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Zones of maximum discontinuity in the western house mouse (*M. m. domesticus*) genetic landscape: a computational geometry method

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Abstract

To represent the zones of maximum genetic discontinuity in a network of geographically located populations of western house mouse from the previously published mitochondrial DNA D-loop sequence datasets which we acquired from the NCBI GenBank database, we applied a computational geometry approach using the Monmonier's maximum difference algorithm implemented in the BARRIER 2.2 software. We defined ten zones where genetic change among populations is locally increased, three of them occur within the Middle East, while seven occur in Europe. Analysis of molecular variance among post-hoc defined regions using the pattern generated by the BARRIER analysis showed that a significant portion of the genetic diversity was because of among groups component.

Introduction

The zones of maximum genetic discontinuity between adjacent populations are very often strongly stabilized and associated in inhospitable regions which act as natural obstacles to gene flow or dispersal [1]. In continental regions physiographic or climatic barriers produce discontinuities between populations. Mountain ranges can constitute significant barriers, especially if they simultaneously separating climatic zones. Darwin and all the pioneers of evolution have accepted the competence of the oceans and aquatic habitats as barriers to dispersal for majority of terrestrial species [2].

The western house mouse (*M. musculus domesticus*) occupies the Middle East and Western Europe regions. It lives almost solely on agricultural lands and human populated areas. Despite of very limited natural dispersal power, it has dispersed into much of rest of the world with humans [3, 4]. Its dispersal and expansion power is sorely tied to human movements. Authentic zoo-archaeological remains [5-7] along with molecular phylogeography [8] have suggested that the precise dispersion of the western house mouse happened in two stage, the first one limited to the east Mediterranean part while the Western Europe was colonized by the most recent waves during the Bronze and Iron ages. This delay in the westward dispersion is considered to be related to the extensive improvement in marine transportation and the stability of the commensal niche in the west Mediterranean parts [6]. Molecular phylogeography and genetic diversity data have proved that the current pattern of differentiation among populations in this subspecies acquired through these historical demographic events [21].

Whenever sampling coordinates are known, the relation of geographic and genetic distances can be evaluated by spatial autocorrelation or regression tests. These methods give some information about the possible structure of the genetic landscape. For example, the low mantel index values reported for commensal house mouse [8-10], suggest that the geographic distance only weakly influenced the pattern of genetic variability or differentiation. However, correlation tests fail when trying to define where genetic barriers exist [11]. The correlation can be high in one zone and low in another zone, and these discrepancies can be difficult to see in a regression diagram since it never defines the areas of genomic discontinuity. Thus, the computational geometry methods are more convenient since they provide the locations and the directions of discontinuities. In order to provide a realistic representation of the genetic discontinuities in *M. m. domesticus* genetic landscape (within the Middle East and western Europe), we reanalyzed the previously published mtDNA D-loop sequence datasets using a computational geometry method, the Monmonier's [12] maximum difference algorithm implemented in the BARRIER 2.2 software [11], which created to infers putative genomic boundaries— i.e. zones of increased change in maps of genomic variation— from genome diversity data.

Materials and Methods

Published mtDNA D-Loop Sequences

Previously published mtDNA D-loop sequence datasets (N = 387; nucleotide positions 15444 to 16253; 809 bp length) of *M. m. domesticus* were acquired from the National Center for Biotechnology Information (NCBI) GenBank (http://www.ncbi.nlm.nih.gov/). Then, according to the reported information from literature and also geographic proximity of samples we classified them to 29 major populations (Fig. 1A). The GenBank accession numbers, references, geographical coordinates, sample sizes, and additional data about populations and samples were acquired from the NCBI GenBank database (Table 1).

