louisiana
132 cluster (Perdereau et al. 2013). This finding, together with similarities in chemical profiles and
133 breeding structures found between France and Louisiana (Perdereau et al. 2010b, Perdereau et
134 al. 2015), suggested that the French population of *R. flavipes* was introduced from Louisiana,
135 most likely during the 17th and 18th centuries via wood and plant trade between New Orleans
136 and the major French ports on the Atlantic coast (Dronnet et al. 2005, Perdereau et al. 2010a,
137 Perdereau et al. 2013).

138 Although the Louisiana origin of the invasive French population appears well supported,
139 several points remain unclear. First, Perdereau et al. (2019) recently identified a French haplotype
140 more closely related to the ‘Eastern cluster’ than the ‘Southern Louisiana cluster’, suggesting
141 multiple native populations from the USA may have invaded France. Additionally, the source(s)
142 of the Canadian and Chilean invasions remain unidentified. Although several populations of *R.*
143 *flavipes* occur in the Northeastern and Midwestern USA (*i.e.*, adjacent to Ontario), the only
144 haplotype found in Canada was shared with populations in Louisiana and France (Perdereau et
145 al. 2013). Therefore, it is unclear whether the Canadian population arose from a primary
146 introduction from Louisiana or from a secondary introduction through France (*i.e.*, bridgehead
147 introduction), as eastern Canada and France share a close historical bond. Similarly, Chile’s

148 unique haplotype was closest to one shared between Louisiana and France (Perdereau et al.
149 2013), raising the same question regarding primary versus secondary introduction. Overall, these
150 findings suggest a complex invasion history for *R. flavipes* and raise the question of how many
151 native populations may have served as sources for the introduced populations and what the role
152 of bridgeheads might be in the global distribution of this species.

153 Here, we used population genetic analyses and approximate Bayesian computation
154 Random Forest (ABC-RF) to investigate the invasion history of *R. flavipes*. Using ddRadSeq, we
155 first generated a SNP dataset sequencing 23 native populations in the USA and six introduced
156 populations in France, Germany, Chile, Uruguay, the Bahamas and Canada. We then assessed
157 patterns of genetic structure within the entire native range of the species, and within each of the
158 introduced populations. Finally, in order to elucidate the invasion history of *R. flavipes*, we
159 compared support for different invasion scenarios modeling the number, size and origin of each
160 introduction event using ABC-RF.

161

162 2 | MATERIALS AND METHODS

163 2.1 | Population sampling and sequencing

164 A total of 257 individuals of *R. flavipes* were collected from 29 populations spanning both native
165 (USA) and different introduced populations in Europe (*i.e.*, France, Germany), North America
166 (Canada and Bahamas) and South America (Chile and Uruguay) (Figure 1; Detailed sampling is
167 provided in Table S1). In addition, 19 individuals of the sister species *R. virginicus* were collected
168 to serve as an outgroup for the phylogenetic analysis. Samples were stored in 96% ethanol at
169 4°C until DNA extraction. Total genomic DNA was extracted from each individual using a modified
170 Gentra Puregene extraction method (Gentra Systems, Inc. Minneapolis, MN, USA). DNA quality
171 was assessed by agarose gel electrophoresis and DNA concentration was measured with Qubit®
172 2.0 Fluorometer (Invitrogen, USA). Non-degraded genomic DNA (100-300ng) was used to
173 construct ddRAD libraries. Libraries were prepared and sequenced at the Texas A&M AgriLife
174 Genomics and Bioinformatics Service facility using SphI and EcoRI restriction enzymes following
175 the protocol of Peterson et al. (2012). Each sample was identified using unique combinatorial
176 barcodes of 6 and 8 base pairs. Samples were amplified through PCR with iProof™ High-Fidelity
177 DNA Polymerase (Bio-Rad). PCR products were purified using AMPure XP beads (Beckman
178 Coulter Inc.). Libraries were size-selected to a range of 300–500 bp using the BluePippin system
179 (Sage Science Inc.). Libraries were sequenced on six flowcell lanes using an Illumina HiSeq 2500
180 (Illumina Inc., USA) to generate 150 bp paired-end reads.

181 The paired-end reads were checked for quality control using FastQC v0.11.8 (Andrews
182 2010). Forward and reverse reads were demultiplexed from their barcodes, assigned to each
183 sample and assembled using Stacks v.2.41 (Rochette et al. 2019). Reads were first aligned to
184 the *R. flavipes* reference genome (Zhou et al. unpublished data, Table S2) using the Burrows-
185 Wheeler Aligner (Li and Durbin 2009). Aligned reads were then run through the reference-based
186 pipeline of Stacks, which built and genotyped the paired-end data, as well as called SNPs using
187 the population-wide data per locus. Only SNPs present in at least 70% of individuals in half of the

188 populations were kept for downstream analyses. Furthermore, SNPs with mean coverage lower
189 than 5x and higher than 200x were removed using VCFtools v.0.1.15 (Danecek et al. 2011), to
190 prevent unlikely SNPs and highly repetitive regions. Low frequency alleles (< 0.05) and highly
191 heterozygous loci (> 0.7) were sorted out, as they likely represent sequencing errors and paralogs
192 (Benestan et al. 2016). A single random SNP was kept for each locus, to prevent linkage
193 disequilibrium that may potentially affect population structure and phylogenetic analyses. The
194 dataset was formatted for downstream software programs using PGDSpider v.2.1.1.5 (Lischer
195 and Excoffier 2011).

196

197 **2.2 | Population structure and phylogenetic relationship**

198 Expected (H_E) and observed (H_o) heterozygosity, inbreeding coefficient (F_{IS}), and population
199 differentiation values (F_{ST}) were calculated using Stacks (Rochette et al. 2019). Population
200 structure among the 23 native and six introduced populations was analyzed using three
201 complementary approaches.

202 First, the most likely number of genetic clusters (*i.e.*, K) in the dataset was estimated, and
203 individuals were assigned into each of them using fastSTRUCTURE v1.040 (Raj et al. 2014). The
204 algorithm ran following an admixture model with allele frequencies correlated and did not use a
205 *priori* information on localities. The algorithm was parallelized and automated using
206 Structure_threader (Pina-Martins et al. 2017), and ran for K ranging from one to 29. The
207 *chooseK.py* function was used to select the most likely number of genetic clusters. Plots were
208 created by Distruct v2.3 (Chhatre 2019) (available at <http://distruct2.popgen.org>).

