Title: Genome-wide divergence among invasive populations of *Aedes aegypti* in California

Running head title (60 chars w/ spaces): Population genomics of California *Aedes aegypti*

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Keywords: *Aedes aegypti*, invasive species, population genomics, California

Abstract word count: 240

Manuscript word count: 3796

Number of figures: 6

Number of tables: 0

Number of Supplementary materials: 3

Abstract

In the summer of 2013, *Aedes aegypti* Linnaeus was first detected in three cities in central California (Clovis, Madera and Menlo Park). It has now been detected in multiple locations in central and southern CA as far south as San Diego and Imperial Counties. A number of published reports suggest that CA populations have been established from multiple independent introductions. Here we report the first population genomics analyses of *Ae. aegypti* based on individual, field collected whole genome sequences. We analyzed 46 *Ae. aegypti* genomes to establish genetic relationships among populations from sites in California, Florida and South Africa. We identified 3 major genetic clusters within California; one that includes all sample sites in the southern part of the state (South of Tehachapi mountain range) plus the town of Exeter in central California and two additional clusters in central California. A lack of concordance between mitochondrial and nuclear genealogies suggests that the three founding populations were polymorphic for two main mitochondrial haplotypes prior to being introduced to California. One of these has been lost in the Clovis populations, possibly by a founder effect. Genome-wide comparisons indicate extensive differentiation between genetic clusters. Our observations support recent introductions of *Ae. aegypti* into California from multiple, genetically diverged source populations. Our data reveal signs of hybridization among diverged populations within CA. Genetic markers identified in this study will be of great value in pursuing classical population genetic studies which require larger sample sizes.

Introduction

Aedes aegypti has a short flight range, usually not actively moving more than 200 m from their breeding source [1], but is exquisitely adapted to hitchhiking in transport vehicles [2]. One central question concerning the populations dynamics of *Ae. aegypti* in CA therefore is whether the established populations at different locations are founded from one source population that spread across the state or if they are the result of other kinds of founding effects. A recent study revealed several, genetically distinct *Ae. aegypti* populations in CA presumably originating from multiple introductions from other sites in the U.S. and/or northern Mexico [3]. Insight into the population structure of CA *Ae. aegypti* beyond this will be necessary to fully understand the dynamics that shape the current pattern of distribution of this invasive vector species.

California (CA) had no known established local populations of *Ae. aegypti* prior to the summer of 2013 when it was detected in three cities in central California: Clovis, Madera and Menlo Park [4, 5, 6]. In the spring and summer of the following year, this mosquito was again found in the same three California locations and for the first time in additional communities in central California and further south in San Diego County (Figure 1). *Ae. aegypti* specimens have been collected over multiple years from some sites and from additional locations in both central and southern CA each year, indicating that *Ae. aegypti* has now become established and is spreading through large parts of the state (Figure 1).

Aedes aegypti is thought to have a short flight range, usually not actively moving more than 200 m from their breeding source [1], but is exquisitely adapted to hitchhiking in transport vehicles [2]. Recent studies revealed several, genetically distinct *Ae. aegypti* populations in CA originating from multiple introductions from other sites in the U.S. and/or northern Mexico [3].

Successful vector control can benefit from population genetics and genomics analyses which can provide estimates of gene flow and identify the genetic basis of phenotypes such as insecticide resistance [7] and host preference [8]. Population genomics studies are especially critical to the

development of control strategies based on genetic manipulation of vectors, which is a matter of growing interest. Modelling, planning and monitoring activities associated with control programs require affordable and rapid assays to distinguish vector sub-populations within a species and a deep understanding of the processes that shape their genetic structure. It is becoming increasingly apparent that hybridization between diverged vector populations may be an import source of new genetic material including alleles that mediate adaptations to facilitate range expansion [9] or that promote the evolution of resistance to insecticides [10]. Analysis of whole-genome sequencing data is the most powerful method to detect even minor admixture [11]. Therefore, we have applied a population genomics approach to study invasive *Ae. aegypti* populations. Here we report a preliminary analysis based on genome sequences of 39 individual *Ae. aegypti*, collected from twelve locations throughout CA, and, for comparison, four specimens from Florida and three from South Africa. The analyses presented here should serve as a starting point for expanded population genomics studies aimed at understanding how invasive mosquito species become established in new locations and how distinct populations interact on the genetic level.

Materials and Methods

Mosquito Collection

Adult female *Ae. aegypti* were collected from 13 cities by personnel from Mosquito Abatement Districts in Fresno, San Diego, and Orange Counties (Figure 2 and Supplementary Table S1). All collections on private properties were conducted after obtaining permission from residents and/or owners. Mosquito samples were individually stored in 80% ethanol prior to DNA extraction.

Whole genome sequencing

103 Genomic DNA was extracted using established protocols [12, 13]. DNA concentrations for each
104 sample were measured using the Qubit dsDNA HS Assay Kit (Life Technologies) on a Qubit instrument
105 (Life Technologies). A genomic DNA library was constructed for each individual mosquito using 20 ng
106 DNA, Qiaseq FX 96 (Qiagen, Valencia, CA), and Ampure SPRI beads (Beckman) following an established
107 protocol [13]. Library concentrations were measured using Qubit (Life Technologies) as described above.
108 Libraries were sequenced as 150 bp paired-end reads using a HiSeq 4000 instrument (Illumina) at the UC
109 Davis DNA Technologies Core.
110
111 Sequence Analysis
112 Raw reads were trimmed using Trimmomatic [14] version 0.36 and mapped to the *Aaeg*L5
113 reference genome [15] using BWA-MEM [16] version 0.7.15. Mapping statistics were calculated using
114 Qualimap version 2.2 [17](Table S1). Freebayes [18] version 1.0.1 was used for variant calling without
115 population prior. We used minimum depth of 8 to call variants for each individual [19]. Only biallelic SNPs
116 were used for further analysis. A missing data threshold of 20% was used to filter SNPs. A phylogenetic
117 tree base on the polymorphism data was constructed using the neighbor-joining algorithm as
118 implemented in PHYLIP [20] version 3.696. Hudson F_{ST} [21], nucleotide diversity (π) and Principal Component
119 Analysis (PCA) analyses was done in Python version 3.4.3 using the scikit-allel module version 0.21.1 [22].
120 The presence of mitochondrial pseudogenes in the nuclear genomes of *Ae. aegypti* could potentially
121 confound SNP calling [23]. Thus we followed the mapping recommendations suggested by Schmidt, et al. [24]
122 and mapped raw reads to the mitochondrial reference genome prior to mapping unmapped reads to the
123 nuclear genome.
124 We used Ae13CLOV028MT (Genbank ID: MH348176) as a reference for mapping the
125 mitochondrial genome because all our specimens contained a deletion between position 14,522 and
126 14,659 compared to the AaegL5 reference genome [24]. Variants in the mitochondrial genome were called