Statistical Analysis

DNA sequences were aligned using the MAFFT version 5 [13] and the probabilistic model of sequence evolution was determined by JmodelTest 2.1.3 [14] using the corrected Akaike information criterion (AICc). The pairwise F_{ST} genetic distances among populations were calculated based on the number of pairwise differences between sequences using the ARLEQUIN 3.5 [15] and the statistical significance of all pairwise F_{ST} values was assessed with permutation method, under 10,000 random permutations. A user friendly graphical approach known as Monmonier's [12] maximum-difference which performed in the software BARRIER version 2.2 [11], was applied to investigate potential genetic discontinuities between adjacent populations. Complete details on the procedure are given in Manni et al. (2004), so that only a brief description of the methodology is presented here. The first stage of the approach is to map the sampled populations according to their geographical coordinates and draw the corresponding Delaunay [16] triangulation network. The resulting Voronoi [17] tessellation is then superimposed over the Delaunay network in order to apply Monmonier's algorithm. The first putative genomic boundary is initiated by drawing a line along the edge of a Voronoi polygon. This line separates the pair of neighboring populations (i.e. populations located on the same Delaunay triangle) for which genetic distance is maximal. The Monmonier's algorithm continues to segregate adjacent pairs of populations on the basis of higher pairwise F_{ST} genetic distances, following the edges of Voronoi polygons. This process is extended until the genetic boundary being traced reaches either the outer limits of the Delaunay network (edge of the map) or a previously established barrier (including itself). Subsequent boundaries can be delimited using the largest remaining pairwise F_{ST} genetic distance among adjacent populations as a starting point. There is no criterion to define the number of genomic boundaries to be recognized in this way, thus we decided to stop at ten. Since there are no specific statistical tests to evaluate the statistical significance of the detected putative genomic boundaries with BARRIER, we ran an algorithmic analysis of molecular variance (AMOVA) [18] using the ARLEQUIN. Testing was accomplished among post hoc defined areas isolated by the software.

Results

By analyzing 809 bp of 387 previously published *M. m. domesticus* mtDNA D-loop sequences, the nucleotide substitution model obtained was HKY [19] coupled with the discrete gamma model [20] of site-specific rate heterogeneity (denoted as the HKY + G model; G = 0.55). The F_{ST} values among population pairs were calculated (Table 2). The ten high-ranking genetic discontinuities identified from BARRIER analysis (Fig. 1B). The number attributed to each barrier indicates its ranking, with 1 being the sharpest. Three of them occur within or near to the Fertile Crescent, one positioned between populations in the eastern arm (boundary No.6), while two positioned between populations in the western arm (boundary No.8 and No.9). The other seven genetic discontinuities (including the sharpest ones) positioned between adjacent populations around the northern shore of Mediterranean Sea (boundaries No.1, No.3 and No.7) and Western Europe (boundaries No.2, No.4, No.5 and No.10). AMOVA— as a test to assess the statistical significance of discontinuities— among post-hoc defined regions using the pattern generated with BARRIER analysis showed that a significant portion (21.57% of total variation) of the total mtDNA diversity was because of among groups component (Table 3).

Discussion

When populations fit the Isolation by Distance (IBD) model, the chances of defining genomic discontinuities dwindle [11]. The low mantel index values reported for commensal house mouse in the literature [8-10] imply the presence of numerous discontinuities in its genetic landscape. Here, the genetic discontinuities statistic in BARRIER analysis graphically defined ten zones where genetic change among adjacent western house mouse populations was locally increased, three of them occur in the Middle East, while seven occur around the Mediterranean basin and Western Europe. AMOVA between post hoc detected areas using the structure obtained in BARRIER analysis confirmed that a significant portion of the total diversity was because of between groups component.

Table-1: Details of the previously published mtDNA D-loop sequences used in this study