209 Second, genetic clustering was estimated using a principal component analysis (PCA)
210 and a discriminant analysis of principal components (DAPC). DAPC uses discriminant functions
211 that maximize variance among groups while minimizing variance within groups (Jombart et al.
212 2010). The most likely number of genetic groups was first inferred by the *find.clusters* algorithm

213 on the principal component analysis (PCA) outputs, with the Bayesian information criterion utilized
214 to select the number of genetic groups. The optimal number of principal components to inform
215 the DAPC (*i.e.*, maximizing discriminatory power between groups, while preventing overfitting)
216 was then defined using the function *optim.a.score*. Both the PCA and DAPC were performed in
217 R (R Core Team 2020) using the *adegenet* package (Jombart 2008).

218 Third, population structure was visualized using the relatedness matrix produced by the
219 RADpainter and fineRADstructure software (Malinsky et al. 2018). This method calculates co-
220 ancestry between samples as an independent assessment of population structure. Analyses ran
221 using default parameters of 100,000 burn-in and 100,000 MCMC iterations, and results were
222 visualized in R through scripts provided with the program (available at
223 http://cichlid.gurdon.cam.ac.uk/fineRAD_structure.html).

224 Phylogenetic relationships among *R. flavipes* individuals were inferred using maximum
225 likelihood (ML) analysis implemented in RAxML v8.2.12 (Stamatakis 2014). Phylogenetic
226 relationships were also estimated using a Bayesian analysis (Figure S5). After filtering, only 16
227 out of the 19 individuals of *R. virginicus* were used as an outgroup; these *R. virginicus* samples
228 were not used in any other analyses. An acquisition bias correction was applied to the likelihood
229 calculations, removing invariant sites from the alignment through the Phrynomics R script
230 (available at <https://github.com/bbanbury/phrynomics/>). The rapid bootstrap analysis and search
231 for the best-scoring maximum likelihood tree was performed using the extended majority rule
232 (MRE)-based bootstopping criterion (Pattengale et al. 2010) under the GTR+G nucleotide
233 substitution model.

234

235 **2.3 | Assessing the invasion history**

236 The global invasion history of *R. flavipes* was inferred through ABC analyses by comparing
237 support for different invasion scenarios. The scenarios varied according to the origin(s) of

238 introduced populations, the founding population size, the bottleneck duration and the admixture
239 rate if multiple sources were detected. To reduce computational effort, model selection and
240 parameter estimation were performed using the recently developed random forests (RF) machine
241 learning method (ABC-RF) available in the *abcrf* R package (Pudlo et al. 2015, Raynal et al.
242 2018). This method requires a reduced number of simulated datasets while still providing robust
243 posterior estimates. To reduce computational effort, we also only tested scenarios relevant to
244 biological and historical data; for example, we did not consider that the Chilean and Canadian
245 introduced populations could be the source of the French population. A step-by-step approach (9
246 different steps divided into 4 parts; fully explained in Supplementary Information 1) was used to
247 infer the different episodes of the invasion history of *R. flavipes*, as this type of approach is
248 commonly performed in ABC studies to distribute the computational effort (Fraimout et al. 2017,
249 Javal et al. 2019, Ryan et al. 2019). The introduced populations in Germany, Uruguay and the
250 Bahamas were not used in ABC computations as they were represented by too few individuals.
251 Briefly, the first part estimated whether each introduced population (*i.e.*, France, Canada and
252 Chile) arose from independent or bridgehead introduction events (Part A). As this first part
253 indicated that the French population may have played a role in the introductions to Canada and
254 Chile, we first sought to decipher the source(s) of the introductions to France alone (Part B). Next,
255 we attempted to identify the sources of the Canadian (Part C) and Chilean (Part D) populations
256 using France as a potential source. For all scenarios tested, introduction events were followed by
257 a decrease in effective population sizes that varied from one to 100 migrants for a duration of zero
258 to 50 years. Divergence time is given in generations, with a generation length of one year.
259 Posterior distributions of preliminary simulated data sets were used to adjust the range of other
260 priors as wide as possible while retaining biological meaning. For each step, 10,000 simulated
261 datasets, including all of the summary statistics implemented in DIYABC v.2.1.0 (Cornuet et al.
262 2014), were generated per scenario from 2,000 randomly sampled SNPs. Priors were set uniform
263 for all model parameters and selected based on historical records. Simulated datasets were first

264 generated by DIYABC, and later exported for model selection and parameter estimation in ABC-
265 RF. The different scenarios tested within each step are provided in the Supplementary
266 Information.

267 **3 | RESULTS**

268 The 257 *R. flavipes* samples yielded an average of 7.0 million paired reads per individual (range:
269 0.03 – 23.5). Twenty-eight individuals were removed due to a significant amount of missing data
270 ($\geq 60\%$) or low coverage ($\leq 9.5\times$). After filtering, the final dataset contained 229 individuals of *R.*
271 *flavipes* from 29 populations and included 51,116 SNPs, with an average coverage of $27\times$ and
272 32% missing data. Weak inbreeding was found within *R. flavipes* populations ($F_{IS} \pm SE = -0.053$
273 ± 0.031). Consequently, values of observed heterozygosity ($H_o \pm SE = 0.196 \pm 0.031$) were higher
274 than values of expected heterozygosity ($H_e \pm SE = 0.135 \pm 0.020$; values for all populations are
275 provided in Table S3).