127 with Freebayes as described for the nuclear genome, but set to single ploidy. Mitochondrial coverage
128 was on average 160 times greater than the nuclear genome coverage with a minimum of 25-fold
129 difference (Supplementary Table S1). Use of properly paired reads for variant calling reduced errors
130 generated by failing to recognize mitochondrial pseudogenes present in the nuclear genome. The
131 Vcf2fasta program [25] was used to extract mitogenome sequences from the VCF file to FASTA format.
132 MEGA version 7.0.26 [26] was used for mitogenome alignment. Mitogenome reference sequences of *Culex*
133 *quinquefasciatus* (Genbank accession number = HQ724617), *Aedes notoscriptus* (KM676219), and *Aedes*
134 *albopictus* (NC_006817) were obtained from GenBank and added to the alignment. Sequences for the
135 thirteen mitochondrial protein-coding genes in *Ae. aegypti* were obtained from GenBank [27], extracted
136 from our dataset, and concatenated for tree construction with the maximum likelihood algorithm
137 implemented in MEGA.
138
139 Data Visualization
140 QGIS version 2.18 was used to create maps. Python matplotlib version 2.2.2
141 (https://matplotlib.org/) was used for generating plots. Inkscape (https://inkscape.org/) version 0.92
142 was used to edit images.
143

144 **Results**

145 We sequenced the genomes of 46 specimens of *Ae. aegypti* from California (N=39), Florida (N=4)
146 and South Africa (N=3) with median genome coverage of 9.6X per sample (Supplementary Table S1).
147 Sequence data is available through NCBI Sequence Read Archive (Study accession number: SRP106694).
148 Data is also available through UC Davis Popl OpenProjects AedesGenomes page [28]: Filtering for biallelic
149 SNPs and a minimum depth of 8 with at most 20% missing data yielded 2,919,917 final high-quality SNPs.

150 Principal Components Analysis based on the genotypes of these SNPs revealed four distinct
151 genetic clusters (Figure 3). The genetic cluster designated GC1 includes all six cities in southern CA and
152 includes one central CA site, Exeter. Samples from Florida also fall within this cluster. The GC2 cluster
153 includes the northernmost sites near the coast in Menlo Park and includes some central CA populations
154 at Madera and Fresno. Populations from the restricted area around Clovis and Sanger in central CA form
155 the GC3 cluster. The GC4 cluster includes all South African *Ae. aegypti* samples. Overall, the distribution
156 of the three *Ae. aegypti* genetic clusters containing CA *Ae. aegypti* have a nearly parapatric distribution
157 with the three groups potentially converging in the Central Valley. The population at Sanger appears to
158 have multiple genetic clusters occurring in sympatry. One specimen from Sanger (Ae17CON058) could
159 be GC2 or a hybrid of GC2 and GC3 given its values of PC2 and PC3 relative to other samples (Figure 3).
160 Other Principal components (PC5 and PC6 in Figure 3) indicate additional population subdivisions further
161 dividing Mission Viejo, Garden Grove, Exeter and Vero Beach samples from the rest of GC2 (Figure 3).
162 This is consistent with a previous report suggesting highly structured populations within southern CA *Ae.*
163 *aegypti* [3]. Our genome-wide SNP-based clustering results show clear subdivision between Clovis and
164 Fresno/Madera/Menlo Park. This may seem slightly different from published SNPchip data [3] but is
165 consistent with the microsatellite-based genetic clustering reported in the same study.
166 Windowed-F_{ST} analysis indicates genome-wide differentiation among the four genetic clusters
167 (Figure 4A -C). The GC1 and GC4 clusters are the most highly diverged (genome-wide average F_{ST} =
168 0.159). Genetic distance between GC1 and the other clusters is intermediate (Figure 4 A and B).
169 Nucleotide diversity (π) is highest in the middle region of each chromosome (Figure 4). These regions
170 correspond to the location of the centromeres (coordinates obtained from personal communications
171 with M. Sharakhova at Virginia Polytechnic Institute). Overall nucleotide diversity is lowest on
172 Chromosome 1, which contains the sex determining locus in *Ae. aegypti*. Overall nucleotide diversity is
173 similar in all population comparisons as indicated by difference in nucleotide diversity ($\Delta\pi = \pi_1 - \pi_2$). As a

174 peculiarity, the South African populations have noticeably higher nucleotide diversity in a region around
175 160-170 Mbp of Chromosome 1 compared to samples from the southern CA GC1.

176 For our only temporal comparison, we compared the genomes of samples obtained in Clovis in
177 2013 with those from samples collected in 2016. Overall genome divergence is negligible (F_{ST}= -0.025 ±
178 0.002). However, a whole genome scan using 1 Mbp windows for F_{ST} values indicates a number of
179 genomic regions with markedly elevated F_{ST} values (>0.1) (Figure 4D). The difference in nucleotide
180 diversity between 2013 and 2016 samples shows a reduction in nucleotide diversity over time in
181 chromosome 2 and 3 (mean π_{2013}- π_{2016} value of 4.48x10^{-5} and 5.20 x10^{-5}, respectively). On the contrary,
182 the nucleotide diversity increased over time on Chromsome 1 (π_{2013}- π_{2016} value of -6.36x10^{-5}). However,
183 an increase in nucleotide diversity in 2016 compared to 2013 is visible in all three chromosomes, some
184 of which also coincides with highly differentiated (F_{ST} >0.1) regions. These highly differentiated regions
185 with relative large nucleotide diversity change may indicate genomic regions under selection
186 presumably as the founding population adapts to local environmental conditions [7].