Samples					Populations		
No.	**Country: City of Origin**	**GenBank Acc. No.**	**Reference**	**Coordinates**	**Classified as Pop. No.***	**Size**	**Mean Coordinates**
1	*Italy: Aeolian Islands*	*JQ646044*	[24]	*38°82´N14°94´E*	*1*	*15*	*38°82´N14°94´E*
2	*Italy: Aeolian Islands*	*JQ646043*		″			
3	*Italy: Aeolian Islands*	*JQ646042*		″			
4	*Italy: Aeolian Islands*	*JQ646041*		″			
5	*Italy: Aeolian Islands*	*JQ646040*		″			
6	*Italy: Aeolian Islands*	*JQ646039*		″			
7	*Italy: Aeolian Islands*	*JQ646038*		″			
8	*Italy: Aeolian Islands*	*JQ646037*		″			
9	*Italy: Aeolian Islands*	*JQ646036*		″			
10	*Italy: Aeolian Islands*	*JQ646035*		″			
11	*Italy: Aeolian Islands*	*JQ646034*		″			
12	*Italy: Aeolian Islands*	*JQ646033*		″			
13	*Italy: Aeolian Islands*	*JQ646032*		″			
14	*Italy: Aeolian Islands*	*JQ646031*		″			
15	*Italy: Aeolian Islands*	*JQ646030*		″			
16	*Iran: Ahvaz*	*EU194640*	[8]	*31°32´N48°66´ E*	*2*	*16*	*31°32´N48°66´E*
17	*Iran: Ahvaz*	*EU194639*		″			
18	*Iran: Ahvaz*	*EU194631*		″			
19	*Iran: Ahvaz*	*EU194629*		″			
20	*Iran: Ahvaz*	*EU194628*		″			
21	*Iran: Ahvaz*	*EU194627*		″			
22	*Iran: Ahvaz*	*EU194626*		″			
23	*Iran: Ahvaz*	*EU194625*		″			
24	*Iran: Ahvaz*	*EU194624*		″			
25	*Iran: Ahvaz*	*EU194623*		″			
26	*Iran: Ahvaz*	*EU194622*		″			
27	*Iran: Ahvaz*	*EU194621*		″			
28	*Iran: Ahvaz*	*EU194620*		″			

Samples					Populations		
No.	**Country: City of Origin**	**GenBank Acc. No.**	**Reference**	**Coordinates**	**Classified as Pop. No.***	**Size**	**Mean Coordinates**
29	*Iran: Ahvaz*	*EU194619*		*″*			
30	*Iran: Ahvaz*	*EU194618*		*″*			
31	*Iran: Ahvaz*	*AB649593*	[25]	*″*			
32	*Iran: Kalat-Bala*	*EU194645*	[8]	*27°32´N56°09´ E*	*3*	*4*	*27˚18´N56˚26´E*
33	*Iran: Bandar-Abbas*	*EU194644*		*27°18´N56°26´ E*			
34	*Iran: Bandar-Abbas*	*EU194643*		*″*			
35	*Iran: Bandar-Abbas*	*EU194637*		*″*			
36	*Bulgaria: Zhitarivo*	*EU194657*	[8]	*42°60´N27°38´ E*	*4*	*15*	*42˚48´N27˚32´E*
37	*Bulgaria: Zhitarivo*	*EU194655*		*″*			
38	*Bulgaria: Zhitarivo*	*EU194651*		*″*			
39	*Bulgaria: Zhitarivo*	*EU194656*		*41°38´N24°43´ E*			
40	*Bulgaria: Zhitarivo*	*EU194654*		*43°24´N27°55´ E*			
41	*Bulgaria: Zhitarivo*	*EU194653*		*42°43´N27°46´ E*			
42	*Bulgaria: Zhitarivo*	*EU194648*		*″*			
43	*Bulgaria: Zhitarivo*	*EU194652*		*42°48´N27°32´ E*			
44	*Bulgaria: Zhitarivo*	*EU194650*		*42°39´N26°59´ E*			
45	*Bulgaria: Zhitarivo*	*EU194649*		*″*			
46	*Turkey: Kırklareli*	*AJ843856*	[10]	*41°41´N27°36´ E*			
47	*Turkey: Kırklareli*	*AJ843855*		*″*			
48	*Turkey: Edirne*	*AJ843848*		*41°27´N26°69´ E*			
49	*Turkey: Edirne*	*AJ843822*		*40°86´N26°63´ E*			
50	*Bulgaria: Vlas*	*AB649605*	[25]	*42°71´N27°75´ E*			
51	*Azerbayjan*	*JX889726*	[26]	*39°20´N45°41´ E*	*5*	*9*	*39˚41´N45˚43´E*
52	*Azerbayjan*	*JX889725*		*″*			
53	*Azerbayjan*	*JX889724*		*″*			
54	*Azerbayjan*	*JX889723*		*″*			
55	*Azerbayjan*	*JX889722*		*″*			
56	*Iran: Mahabad*	*JN416768*	[27]	*36°76´N45°72´ E*			
57	*Iran: Jolfa*	*JN416767*		*38°95´N45°63´ E*			
58	*Georgia: Alazani*	*JX658122*	[28]	*41°56´N45°95´ E*			
59	*Georgia: Chirakskaya*	*AF506184*	[29]	*41°70´N44°79´ E*			
60	*Italy*	*AY560817*	[30]	*42°36´N14°14´ E*	*6*	*14*	*42˚28´N13˚33´E*
61	*Italy*	*AY560808*		*42°35´N13°74´ E*			
62	*Italy*	*AY560829*		*41°87´N12°87´ E*			
63	*Italy*	*AY560819*		*42°04´N13°23´ E*			
64	*Italy*	*AY560821*		*42°09´N13°30´ E*			
65	*Italy*	*AY560820*		*42°17´N13°05´ E*			
66	*Italy*	*AY560830*		*42°28´N13°33´ E*			
67	*Italy*	*AY560805*		*42°48´N13°16´ E*			
68	*Italy*	*AY560807*		*42°93´N12°99´ E*			
69	*Italy*	*AY560828*		*43°06´N13°00´ E*			
70	*Italy*	*AY560804*		*42°48´N13°16´ E*			
71	*Italy*	*AY560806*		*42°28´N13°33´ E*			
72	*Italy*	*AY560822*		*41°87´N12°87´ E*			
73	*Italy*	*AY560809*		*41°89´N12°48´ E*			
74	*Italy*	*AY560826*	[30]	*41°63´N14°25´ E*	*7*	*10*	*41˚49´N14˚95´E*
75	*Italy*	*AY560812*		*41°49´N14°95´ E*			
76	*Italy*	*AY560815*		*41°52´N15°38´ E*			
77	*Italy*	*AY560827*		*41°63´N15°83´ E*			
78	*Italy*	*AY560814*		*41°24´N15°44´ E*			
79	*Italy*	*EU194661*	[8]	*41°08´N14°25´ E*			
80	*Italy*	*AY560825*	[30]	*41°63´N15°83´ E*			
81	*Italy*	*AY560813*		*41°63´N14°25´ E*			
82	*Italy*	*AY560810*		*″*			
83	*Italy*	*AY560811*		*″*			
84	*Italy*	*AY560816*	[30]	*40°03´N15°86´ E*	*8*	*5*	*39˚ 22´N16˚09´E*
85	*Italy*	*AY560818*		*39°22´N16°09´ E*			
86	*Italy: Calabria*	*GU384342*		*39°14´N16°04´ E*			
87	*Italy: Calabria*	*GU384341*		*″*			
88	*Italy: Calabria*	*JQ646045*	[24]	*39°00´N16°83´ E*			
89	*Iran: Famenin*	*EU194617*	[8]	*35°11´N48°97´ E*	*9*	*9*	*35˚11´N48˚97´E*