276

277 **3.1 | Population structure**

278 Strong genetic structure was uncovered among the *R. flavipes* individuals from fastSTRUCTURE,
279 with $K = 4$ best explaining the structure in the data (Figure 1). At this value of K , more than half of
280 the individuals in the dataset (57.2%) were clearly assigned to one of the four clusters (assignment
281 probability higher than 99%; 73.3% of individuals were assigned to a unique cluster probability
282 higher than 80%). However, the strong genetic structure uncovered among individuals in the
283 native range was inconsistent with their geographic origin, as neighboring samples often exhibited
284 completely different assignment profiles (Figure 1). This pattern was also found when populations
285 from the native range were analyzed separately (Figure S1). In the French introduced range, most
286 samples could be assigned to the same cluster, although some samples from the Paris region
287 had a mixed assignment; a similar mixed assignment was found for the lone German sample. A
288 comparable pattern was observed in the Chilean introduced range, with most samples displaying
289 fixed assignments and only a few with mixed assignments. Although a single genetic group was
290 mostly found within each introduced population (France, Chile and Canada), the three introduced

291 populations were separately assigned to three different genetic groups and did not segregate into
292 a single '*introduced*' cluster; a finding also uncovered at lower values of K (Figure S2). Because
293 the genetic clustering of the native range did not consistently align with geographic origin, inferring
294 a source population for each introduced population becomes difficult. For example, most samples
295 from Chile were assigned to the same cluster as samples from New York, Wisconsin and Texas.
296 Similarly, although the introduced population in France shared its strongest tie to the native range
297 with Arkansas, France also had ties with Louisiana, Missouri and even one sample in South
298 Carolina. The origin of the samples in Canada was even more complicated, as the genetic cluster
299 present in this population was spread across most native localities. Similar findings were
300 uncovered for different values of K (Figure S2).

301 Similar results to that of fastSTRUCTURE were uncovered using the PCA and DAPC
302 approach (Figure 2). The PCA indicated strong differentiation across the *R. flavipes* samples, as
303 they broadly segregated along the two axes. For most localities, genetic clustering was not
304 associated with geography, as samples from a given locality did not always cluster together.
305 Likewise, low genetic similarity was observed between geographically neighboring localities.
306 Interestingly, such a pattern was also found to a lesser extent in the introduced populations of
307 France and Chile (only a single sample was available from Germany and Uruguay, and just two
308 from the Bahamas). In France, most of the samples segregated together, except for six individuals
309 from the Paris region, which clustered separately from the rest of the main population and had
310 mixed assignments. A similar pattern was observed for the samples from Chile, with three
311 samples clustering apart from the main Chilean population. Interestingly, fastSTRUCTURE found
312 the occurrence of two and three genetic clusters in the Chilean and French populations
313 respectively, when those populations were analyzed separately (Figure S3). The *find.clusters*
314 algorithm found the best support for four genetic clusters in the dataset (Figure 2). Notably, the
315 introduced localities of *R. flavipes* did not cluster together; instead, the different introduced

316 populations were spread across the four different DAPC clusters, with some even split between
317 two clusters (Chile and France). Remarkably, a similar pattern was observed from localities within
318 the native range, with samples from a given locality clustering into two (e.g., Texas, Mississippi,
319 Wisconsin) or even three (Louisiana) distinct DAPC clusters.

320 The co-ancestry matrix highlighted similar patterns when clustering individuals based on
321 their level of relatedness (Figure 3). Using fineRADstructure, all samples from a given locality
322 were no more related to one another than they were to samples from another locality (Figure 3).
323 This result is indicative of a weak geographic structure in the native range, as most localities were
324 disjunct in the co-ancestry matrix. Notably, the same pattern was observed for the introduced
325 populations, with clustering observed in two (Canada) or three (France and Chile) distinct co-
326 ancestry groups. Accordingly, although significant, the mean genetic differentiation between
327 populations was rather low (mean $F_{ST} \pm SE = 0.091 \pm 0.054$; pairwise F_{ST} values between each
328 pair of populations is provided in Figure S4).

329

330 **3.2 | Phylogenetic relationship**

331 The ML phylogeny was constructed on 29,875 SNPs after filtering out invariant sites, using 650
332 bootstrap replicates, as suggested by the MRE-based bootstopping-criterion. Overall, the tree
333 was consistent with results from the clustering analyses, despite weak bootstrap support
334 throughout the topology (Figure 4). Interestingly, the entire introduced range did not fall out as a
335 single clade; instead, introduced populations arose throughout different branches of the tree.
336 Furthermore, all invasive populations fall out as at least two (Canada and Bahamas) or more
337 different clades (France and Chile). This result also suggests that different introduced populations
338 arose from separate introduction events out of the native range, and that there were several

339 introduction events in most invasive populations (similar findings were found when Bayesian
340 inferences were used to build the tree; Figure S5).

341

342 **3.3 | Invasion history**

343 Part A of the ABC analysis found that introduced populations in Canada and Chile most likely
344 originated, at least partially, from bridgehead introductions from the previously introduced
345 population in France (Figure 5), rather than directly from the native range (Supplementary
346 Information 1). The RF votes were mostly split between three scenarios describing a bridgehead
347 introduction from France to either Canada (220 RF votes), Chile then Canada (221 RF votes) or
348 both countries (215 RF votes).

349 When analyzing the introduced French population alone in part B, the first step found that
350 this introduced population could not be unambiguously assigned to a single origin, as all three
351 regions of the native range received a substantial amount of support (*Louisiana/Mississippi*: 417
352 RF votes, *East*: 414 RF votes and *Central*: 169 RF votes). The '*least bad*' single introduction event
353 scenario (151 RF votes) was outvoted when compared against a two-population admixture
354 scenario (319 RF votes, second step); and this two-population admixture scenario (271 RF votes)
355 was itself outvoted by scenarios simulating the contemporary French population arising through
356 admixture of all three native regions (394 RF votes, third step). When groups of scenarios were
357 compared, the group of scenarios with admixture outvoted the group without admixture in the
358 second step (660 against 340 RF votes); and the group of scenarios with three-population
359 admixture outvoted the group with two-population admixture in the third step (612 against 388 RF
360 votes). The fourth step of part B (further dividing the native range) found that Massachusetts,
361 Maryland and New York (222 RF votes) obtained the highest support as the origin for the French
362 population. However, several other source populations obtained a significant number of RF votes,

363 casting doubt on the ability to undeniably assign the introduced population of France to a unique
364 source. This ambiguity is further emphasized when the scenarios were divided into groups, as
365 both the Southeastern region (504 RF votes) and the rest of the native range (496 RF votes)
366 obtained an almost identical number of RF votes. Overall, these findings suggest the occurrence
367 of multiple introduction events out of the native range. However, at both large (step1) and finer
368 scales (step4), no scenario received a majority vote, preventing a definitive determination of the
369 source for the introduced population in France and calling for caution in the appraisal of the
370 estimated parameters.