187 Differentiation among populations within GC2 (F_{ST}=-0.052 ~ -0.007) and GC3 (F_{ST}=-0.131 ~ -
188 0.045) is minimal (Table S2). However, differentiation between some populations within GC1 is fairly
189 high (F_{ST}=0.006 ~ 0.210), especially between Exeter and the southern CA samples (F_{ST}=0.094 ~ 0.197).
190 This suggests potential substructure within GC2 separating Exeter and Florida samples from other
191 southern CA samples (Figure 3 and Figure 5). The F_{ST} distance between one sample from the town of
192 Sanger (sample Ae17CON058) to GC2 and GC3 clusters were equivalent (Table S2) and its placement in
193 the PCA (Figure 3) and phylogenetic tree (Figure 5) suggest that this individual could be a GC2/GC3
194 hybrid.

195 Estimates of F_{ST} derived from whole genome sequence data have been shown to be accurate
196 even with very small sample sizes (i.e. N=2/population [29]). This is due to the very large number of SNPs
197 (i.e. n>>1,000 loci) used in these analyses. Using conservative SNP calling with a minimum depth of 8 we

198 were able to calculate F_{ST} values between pairs of genetic clusters based on 2.1 – 6.3 million SNPs (mean
199 = 4.0 million). This well exceeds the number of loci required for an accurate assessment of F_{ST}. In
200 addition, we evaluated various read depths and missing data ratios and observed results consistent with
201 those we report here (data not shown).

202 Mitogenome sequence analysis revealed two major mitochondrial lineages in CA *Ae. aegypti*
203 (Figure 6). One lineage includes the *Ae. aegypti* reference sequence and is represented in all four genetic
204 clusters, the other was present in samples from GC1, GC2 and GC4. Samples from Florida and South
205 Africa are distributed among the two major lineages suggesting that these lineages might be present
206 throughout the global range of *Ae. aegypti*.

207

208

209 **Discussion**

210 Using nuclear genome sequence data we identified three major genetic clusters among CA *Ae.*
211 *aegypti*. These correspond roughly to geographic regions in the state (Figure 2 and 3). Our data support
212 the hypothesis that *Ae. aegypti* in CA currently exists as multiple, mostly isolated populations. High
213 genetic distance ($F_{ST} > 0.1$) as well as genome-wide differentiation (Figure 4) support multiple
214 introductions into CA from genetically distinct source populations as the most plausible history of this
215 invasion.

216 Two major mitochondrial lineages are present within California populations, probably
217 corresponding to previously described global clades [24, 30]. However, their genealogy differs from the
218 nuclear genome genealogy (Figures 5 and 6). This is comparable to a previous study using ND4 sequence
219 analysis of *Ae. aegypti* populations introduced to Florida [31]. The lack of geographic clustering of
220 mitochondrial lineages therefore appears to be common in invasive *Ae. aegypti* populations and is likely
221 due to the saltatory nature of dispersal in this species. The incongruence between nuclear and

222 mitochondrial gene genealogies could be due to different evolutionary rates between different loci
223 producing differing topologies [32, 33, 34]. It is possible that mitochondrial lineages capture historic
224 divergence events, while nuclear genome divergence reflects relatively recent divergence. Linkage
225 disequilibrium decays rapidly in mosquito genomes as seen in *Anopheles arabiensis* [35]. Thus, any contact
226 between two distinct *Ae. aegypti* populations may have resulted in relatively recent gene flow
227 homogenizing populations within a locality. In this case mitochondrial markers appear to be less useful
228 to determine relatively recent population divergence events in *Ae. aegypti*.

229 We investigated the possibility of generating SNP genotypes that are compatible with the
230 existing *Ae. aegypti* SNP chip dataset [36] to allow for a direct comparison of our results with those
231 previously published. The SNP positions provided in Evans et al. [36] were based on the initial genome
232 assembly AaegL1 [37]. Our BLAST results comparing AaegL1-based SNP sequences to the AaegL5 assembly
233 revealed numerous and significant differences, including duplicated regions (multiple matching with
234 high (>98%) similarity), sequence differences (arising from indel mutations), non-biallelic SNPs,
235 polymorphisms surrounding the target SNPs, etc. These often resulted in mismatched genotype calls
236 between the two different platforms, most likely displaying at least partially unintended haplotype calls
237 with the SNP chip. Due to these problems a direct comparison of SNP genotype calls using the published
238 SNP chip data with those generated from genome sequence data is deemed inappropriate and we highly
239 recommend taking this into account when applying SNP chip analyses in the future.

240 Microsatellite data from Gloria-Soria, et al. [4] and Pless, et al. [3] indicated that San Mateo (=Menlo
241 Park), Madera and Fresno samples were genetically similar to samples from the southeastern USA which
242 includes samples from Louisiana, Georgia and Florida. Pless, et al. [3] also included a population from
243 Exeter, CA that was also classified together with other central CA samples and south central and
244 southeast USA populations based on microsatellite profiles. This appears to be inconsistent with our
245 results. Our analysis placed the three central CA populations (Menlo Park, Madera and Fresno) in a

246 group (GC3) distinct from the group containing the southeast USA populations (Vero Beach and Key
247 West, Florida). In our analysis, the samples from Florida clustered with populations from Exeter, CA and
248 southern CA (GC1, Figure 3).

249 Contrary to the microsatellite data, the SNP chip data from the same study [3] groups the Exeter
250 population apart from all other CA populations including those in central CA, consistent with our
251 genome-wide SNP data. Unfortunately, their SNP chip data clustering results did not include samples
252 from the southeast USA preventing direct comparison with their SNP clustering result. This, however,
253 could support the view that the Exeter population, introduced in 2014 is distinct from all other CA
254 populations and that it was introduced independently, rather than resulting from local spread of *Ae.*
255 *aegypti* within CA.