Samples					Populations		
No.	Country: City of Origin	GenBank Acc. No.	Reference	Coordinates	Classified as Pop. No.*	Size	Mean Coordinates
90	*Iran: Famenin*	*EU194616*		*″*			
91	*Iran: Famenin*	*EU194615*		*″*			
92	*Iran: Famenin*	*EU194614*		*″*			
93	*Iran: Famenin*	*EU194613*		*″*			
94	*Iran: Famenin*	*EU194612*		*″*			
95	*Iran: Famenin*	*EU194609*		*″*			
96	*Iran: Hamadan*	*EU194611*		*34°80´N48°51´ E*			
97	*Iran: Hamadan*	*EU194610*		*34°80´N48°51´ E*			
98	*France*	*KC139188*	[31]	*48°66´N06°99´ E*	*10*	*12*	*48˚66´N06˚99´E*
99	*France*	*KC139189*		*″*			
100	*France*	*KC139190*		*″*			
101	*France*	*KC139191*		*″*			
102	*France*	*KC139192*		*″*			
103	*France*	*KC139193*		*″*			
104	*France*	*KC139194*		*″*			
105	*France*	*KC139195*		*″*			
106	*France*	*KC139196*		*″*			
107	*France*	*KC139197*		*″*			
108	*France*	*KC139198*		*″*			
109	*France*	*KC139199*		*″*			
110	*France*	*KC139170*	[31]	*44°31´N03°51´ E*	*11*	*19*	*44˚31´N03˚51´E*
111	*France*	*KC139171*		*″*			
112	*France*	*KC139172*		*″*			
113	*France*	*KC139173*		*″*			
114	*France*	*KC139174*		*″*			
115	*France*	*KC139175*		*″*			
116	*France*	*KC139176*		*″*			
117	*France*	*KC139177*		*″*			
118	*France*	*KC139178*		*″*			
119	*France*	*KC139179*		*″*			
120	*France*	*KC139180*		*″*			
121	*France*	*KC139181*		*″*			
122	*France*	*KC139182*		*″*			
123	*France*	*KC139183*		*″*			
124	*France*	*KC139184*		*″*			
125	*France*	*KC139185*		*″*			
126	*France*	*KC139186*		*″*			
127	*France*	*KC139187*		*″*			
128	*France: Montpellier*	*AB649592*	[25]	*43°61´N03°87´ E*			
129	*France*	*KC139158*	[31]	*48°64´N03°49´ E*	*12*	*13*	*48˚64´N03˚49´E*
130	*France*	*KC139159*		*″*			
131	*France*	*KC139160*		*″*			
132	*France*	*KC139161*		*″*			
133	*France*	*KC139162*		*″*			
134	*France*	*KC139163*		*″*			
135	*France*	*KC139164*		*″*			
136	*France*	*KC139165*		*″*			
137	*France*	*KC139166*		*″*			
138	*France*	*KC139167*		*″*			
139	*France*	*KC139168*		*″*			
140	*France*	*KC139169*		*″*			
141	*France: Paris*	*HQ185282*	[32]	*48°85´N02°35´ E*			
142	*France*	*KC139136*	[31]	*43°34´N01°42´ E*	*13*	*23*	*43˚34´N01˚42´E*
143	*France*	*KC139137*		*″*			
144	*France*	*KC139138*		*″*			
145	*France*	*KC139139*		*″*			
146	*France*	*KC139140*		*″*			
147	*France*	*KC139141*		*″*			
148	*France*	*KC139142*		*″*			
149	*France*	*KC139143*		*″*			
150	*France*	*KC139144*		*″*			