371 Part C aimed at analyzing the origins of the Canadian introduced population, using the
372 French introduced population as a potential source. ABC-RF analyses revealed that the most
373 probable scenario for the origin of the Canadian population was an introduction from a French
374 bridgehead and its admixture with a separate introduction event from the native range (405 RF
375 votes), rather than originating entirely from the native range (227 RF votes) or a French
376 bridgehead (368 RF votes). The presence of a French bridgehead is also supported, as the group
377 of scenarios including a bridgehead event (623 RF votes) outvoted the group without a
378 bridgehead event (377 RF votes). When the native range was further divided, ABC-RF analyses
379 also failed to confidently link the origin of the Canadian introduced population to a unique
380 geographic region, as several source populations obtained a significant number of RF votes. This
381 doubt is also emphasized when groups of scenarios were compared, as both the Southeastern
382 region (520 RF votes) and the rest of the native range (480 RF votes) obtained a similar number
383 of RF votes.

384 A similar invasion history was identified for Chile in part D, as a bridgehead from France
385 combined with an additional introduction event from the native range was found most likely (506
386 RF votes), rather than entirely from the native range (339 RF votes) or a French bridgehead (155
387 RF votes). Similar to the origin of the introduced populations of France and Canada, ABC-RF did

388 not confidently infer the source of the Chilean population when the native range was divided.
389 Several source populations obtained a similar number of RF votes when each scenario was
390 analyzed separately, and the Southeastern group of scenarios (539 RF votes) obtained a similar
391 number of RF votes to the group that included the rest of the native range (461 RF votes). Overall,
392 the ABC results cast doubt on the ability to connect each introduced population to one or a few
393 specific source populations, as most simulated scenarios poorly fit the observed dataset with no
394 scenario receiving a clear majority of the votes. This finding is also suggested by the divergence
395 between the simulated and observed datasets present in the LDA graphs, potentially highlighting
396 that more sophisticated scenarios are needed to better explain the data. Although all of the
397 posterior probabilities and posterior parameter estimates are provided in the Supplementary
398 Information for the '*least bad*' scenario in each step, we call for caution in interpreting those values
399 given the ambiguous results obtained in most steps.

400 4 | DISCUSSION

401 Our study provides insights into the invasion history of the termite *Reticulitermes flavipes*,
402 highlighting frequent and recent human-mediated jump dispersal in both the native and introduced
403 range of this species. We first revealed strong genetic structure among individuals within the
404 native range of this species with individuals grouping into four distinct clusters. Yet, these clusters
405 were not strictly associated with geography, as highly different individuals were found in the same
406 locality and highly similar ones in localities separated by several thousand kilometers. This finding
407 indicates extensive movement of colonies throughout the native range, likely through human
408 transportation of wood. We also highlight a complex invasion history with multiple introduction
409 events out of the native range and bridgehead spread from the introduced population in France.
410 The apparent genetic shuffling within the native range limits our ability to assign an exact source
411 population(s) for the different introduced ranges. However, similar to the effect of multiple
412 introductions into the invasive range, admixture in the native range prior to invasion can potentially
413 favor invasion success by increasing the genetic diversity later conveyed to the introduced
414 ranges.

415 Our findings revealed the occurrence of multiple introductions from different native
416 localities serving as sources for the invasive ranges of France, Chile and Canada. Additionally,
417 Canada and Chile received secondary invasions from the introduced population in France, which
418 acted as a bridgehead. Some previous results indicated that there may have been several
419 introductions into France (Perdereau et al. 2019). *Reticulitermes flavipes* was first reported in
420 Europe (Austria) in 1837 and was first reported in France as *R. santonensis* in 1924 (Feytaud
421 1924), where it was widespread and therefore probably introduced much earlier (Bagnères et al.
422 1990). Despite being unable to definitively link its source population(s) to the New Orleans region
423 as previously suggested (Perdereau et al. 2013, 2015), our data, based on a larger sample size
424 and more informative markers, do not rule out this possibility. Our data instead suggest that

425 individuals genetically similar to this invasive population were found across the entire native
426 range, from Louisiana to Maryland. However, it is possible that the French population originated
427 from colonies originally from the New Orleans region that had been transported elsewhere within
428 the native range, such as South Carolina or Arkansas. Such long-distance jump dispersal within
429 the native range can therefore hamper the clear identification of the source population(s).
430 Likewise, although our results suggest that the Canadian and Chilean introduced populations
431 originated from admixture between the introduced population of France and native localities in
432 the northern range of *R. flavipes*, these results suffer from low confidence, potentially due to
433 genetic mixing between native localities. Although the French connections with Louisiana and
434 eastern Canada are well-established, France also has historical ties with Chile. Notably, most of
435 the human immigrants to Chile between the 18th and 20th centuries come from the Basque region
436 of Southern France (Fernandez-Domingo 2006), where *R. flavipes* occurs. During the 18th
437 century, Chile experienced massive immigration from this region, reaching 27% of the total
438 Chilean colonial population. Overall, these findings indicate that jump dispersal may not be
439 restricted to a single region within the native range of this species. Instead, such dispersal appears
440 common in *R. flavipes* in both its native and invasive ranges, suggesting that this species
441 possesses traits that promote its spread and have contributed to its global distribution.