256 Pless, et al. [3] PCA analyses of the SNP chip data separated Clovis (GC3) from the GC2 cluster with
257 some overlap. The larger number of SNPs used in our analysis (>2.9 million biallelic SNPs compared to
258 15,698 SNPs) may have increased the resolution, allowing us to confidently separate the two. Our data
259 together with previous reports strongly support multiple introductions of *Ae. aegypti* in California. The
260 most likely scenario includes four independent introductions: (i) Clovis area; probably in 2013 (ii)
261 Madera area; probably in 2013 (iii) southern CA, probably in 2014 (iv) Exeter, probably in 2014
262 introduced from someplace in the southeast USA like Florida. The years are based on reports from the
263 California vector control districts. This scenario is also in line with most of the results published based on
264 microsatellites and SNP chip data [3]. From our data the origin of the introductions remains dubious with
265 only the Exeter population showing signs of presumable derivation from the southeast USA.
266 The degree of genetic differentiation found in the Clovis population between the years 2013 and 2016
267 (Figure 4D) indicates the population is undergoing rapid changes in its genome, potentially reflecting
268 local adaptation, or, less likely, drift. The only other longitudinal investigation of a CA population of *Ae.*
269 *aegypti* that we are aware of compares genotypes of samples from 2013 and 2015 from Madera,

270 detecting almost no change within these two years [3]. Further investigation on genic features showing
271 significant differences between the two time points may shed light on the genes involved in local
272 adaptation at Clovis and the particular circumstances that drove it.

273 The geographic origin of CA *Ae. aegypti* populations and the means by which they were
274 introduced remains unclear. Perhaps the most interesting open question is what conditions facilitated
275 multiple introductions? Answering these questions is beyond the scope of this study and requires
276 additional data. Investigating samples from different origins using the same NGS platform may provide a
277 clearer description of *Ae. aegypti* invasion history in CA. In addition, investigation describing genomic
278 changes over time may provide information on local adaptation and potentially will be useful for the
279 control of the species in California.

280

281 **Acknowledgments**

282 We thank Orange County Mosquito and Vector Control District team (Mr. Michael Hearst,
283 District Manager), Community Health Division of the Department of Environmental Health (Ms. Rebecca
284 Lafreniere, Chief and Ms. Elizabeth Pozzebon, Director), Greater Los Angeles Mosquito and Vector
285 Control District (Dr. Susan Kluh), and Dr. Christopher Barker (UC Davis) for providing specimens. We
286 thank Youki Yamasaki, Allison Chang, Parker Houston, Allison Weakley, Kendra Person, Hans Gripkey for
287 assisting DNA extraction and library preparations for this study. Special thanks to Dr. Bradley Main for
288 his comments to the manuscript. This project was funded by the UC Davis Bridge Funding Program,
289 School of Veterinary Medicine Vector-borne Disease Pilot Grant Program, DARPA Safe Gene Program
290 and the CDC Pacific Southwest Regional Center of Excellence grant. We thank personnel from
291 Consolidated Mosquito Abatement District and Delta, Greater LA County and San Mateo County Vector
292 Control Districts and Fresno, Madera County and Orange County Mosquito and Vector Control Districts
293 and San Diego County Dept. of Environmental Health, Vector Control for collecting samples used in this

294 study. We also thank Dr. Leo Braack (University of Pretoria, South Africa) for assisting AJC in collection of
295 South African samples and Dr. Danny Governer and SANParks for permitting collection from Shingwedzi
296 in the Kruger National Park.

297

298 **FIGURE LEGENDS**

299 **Figure 1. History of the recent *Ae. aegypti* invasion in California.** The respective year of the first
300 detection of the species in each site is displayed on the map. * 2018 data is surveillance data available as
301 of July, 31, 2018. Data was derived from CalSurv Maps [38] and the CleanTOPO2 basemap [39] was used as
302 background.

303 **Figure 2. Geographic origin of *Ae. aegypti* used in this study.** Left map shows location of all samples
304 from California with the inset enlarging the Fresno/Clovis area. Top right shows a world map, bottom
305 central shows a Florida map and bottom right a South Africa map with all respective sampling locations.
306 CleanTOPO2 basemap [39] was used as background.

307 **Figure 3. Genetic Clusters of *Ae. aegypti* based on PCA analysis.** Principal Component Analysis based on
308 the SNP data. Principal component 1 (PC1) accounts for 6.3% of SNPs that are separating South Africa
309 population (GC4) from United States (US) populations. PC2 accounts for 5.6% of SNPs that separates US
310 populations into three groups (namely GC1, GC2 and GC3). PC3 accounts for 4.4% of SNPs separating
311 Central California population into two groups (GC2 and GC3). PC4 accounts for 4.2% of SNPs separating
312 Southern California population from Exeter (Central California) and Vero Beach, Florida populations. PC5
313 (3.2% SNPs) and PC6 (3.1% SNPs) further divide GC1 cluster separating Exeter, Garden Grove and
314 Mission Viejo and Vero Beach samples.

315 **Figure 4. Genome-wide comparison of *Ae. aegypti* populations revealing broad highly differentiated**
316 **(F_{ST}>0.1) genomic regions.** F_{ST} is marked in black dots. Nucleotide diversity (π) is marked in red for GC1,
317 blue for GC2, green for GC3 and light purple for GC4. Difference in nucleotide diversity ($=\pi_1 - \pi_2$) is

318 marked in in gray. A: GC1 (Southern California, N=18) vs GC2 (Central California – Menlo Park, Madera
319 and Fresno, N=9). B: GC1 (Southern California, N=18) vs GC3 (Central California – Clovis, N=7). C: GC1
320 (Southern California, N=18) vs GC4 (South Africa, N=3). D: Clovis 2013 (N=3) vs 2016 (N=4). Values were
321 calculated using 1Mbp windows with 500Kbp steps. Vertical gray bars indicate the location of
322 centromeres. Other comparisons of GC2 vs GC3, GC2 vs GC4 and GC3 vs GC4 are provided in
323 Supplementary Figure S1.

324 **Figure 5. Neighbor-joining tree based on pairwise nuclear genome-wide F_{ST}.** Populations within GC1
325 designated in red (CA) and purple (Florida and Exeter, CA), GC2 in blue, GC3 in green, and GC4 in
326 magenta.

327 **Figure 6. Maximum Likelihood tree based on mitochondrial protein-coding genes.** Sample-specific
328 sequences for all protein-coding genes were aligned and concatenated. Labelling refers to the Principal
329 Component Analysis and resulting genetic clusters (GCs).