Samples					Populations		
No.	**Country: City of Origin**	**GenBank Acc. No.**	**Reference**	**Coordinates**	**Classified as Pop. No.***	**Size**	**Mean Coordinates**
151	*France*	*KC139145*		*"*			
152	*France*	*KC139146*		*"*			
153	*France*	*KC139147*		*"*			
154	*France*	*KC139148*		*"*			
155	*France*	*KC139149*		*"*			
156	*France*	*KC139150*		*"*			
157	*France*	*KC139151*		*"*			
158	*France*	*KC139152*		*"*			
159	*France*	*KC139153*		*"*			
160	*France*	*KC139154*		*"*			
161	*France*	*KC139155*		*"*			
162	*France*	*KC139156*		*"*			
163	*France*	*KC139157*		*"*			
164	*France: Toulouse*	*AB649591*	[25]	*43°60´N01°44´ E*			
165	*France*	*KC139124*	[31]	*46°37´N07°00´ E*	*14*	*12*	*46˚35´N06˚13´E*
166	*France*	*KC139125*		*"*			
167	*France*	*KC139126*		*"*			
168	*France*	*KC139127*		*"*			
169	*France*	*KC139128*		*"*			
170	*France*	*KC139129*		*"*			
171	*France*	*KC139130*		*"*			
172	*France*	*KC139131*		*"*			
173	*France*	*KC139132*		*"*			
174	*France*	*KC139133*		*"*			
175	*France*	*KC139134*		*"*			
176	*France*	*KC139135*		*"*			
177	*France*	*KC139091*	[31]	*47°47´N00°56´ W*	*15*	*18*	*47˚47´N00˚56´W*
178	*France*	*KC139092*		*"*			
179	*France*	*KC139093*		*"*			
180	*France*	*KC139094*		*"*			
181	*France*	*KC139095*		*"*			
182	*France*	*KC139096*		*"*			
183	*France*	*KC139097*		*"*			
184	*France*	*KC139098*		*"*			
185	*France*	*KC139099*		*"*			
186	*France*	*KC139100*		*"*			
187	*France*	*KC139101*		*"*			
188	*France*	*KC139102*		*"*			
189	*France*	*KC139103*		*"*			
190	*France*	*KC139104*		*"*			
191	*France*	*KC139105*		*"*			
192	*France*	*KC139106*		*"*			
193	*France*	*KC139107*		*"*			
194	*France*	*KC139108*		*"*			
195	*Germany*	*KC139200*	[31]	*48°78´N8°645´ E*	*16*	*12*	*48˚78´N08˚64´E*
196	*Germany*	*KC139201*		*"*			
197	*Germany*	*KC139202*		*"*			
198	*Germany*	*KC139203*		*"*			
199	*Germany*	*KC139204*		*"*			
200	*Germany*	*KC139205*		*"*			
201	*Germany*	*KC139206*		*"*			
202	*Germany*	*KC139207*		*"*			
203	*Germany*	*KC139208*		*"*			
204	*Germany*	*KC139209*		*"*			
205	*Germany*	*KC139210*		*"*			
206	*Germany*	*KC139211*		*"*			
207	*Germany*	*KC139109*	[31]	*51°12´N7°374´ E*	*17*	*15*	*51˚12´N07˚37´E*
208	*Germany*	*KC139110*		*"*			
209	*Germany*	*KC139111*		*"*			
210	*Germany*	*KC139112*		*"*			