442 The genetic patterns observed in the native range of *R. flavipes* may be explained by
443 numerous and recent jump dispersal events across the native range, likely mediated via human
444 trade and transportation. This finding exemplifies species spread by *stratified dispersal*, whereby
445 individuals disperse at different spatial scales, from local to long-distance movement (Shigesada
446 et al. 1995). Local scale dispersal relies on the biological dispersal ability of the species, ranging
447 from short-range (*i.e.*, budding) to moderate dispersal (*i.e.*, nuptial flights). In contrast, long-
448 distance dispersal is often human-mediated and therefore considered stochastic and difficult to
449 identify. Notably, our study revealed both genetically distinct individuals inhabiting the same

450 locality and genetically similar individuals separated by several thousand kilometers. The
451 geographic distance separating highly similar individuals far exceeds the biological dispersal
452 ability of this species, which suggests that these individuals were artificially transported to a
453 different locality. Additionally, the finding of genetically distinct individuals within the same or
454 adjacent localities indicates a low level of mixing between those individuals. This may stem from
455 reduced local dispersal, whereby transported individuals inbreed and do not disperse far from
456 their landing point. A high proportion of new reproductives of *R. flavipes* do in fact couple with
457 their nestmates during mating flights (25%); however, the proportion of inbred founders is
458 significantly reduced among established colonies (DeHeer and Vargo 2006). Therefore, this
459 inbreeding depression may select against the interbreeding of artificially transported colonies.
460 Also, *R. flavipes* usually disperses through nuptial flights, which should enhance gene flow over
461 large scales (Vargo 2003). Consequently, a scenario where transported individuals interbreed
462 and do not disperse far from their landing point may not alone explain the pattern observed in this
463 study. The finding of highly genetically different individuals within the same locality therefore
464 suggests that some of the long-distance jump dispersal events are probably too recent to allow
465 transported individuals to admix with local colonies and homogenize the gene pool within
466 populations.

467 The global spread of invasive species is strongly influenced by long-distance jump
468 dispersal events, even once established within an introduced range (Suarez et al. 2001). Jump
469 dispersal events are more effective, and often required, for species to rapidly reach a widespread
470 distribution (Gippet et al. 2019, Bertelsmeier 2021). For example, the worldwide distribution of the
471 Argentine ant has been shown to primarily stem from human-mediated jump dispersal, rather than
472 from its classical spread through colony budding, as the latter would have to be three orders of
473 magnitude higher to explain its actual distribution (Suarez et al. 2001). This finding is also typified
474 in the global distribution of the red imported fire ant *Solenopsis invicta*, which utilized long-range

475 jump dispersal to first invade the southeastern USA, and subsequently Asia and Australia from
476 this USA bridgehead (Ascunce et al. 2011). In general, human-mediated jump dispersal appears
477 common in eusocial invaders with a global distribution, like ants (Bertelsmeier et al. 2017, 2018)
478 and termites (Buczowski and Bertelsmeier 2017, Blumenfeld and Vargo 2020). These multiple
479 long-distance movements are also observed among regions within invasive ranges, across a wide
480 variety of taxa, such as the aforementioned *S. invicta* throughout the southern USA (Lofgren
481 1986) and China (Ascunce et al. 2011), the western mosquitofish *Gambusia affinis* in New
482 Zealand (Purcell and Stockwell 2015), and plants in China (Horvitz et al. 2017). Many studies
483 have demonstrated the role of human-mediated jump dispersal in shaping invasive distributions
484 and genetic diversity. However, it often remains unclear whether long-distance dispersal pre-
485 exists in the native range of invasive species, and whether it plays a role in determining the pattern
486 of genetic diversity observed at the global scale of these species.

487 Native ranges of many invasive species often remain geographically structured (Voisin et
488 al. 2005, Beck et al. 2008, Leinonen et al. 2008, Verhoeven et al. 2011). For example, native
489 populations of *S. invicta* are strongly geographically differentiated (Ross et al. 2007). Though rare
490 long-distance dispersal of *S. invicta* has been reported (Ahrens et al. 2005), these events
491 occurred far in the past and have been attributed to strong winds during nuptial flights or the
492 rafting of entire colonies during flooding events (Hölldobler and Wilson 1990), rather than from
493 human-mediated transport (Ahrens et al. 2005). Native populations of another termite invader
494 *Coptotermes formosanus* in China are highly structured, with distinct native populations
495 representing different genetic clusters (Blumenfeld et al. 2021). This structuring suggests reduced
496 gene flow across populations, and therefore a limited number of human-mediated dispersal
497 events within the native range of this species. Our results stand in sharp contrast with the strong
498 population structure commonly uncovered within the native ranges of invasive species, as
499 frequent jump dispersal appears to have occurred in the native range of *R. flavipes*.

500 Understanding the factors driving the differences between *C. formosanus* and *R. flavipes* may
501 shed light on key evolutionary mechanisms underlying their invasion success. Furthermore, while
502 most studies focus on unraveling invasion pathways out of a native range, our results stress the
503 need to consider evolutionary processes and human-mediated dispersal that may already be
504 present within the native range of an invasive species, as these can affect the level and
505 distribution of genetic diversity in both the native and invasive ranges.

506 Extensive human-mediated jump dispersal has been reported in the native range of a few
507 species. For example, in the invasive tree *Acacia pycnantha*, extensive transport and replanting
508 throughout its native Australian range prior to its introduction to South Africa resulted in highly
509 admixed genotypes already present in the native range. This feature has consequently prevented
510 an accurate identification of the native source population(s), as highly admixed genotypes and
511 comparable genetic diversity were present in both ranges of the species (Le Roux et al. 2013). A
512 similar pattern has been found in the North American rangeland weed, *Centaurea diffusa*, where
513 an extremely low level of population structure in the native range hindered the assignment of its
514 introduced population to its likely native source location (Marrs et al. 2008). However, the genetic
515 patterns observed in the *Acacia* and *Centaurea* plants are slightly different than the one observed
516 in *R. flavipes*, as the inability to pinpoint the origins of invasive populations of these plants stems
517 from the near-panmixia found across the native range (Marrs et al. 2008, Le Roux et al. 2013).
518 Therefore, the patterns in these other species most likely stem from an ancient and continuous
519 genetic shuffling throughout the native range. In contrast, the lack of geographic structure despite
520 highly genetically different individuals indicates recent and stochastic long-distance dispersal in
521 *R. flavipes*. Consequently, the genetic structure of *R. flavipes* may have been different (with less
522 admixture) in both the native and invasive range(s) a few centuries ago, at the beginning of the
523 French, Canadian and Chilean invasions. The complex genetic structure currently observed,

524 together with multiple introduction events, makes it difficult to accurately reconstruct the invasion
525 history of this species.