330

331 **Supplementary materials**

332 **Table S1.** Sample metadata including geographic coordinates, collection date and genome sequencing
333 related metric.

334 **Table S2.** Pairwise F_{ST} values based on nuclear genome SNP data.

335 **Figure S1.** Genome-wide comparison of *Ae. aegypti* populations comparing GC2 vs GC3, GC2 vs GC4 and
336 GC3 vs GC4.

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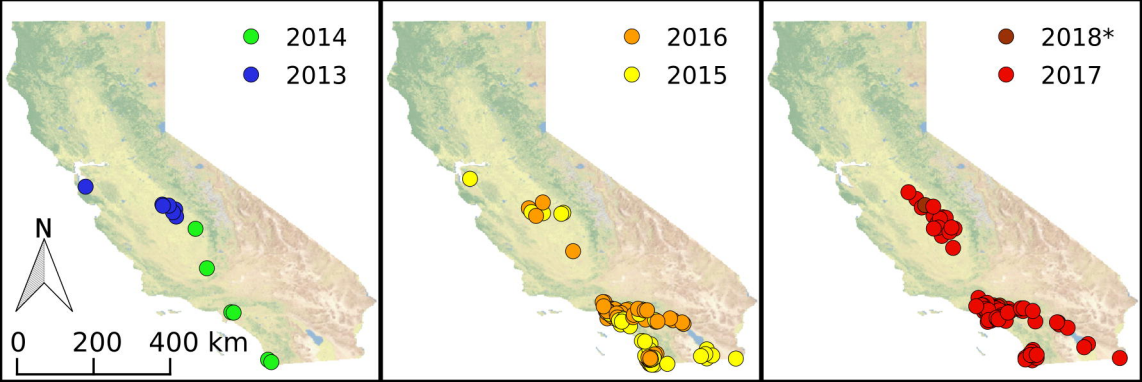
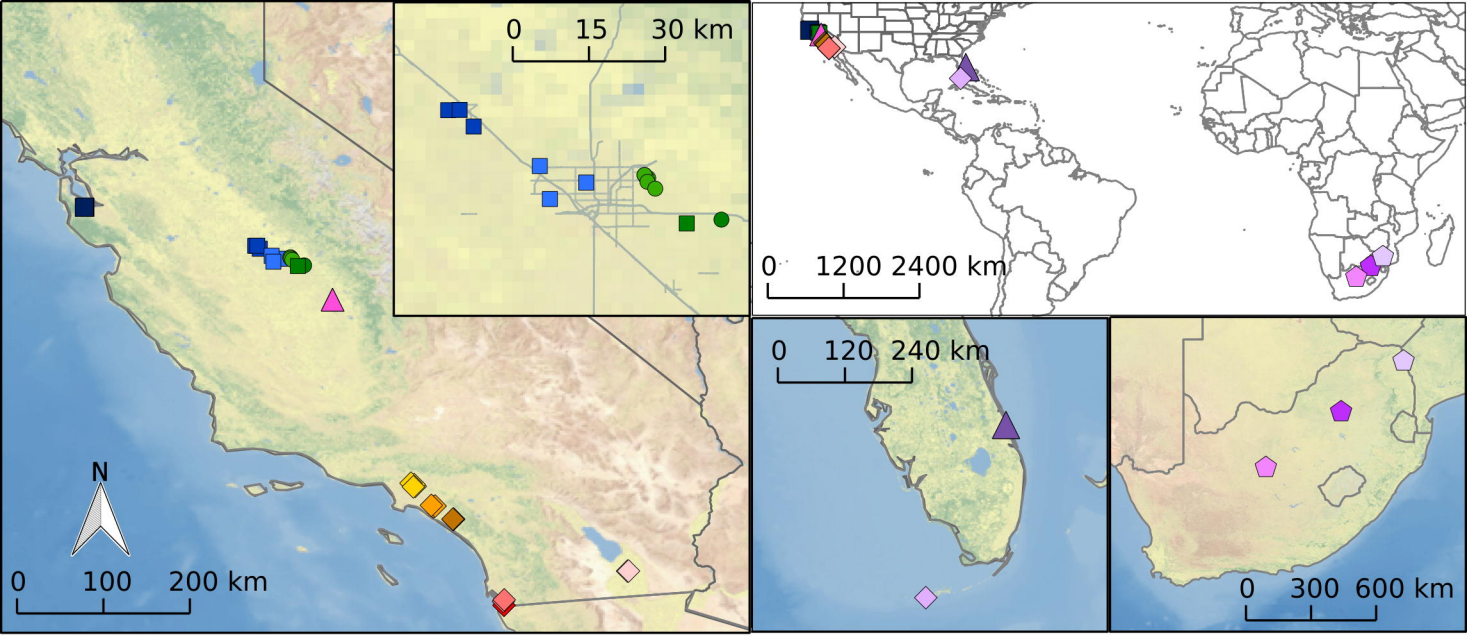