Samples					Populations		
No.	**Country: City of Origin**	**GenBank Acc. No.**	**Reference**	**Coordinates**	**Classified as Pop. No.***	**Size**	**Mean Coordinates**
211	*Germany*	*KC139113*		″			
212	*Germany*	*KC139114*		″			
213	*Germany*	*KC139115*		″			
214	*Germany*	*KC139116*		″			
215	*Germany*	*KC139117*		″			
216	*Germany*	*KC139118*		″			
217	*Germany*	*KC139119*		″			
218	*Germany*	*KC139120*		″			
219	*Germany*	*KC139121*		″			
220	*Germany*	*KC139122*		″			
221	*Germany*	*KC139123*		″			
222	*Israel*	*EU938924*	[33]	*31°04´N34°85´ E*	*18*	*16*	*31˚04´N34˚85´E*
223	*Israel*	*EU938923*		″			
224	*Israel*	*EU938922*		″			
225	*Israel*	*EU938921*		″			
226	*Israel*	*EU938920*		″			
227	*Israel*	*EU938919*		″			
228	*Israel*	*EU938918*		″			
229	*Israel*	*EU938917*		″			
230	*Israel*	*EU938916*		″			
231	*Israel*	*EU938915*		″			
232	*Israel*	*EU938914*		″			
233	*Israel: Ortal*	*AF506187*	[29]	*33°08´N35°75´ E*			
234	*Israel: Ortal*	*AF506186*		*33°08´N35°75´ E*			
235	*Israel: Jerusalem*	*AF506185*		*31°76´N35°21´ E*			
236	*Israel: Keshet*	*AF506183*		*32°98´N35°80´ E*			
237	*Israel: Kursi Beach*	*JX658105*	[28]	*32°82´N35°66´ E*			
238	*Iran: Kuli Alireza*	*JX658120*	[28]	*31°26´N49°65´ E*	*19*	*7*	*31˚26´N49˚65´E*
239	*Iran: Kuli Alireza*	*JX658119*		*31°26´N49°65´ E*			
240	*Iran: Ize*	*JX658118*		*31°83´N49°87´ E*			
241	*Iran: Ize*	*JX658117*		″			
242	*Iran: Simili*	*JX658116*		*31°69´N49°42´ E*			
243	*Iran: Simili*	*JX658115*		″			
244	*Iran: Simili*	*JX658114*		″			
245	*Italy: Bassa*	*EU194663*	[8]	*43°72´N10°87´ E*	*20*	*9*	*45˚22´N10˚35´E*
246	*Italy: Costa*	*EU194660*		*45°91´N11°69´ E*			
247	*Italy: San Georgio*	*EU194675*		*45°32´N11°54´ E*			
248	*Italy: Reggiolo*	*EU194659*		*44°91´N10°80´ E*			
249	*Italy: Cadimarco*	*EU194674*		*45°22´N10°35´ E*			
250	*Italy: Aselli*	*EU194673*		*45°08´N10°01´ E*			
251	*Italy: Cascina Speranza*	*EU194670*		*45°62´N09°83´ E*			
252	*Italy: Zanica*	*EU194671*		*45°99´N9°998´ E*			
253	*Italy: Aselli*	*EU194666*		*45°08´N10°01´ E*			
254	*Italy: Mezzanino*	*EU194658*	[8]	*45°20´N09°33´ E*	*21*	*12*	*45˚28´N09˚08´E*
255	*Italy: Corbesate*	*EU194667*		*45°23´N09°25´ E*			
256	*Italy: Corazza*	*EU194662*		*44°99´N09°01´ E*			
257	*Italy: Cascina Verdura*	*EU194676*		*45°41´N09°19´ E*			
258	*Italy: Binasco*	*AB649587*	[25]	*45°33´N09°09´ E*			
259	*Italy: Trovo*	*EU194672*	[8]	*45°28´N09°08´ E*			
260	*Italy: Cislago*	*AB649586*	[25]	*45°66´N8°974´ E*			
261	*Italy: Nosate*	*EU194668*	[8]	*45°55´N8°719´ E*			
262	*Italy: Invotio*	*EU194669*		*45°78´N8°503´ E*			
263	*Italy: Arioti*	*EU194665*		*45°30´N8°026´ E*			
264	*Italy: Arioti*	*EU194664*		″			
265	*Italy: Aosta*	*AB649589*	[25]	*45°73´N7°313´ E*			
266	*Turkey: Rize*	*AJ843836*	[10]	*41°02´N40°52´ E*	*22*	*12*	*41˚12´N37˚28´E*
267	*Turkey: Trabzon*	*AJ843834*		*41°00´N39°71´ E*			
268	*Turkey: Trabzon*	*AJ843867*		*41°05´N39°33´ E*			
269	*Turkey: Ordu*	*AJ843866*		*41°12´N37°28´ E*			