526 The invasion success of termites is tightly linked with their ability to eat wood, nest in wood
527 and cultivated plants, and readily generate secondary reproductives, as all 28 species of invasive
528 termites share these three traits (Evans et al. 2013, Eyer and Vargo 2021). These traits may
529 enhance the frequency of human-mediated dispersal because any piece of wood serving as a
530 nest or foraging site has the potential to become a viable propagule (Evans et al. 2010, Evans et
531 al. 2013). However, these traits are common in lower termites like *R. flavipes* and *C. formosanus*,
532 therefore their occurrence in both species cannot explain why *R. flavipes* has experienced a
533 greater frequency of long-distance dispersal than *C. formosanus*. In *R. flavipes*, repeated human-
534 mediated dispersal could reflect a higher degree of propagule pressure from different USA
535 regions, representing multiple hubs of intense human activity and timber production. Forests and
536 timber production are unequally distributed across the eastern USA (Brown et al. 1999, Howard
537 and Liang 2019), and may therefore require significant wood transportation throughout this part
538 of the country from high to low timber-producing regions. Similarly, the frequency of human-
539 mediated dispersal may reflect the connectivity between native regions. In the introduced
540 population of *R. flavipes* in France, the distribution of genetic diversity is associated with the
541 construction of the railway network and stations, highlighting its possible role in spreading termites
542 over long distances (Andrieu et al. 2017, Suppo et al. 2018, Perdereau et al. 2019). In the USA,
543 about 14,000km of track were active by 1850, mainly in the eastern USA (141,000km in 1880 and
544 over 400,000km in 1916) (United States Census Bureau 1890, Chandler 1965). In contrast, the
545 first 10km railway was built in China in 1881, but less than 13,000km were in use by 1948 for the
546 whole country. This difference in connectivity may explain the numerous long-distance dispersal
547 events in the native range of *R. flavipes* and their absence in the Chinese native range of *C.*
548 *formosanus*. Interestingly, the USA railroad network has been suggested to represent a major

549 dispersal mode for the invasive population of *C. formosanus* (Austin et al. 2008). Overall, many
550 invasive social insect species originate from South America or East Asia (Tsutsui et al. 2000,
551 Heller 2004, Ross et al. 2007, Eyer et al. 2018a, Eyer et al. 2018b, Eyer et al. 2020). The
552 population structure observed in most native populations of invasive termites may simply reflect
553 the reduced connectivity between native regions in these areas, potentially resulting from a lack
554 of internal trade among regions or difficulty in reaching isolated geographic areas. Our findings in
555 *R. flavipes* indicate that frequent long-distance dispersal may already be present within the native
556 ranges of some invasive species, especially those originating from regions with a long history of
557 dense transport networks.

558 Native populations of many invasive species often remain geographically isolated and
559 locally adapted (Verhoeven et al. 2011). In the introduced range, a temporary loss of local
560 adaptation through admixture has been suggested to alter the fitness consequences of admixture
561 in recent invaders (Verhoeven et al. 2011). In our study, the levels of admixture observed in the
562 introduced populations of France and Chile may be explained by numerous introductions from
563 distinct source populations and their interbreeding within the invasive range. However, we cannot
564 rule out the possibility that populations were already admixed before propagules were transported
565 worldwide. Similarly, it is possible that admixed introduced populations re-invaded the native
566 range of *R. flavipes*. In the native range of species, long-distance dispersal enhances gene flow
567 between distant populations that are otherwise isolated. Similar to post-introduction increases of
568 genetic diversity through multiple introduction events (Kolbe et al. 2004, Stenoien et al. 2005,
569 García et al. 2017), admixture between native populations prior to an introduction event may
570 enhance the amount of genetic diversity brought to the invasive range. Admixture may improve
571 invasion success through recombination of distinct genotypes, potentially creating novel
572 combinations of traits, and/or increasing the level of genetic diversity upon which natural selection
573 can act. Pre- or post-introduction admixture may also relax the inbreeding load by reducing the

574 expression of recessive deleterious alleles or lead to heterosis effects, potentially improving the
575 establishment and early success of invasive species (Ellstrand and Schierenbeck 2000, Drake
576 2006, Keller and Taylor 2008, Hahn and Rieseberg 2016). Overall, increased genetic diversity via
577 admixture may favor subsequent introductions given the novel selection pressures invasive
578 species face in their new environments (Verhoeven et al. 2011).

579

580 *Conclusion*

581 In this study, we infer the occurrence of long-distance jump dispersal in the native range of the
582 termite *R. flavipes*. This long-distance dispersal may facilitate admixture between populations that
583 are otherwise isolated. Admixture in native populations prior to introduction may favor invasion
584 success by increasing the amount of genetic diversity brought to the introduced range, achieving
585 an effect similar to that produced by multiple introductions from the native range. However, pre-
586 introduction admixture may not be as common as multiple introduction scenarios (*i.e.*, post-
587 introduction admixture), because the benefits of admixture in the novel environment of the
588 invasive range are probably higher, and the costs smaller (Rius and Darling 2014). As native
589 populations are locally adapted, long-distance dispersal and admixture may disturb this local
590 adaptation, thereby reducing population fitness (Verhoeven et al. 2011, Palacio-Lopez et al.
591 2017). In contrast, populations in invaded ranges are generally too recent to be locally adapted
592 (but see Batz et al. 2020). This lack of local adaptation may release introduced populations from
593 maintaining specific locale-selected allelic combinations, and thereby fully benefit from admixture
594 in early stages of the invasion. The relative roles of pre-and post-introduction admixture in
595 biological invasions should be fertile ground for future studies.

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603

604 **DATA ACCESSIBILITY**

605 The data reported in this study will be deposited in the Open Science Framework database upon
606 acceptance, <https://osf.io>. <https://osf.io> (<https://doi.org/10.17605/OSF.IO/R537U>). Raw sequence
607 files are deposited at the National Center for Biotechnology Information under BioProject
608 accession number PRJNA667438.