2014
2013
N
0
200
400 km
2016
2015
2018*
2017



Southern California

- ELA
- Garden Grove
- Mission Viejo
- San Diego
- Brawley
- Chula Vista

Central California

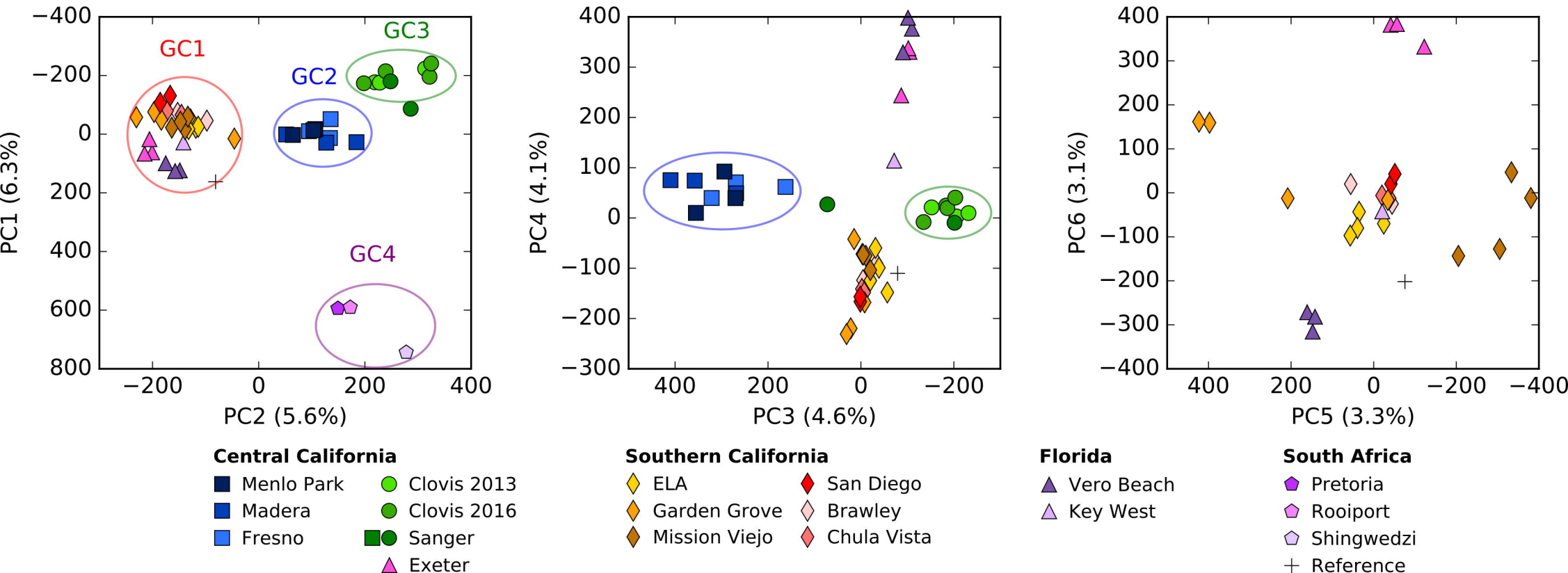
- Menlo Park
- Madera
- Fresno
- Clovis 2013
- Clovis 2016
- Sanger
- Exeter

Florida

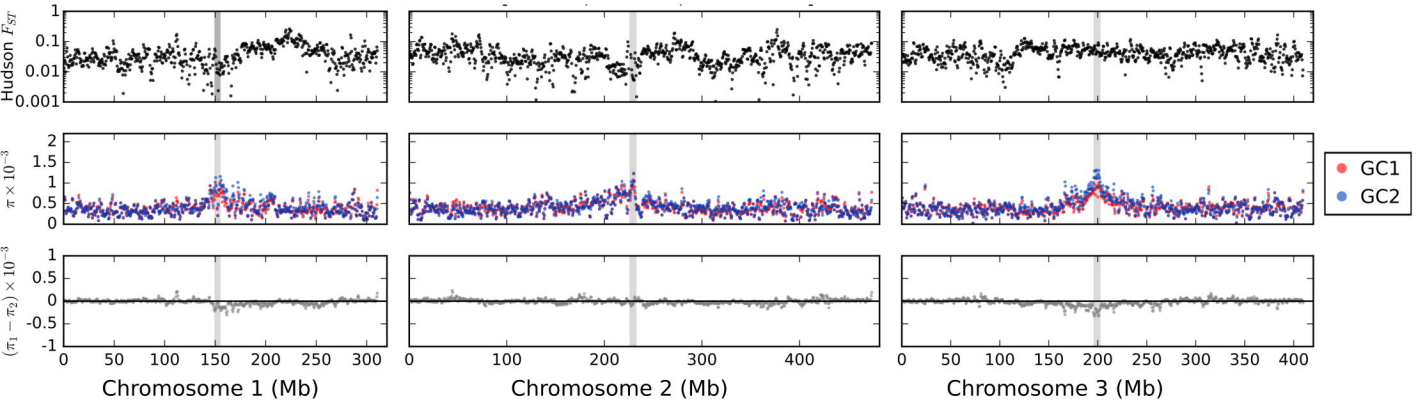
- Vero Beach
- Key West

South Africa

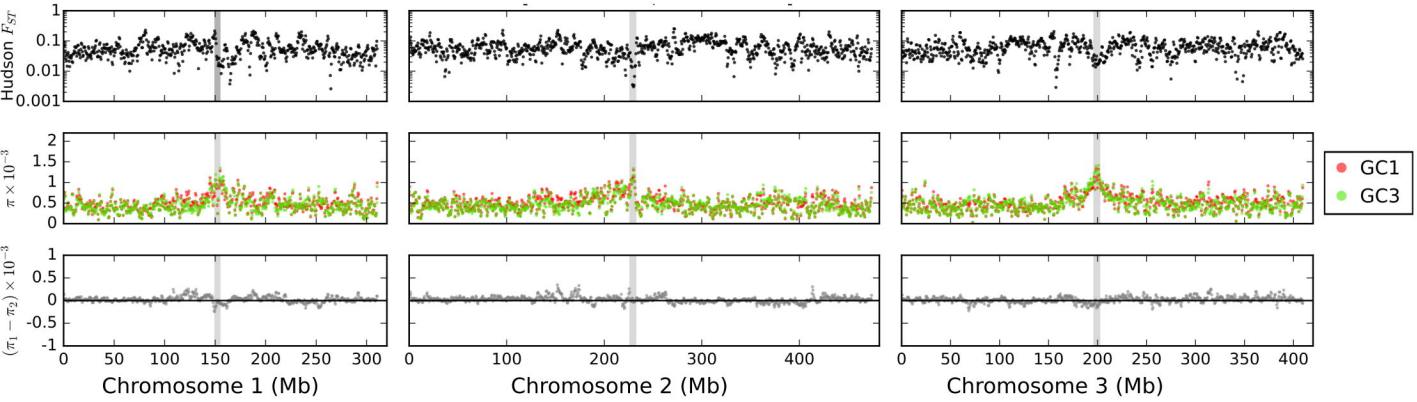
- Pretoria
- Rooiport
- Shingwedzi


GC1
GC2
GC3
GC4
PC1 (6.3%)
PC2 (5.6%)
PC4 (4.1%)
PC3 (4.6%)
PC6 (3.1%)
PC5 (3.3%)
Central California
Menlo Park
Madera
Fresno
Clovis 2013
Clovis 2016
Sanger
Exeter
Southern California
ELA
Garden Grove
Mission Viejo
San Diego
Brawley
Chula Vista
Florida
Vero Beach
Key West
South Africa
Pretoria
Rooiport
Shingwedzi
Reference