Samples					Populations		
No.	**Country: City of Origin**	**GenBank Acc. No.**	**Reference**	**Coordinates**	**Classified as Pop. No.***	**Size**	**Mean Coordinates**
270	*Turkey: Samsun*	*AJ843865*		*41°25´N36°54´ E*			
271	*Turkey: Samsun*	*AJ843851*		*41°43´N36°14´ E*			
272	*Turkey: Sinop*	*AJ843861*		*42°02´N35°15´ E*			
273	*Turkey: Sivas*	*AJ843838*		*39°74´N37°01´ E*			
274	*Turkey: Samsun*	*AJ843864*		*41°62´N35°63´ E*			
275	*Turkey: Samsun*	*AJ843863*		*41°61´N35°56´ E*			
276	*Turkey: Sinop*	*AJ843860*		*42°02´N35°15´ E*			
277	*Turkey: Samsun*	*AJ843862*		*41°61´N35°56´ E*			
278	*Portugal: lisbon*	*GQ242020*	[34]	*38°72´N09°15´ W*	*23*	*14*	*38˚17΄N08˚56΄W*
279	*Portugal: Sines*	*GQ242019*		*37°95´N08°86´ W*			
280	*Portugal: Sines*	*GQ242018*		*″*			
281	*Portugal: Vila Nova Mil Fontes*	*GQ242017*		*37°75´N08°76´ W*			
282	*Portugal: Lagos*	*GQ242016*		*37°10´N08°67´ W*			
283	*Portugal: Porto*	*GQ242015*		*41°15´N08°62´ W*			
284	*Portugal: faro*	*GQ242014*		*37°01´N07°93´ W*			
285	*Portugal: lisbon*	*GQ242013*		*38°72´N09°15´ W*			
286	*Portugal: Vila Franca de Xira*	*GQ242012*		*38°95´N08°98´ W*			
287	*Portugal: Vila Franca de Xira*	*GQ242011*		*″*			
288	*Portugal: Peniche*	*GQ242010*		*39°36´N09°38´ W*			
289	*Portugal: Setubal*	*GQ242009*		*38°52´N08°89´ W*			
290	*Portugal: Grandola*	*GQ242008*		*38°17´N08°56´ W*			
291	*Portugal: Grandola*	*GQ242007*		*″*			
292	*Italy: Sardinia*	*JQ646051*	[24]	*40°11´N09°01´ E*	*24*	*4*	*40˚11΄N09˚01΄E*
293	*Italy: Sardinia*	*JQ646050*		*″*			
294	*Italy: Sardinia*	*JQ646049*		*″*			
295	*France: Corse*	*AB649590*	[25]	*42°30´N9°149´ E*			
296	*Iran: Shavour*	*EU194642*	[8]	*31°87´N48°34´ E*	*25*	*10*	*31˚87΄N48˚34΄E*
297	*Iran: Shavour*	*EU194641*		*″*			
298	*Iran: Shavour*	*EU194638*		*″*			
299	*Iran: Shavour*	*EU194636*		*″*			
300	*Iran: Shavour*	*EU194635*		*″*			
301	*Iran: Shavour*	*EU194634*		*″*			
302	*Iran: Shavour*	*EU194633*		*″*			
303	*Iran: Shavour*	*EU194632*		*″*			
304	*Iran: Shavour*	*EU194630*		*″*			
305	*Iran: Choqa Zambil*	*JX658113*	[28]	*32°02´N48°51´ E*			
306	*Turkey: Harran*	*JX658109*	[28]	*36°86´N39°03´ E*	*26*	*10*	*37˚06΄N37˚38΄E*
307	*Turkey: Urfa*	*AJ843842*	[10]	*37°15´N38°79´ E*			
308	*Turkey: Adıyaman*	*AJ843826*		*37°70´N37°86´ E*			
309	*Turkey: Gaziantep*	*AJ843827*		*37°06´N37°38´ E*			
310	*Turkey: Adana*	*AJ843871*		*38°26´N36°22´ E*			
311	*Turkey: Mersin*	*AJ843833*		*36°80´N34°63´ E*			
312	*Turkey: Hatay*	*AJ843837*		*36°03´N36°15´ E*			
313	*Turkey: Adana*	*JX658108*	[28]	*37°00´N35°32´ E*			
314	*Turkey: Harran*	*JX658109*		*36°86´N39°03´ E*			
315	*Turkey: Hatay*	*AJ843837*	[10]	*36°03´N36°15´ E*			
316	*Spain: Barcelona*	*GU384360*	[35]	*42°20´N03°13´ E*	*27*	*16*	*41˚05΄N00˚87΄E*
317	*Spain: Barcelona*	*GU384359*		*41°25´N01°47´ E*			
318	*Spain: Barcelona*	*GU384358*		*41°32´N01°23´ E*			
319	*Spain: Barcelona*	*GU384357*		*41°18´N02°01´ E*			