609

610 **AUTHOR CONTRIBUTIONS**

611 ELV and AGB designed the study. EP, SD, FD, AGB and ELV collected the data. LNLJ performed
612 the molecular analyses. AJB, PAE, LNLJ and PTS analyzed the data. PAE and AJB wrote the
613 paper with contributions of ELV.

614

615 **SUPPLEMENTARY MATERIAL**

616 *Additional material may be found in the online version of this article.*

617 **Table S1:** Sampling information for every individual used in this study.

618

619 **Table S2:** Number of samples, observed and expected heterozygosity, FIS and nucleotide
620 diversity for each population.

621 **Table S3:** Number of samples, observed and expected heterozygosity, FIS and nucleotide
622 diversity for each population.

623 **Figure S1:** fastSTRUCTURE assignment for individuals from native populations of *R. flavipes* for
624 K ranging from 2 to 4.

625 **Figure S2:** fastSTRUCTURE assignment for each individual of *R. flavipes* for K ranging from 2 to
626 5.

627 **Figure S3:** fastSTRUCTURE assignment for individuals from invasive populations of France and
628 Chile.

629 **Figure S4:** Pairwise F_{ST} matrix between each pair of populations of *R. flavipes*.

630 **Figure S5:** Bayesian inferences tree of *Reticulitermes flavipes*. Native populations are highlighted
631 in grey; introduced populations are highlighted in reddish colors.

632

633

634 **Supplementary Information 1:** A detailed description of the step-by-step ABC RF analysis is
635 covered, including: 1) priors used for the analyses, 2) graphical representation and random forest
636 votes for each scenario within each step, 3) an overall PCA of the simulated datasets for every
637 scenario for each step and 4) parameter estimates for the final invasion model.

638

639 **FIGURE LEGENDS**

640 **Figure 1:** Sampling map and fastSTRUCTURE assignment for each individual of *R. flavipes* for
641 $K = 4$. Each vertical bar represents an individual and each color represents a distinct genetic
642 cluster. Individual fastSTRUCTURE assignments are geographically located in the native and
643 introduced ranges of *R. flavipes*.

644 **Figure 2:** Principal Component Analysis (PCA) of *Reticulitermes flavipes* individuals. Each circle
645 represents an individual. Each individual is colored according to its population of origin; introduced
646 populations are depicted in reddish colors, native populations are colored in grey. Individuals are
647 grouped according the Discriminant Analysis of Principal Components (DAPC) with best support
648 for $K = 4$ genetic clusters.

649 **Figure 3:** Co-ancestry matrix between each pair of individuals inferred using fineRADstructure.
650 Each pixel represents a pair of individuals. Co-ancestry coefficients between two individuals are
651 designated on a color spectrum. Low values are shown in yellow; higher values are shown in
652 darker colors.

653 **Figure 4:** Maximum likelihood phylogenetic tree of *Reticulitermes flavipes* individuals from
654 RAxML. Individuals are colored according to their fastSTRUCTURE assignments ($K = 4$).
655 Samples from the introduced ranges are highlighted with an emphasized tip. The phylogenetic
656 tree is rooted with 16 *R. virginicus* samples.

657 **Figure 5:** Graphical representation of the invasion pathway of *Reticulitermes flavipes* out of the
658 eastern USA inferred through ABC RF in France, Canada and Chile. The estimated time of
659 introduction and rate of admixture is provided for each introduction event. The large 95%CI
660 however calls for caution in interpreting those values. All scenarios tested and results for each
661 ABC step, as well as all of the posterior parameter estimates, are provided in the Supplementary
662 Information.

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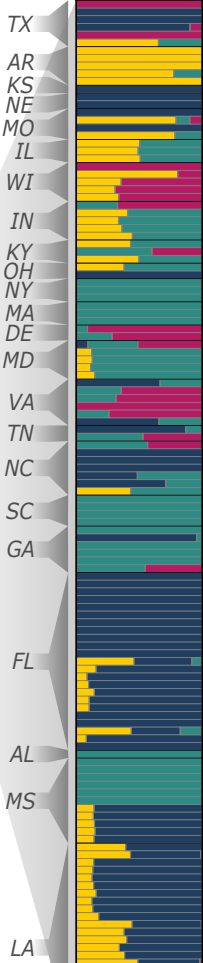
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United States