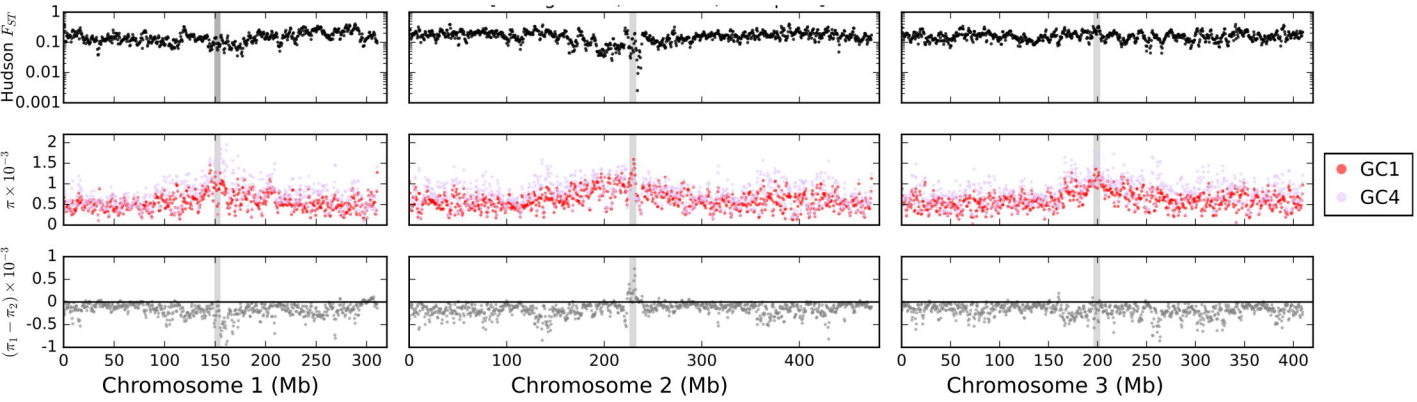
A: GC1 (Southern CA, N=18) vs GC2 (Menlo Park, Madera and Fresno, N=9) - overall F_{ST} = 0.039 ± 0.001



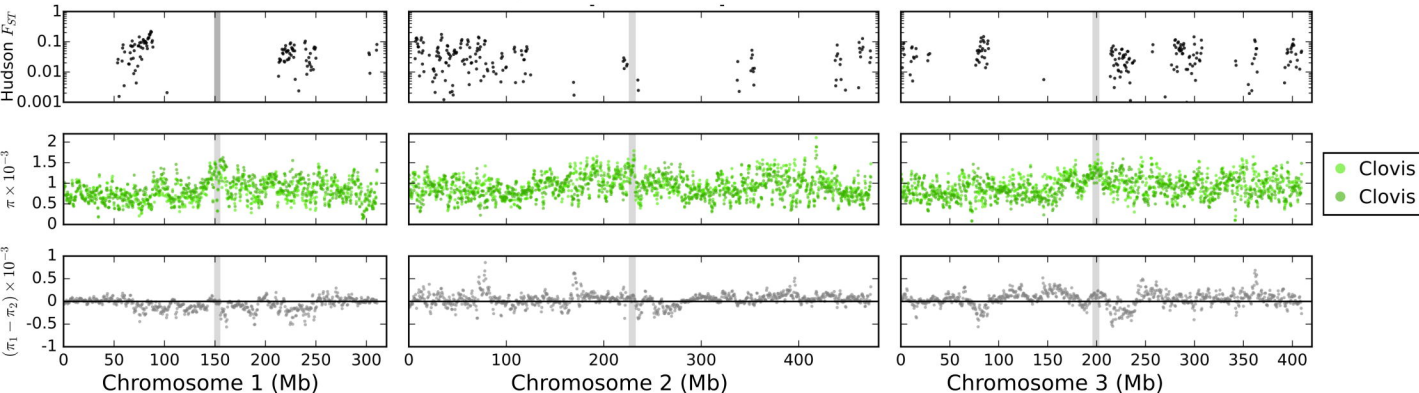
B: GC1 (Southern CA, N=18) vs GC3 (Clovis, N=7) - overall F_{ST} = 0.056 ± 0.002