Canada

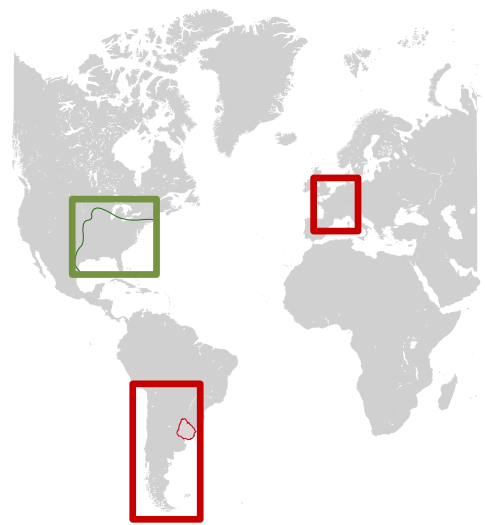
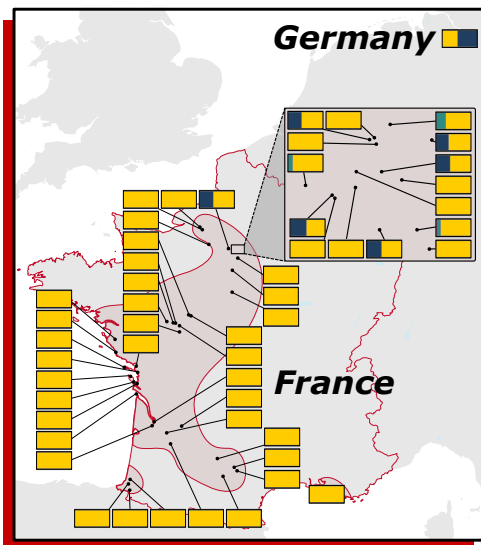
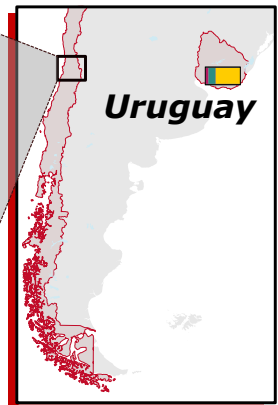
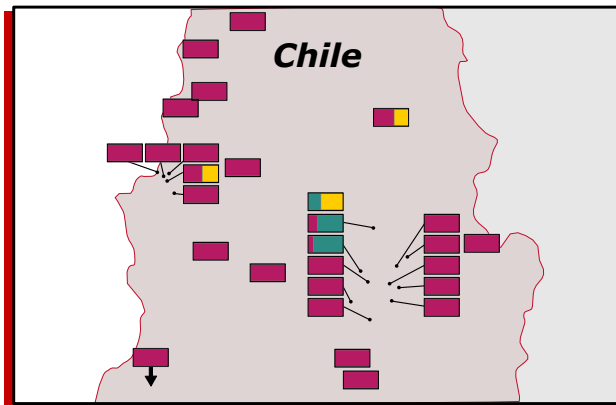
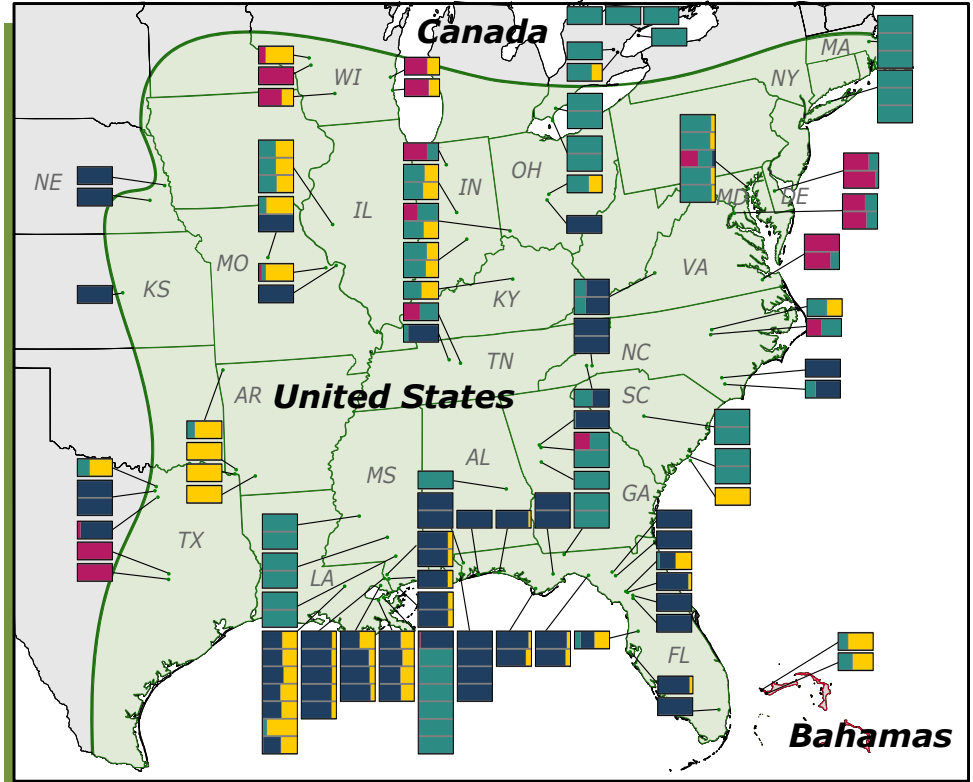
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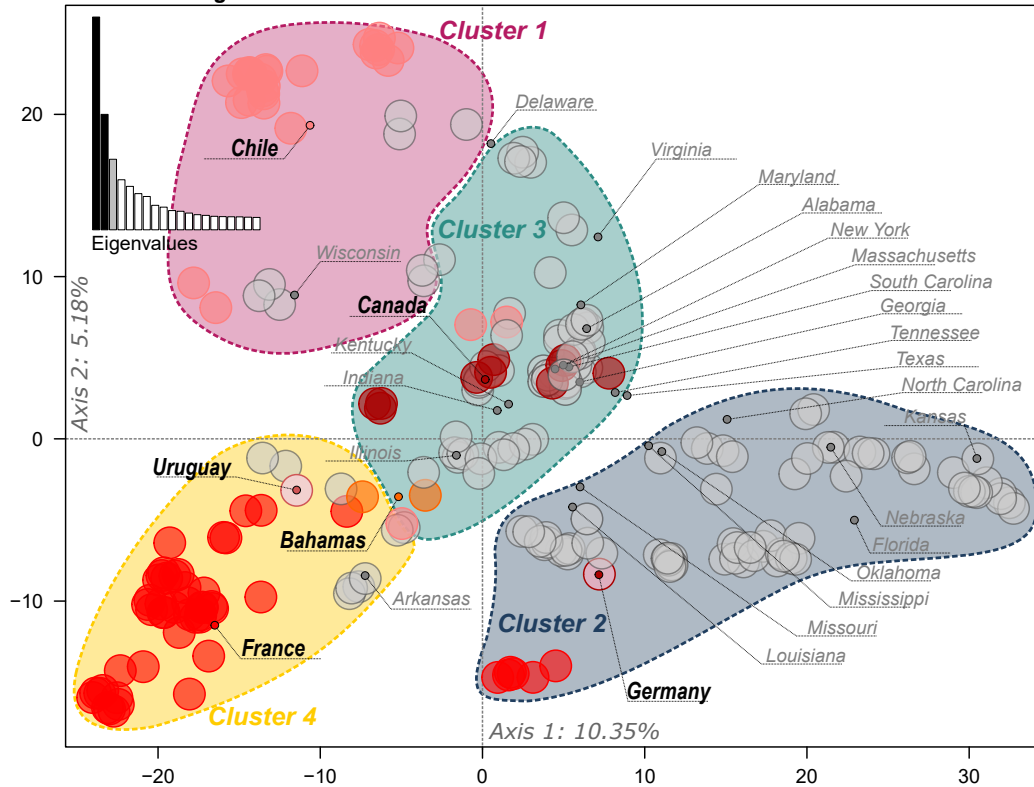
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PCA clustering



DAPC clustering