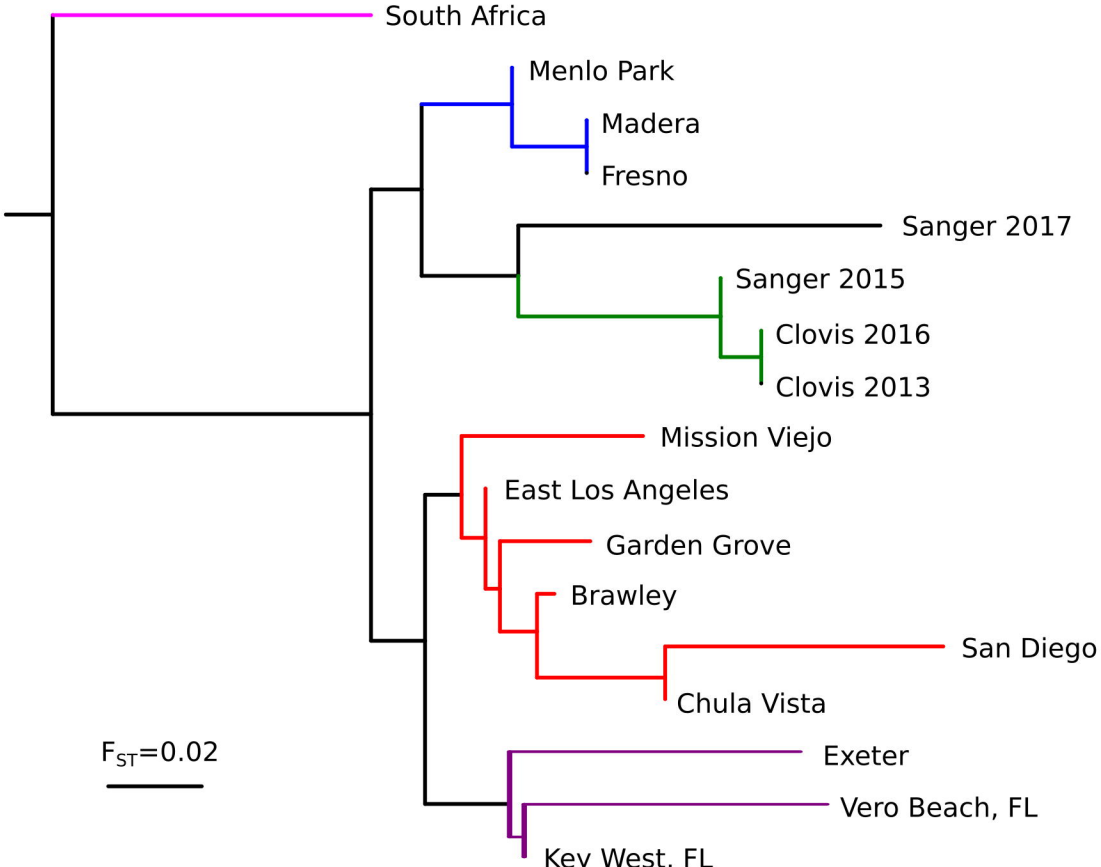


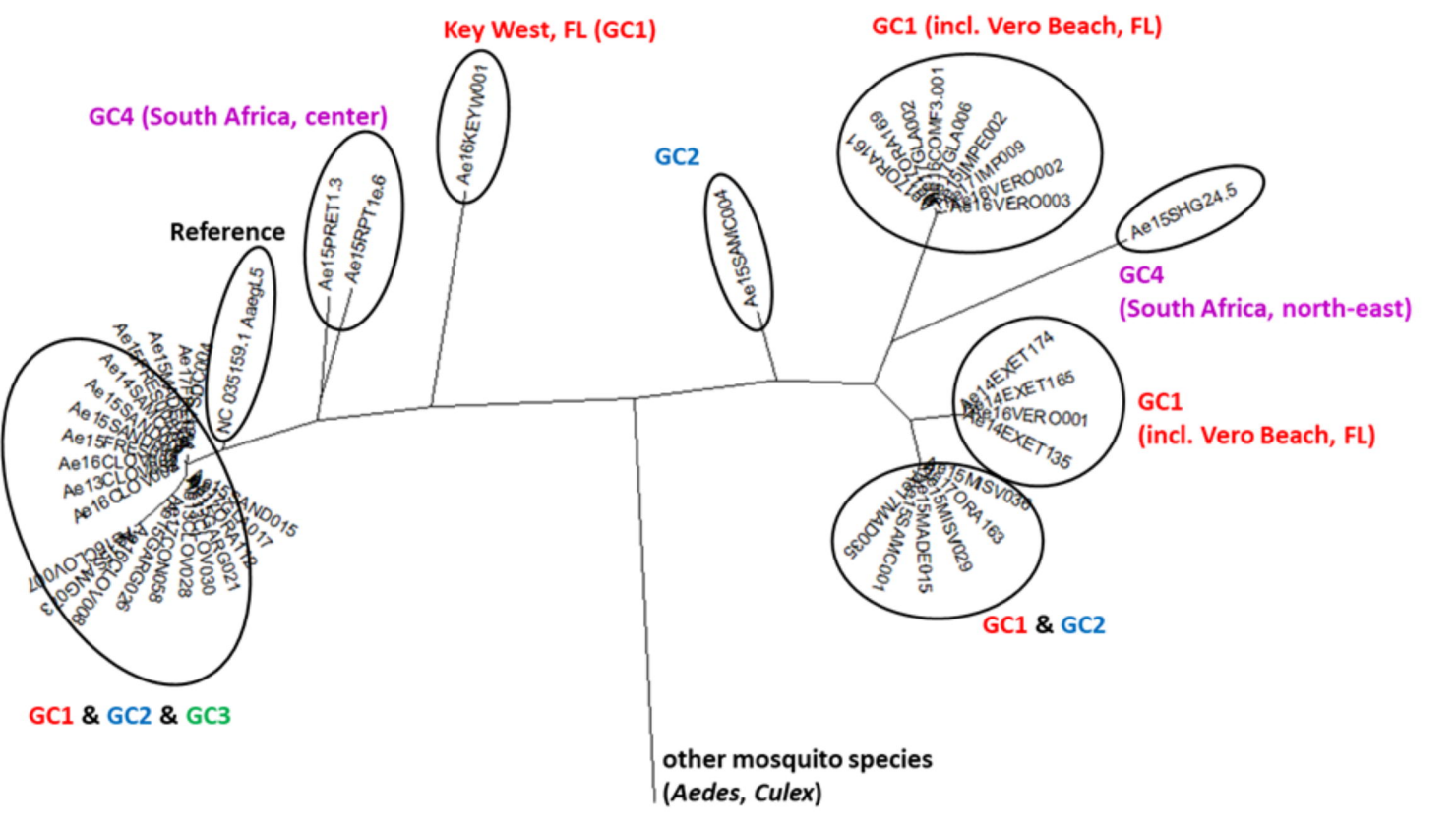
C: GC1 (Southern CA, N=18) vs GC4 (South Africa, N=3) - overall F_{ST} = 0.159 ± 0.003



D: Clovis 2016 (N=4) vs 2013 (N=3) - genome-wide F_{ST} = -0.025 ± 0.002




South Africa
Menlo Park
Madera
Fresno
Sanger 2017
Sanger 2015
Clovis 2016
Clovis 2013
Mission Viejo
East Los Angeles
Garden Grove
Brawley
San Diego
Chula Vista
Exeter
Vero Beach, FL
Key West, FL
F_{ST}=0.02


Key West, FL (GC1)
GC1 (incl. Vero Beach, FL)
GC4 (South Africa, center)
GC2
Reference
Ae16KEYW001
Ae15PRET1.3
Ae15RPT1e.6
Ae15SAMC004
NC 035159.1 AaegL5
Ae15SHG24.5
GC4
(South Africa, north-east)
GC1
(incl. Vero Beach, FL)
GC1 & GC2
GC1 & GC2 & GC3
other mosquito species
(*Aedes*, *Culex*)