Samples					Populations		
No.	**Country: City of Origin**	**GenBank Acc. No.**	**Reference**	**Coordinates**	**Classified as Pop. No.***	**Size**	**Mean Coordinates**
320	*Spain: Barcelona*	*GU384355*		*43°48´N05°28´ E*			
321	*Spain: Barcelona*	*GU384356*		*41°19´N01°49´ E*			
322	*Spain: Barcelona*	*GU384354*		*41°10´N01°01´ E*			
323	*Spain: Barcelona*	*GU384353*		*41°31´N01°42´ E*			
324	*Spain: Barcelona*	*GU384352*		*43°48´N05°28´ E*			
325	*Spain: Barcelona*	*GU384351*		*41°17´N01°33´ E*			
326	*Spain: Barcelona*	*GU384350*		*43°48´N05°28´ E*			
327	*Spain: Barcelona*	*GU384349*		*41°27´N01°01´ E*			
328	*Spain: Barcelona*	*GU384348*		*41°42´N01°32´ E*			
329	*Spain: Barcelona*	*GU384347*		*41°21´N01°46´ E*			
330	*Spain: Barcelona*	*GU384346*		*41°23´N01°36´ E*			
331	*Spain: Barcelona*	*GU384345*		*41°29´N01°00´ E*			
332	*United Kingdom*	*FM211631*		*51°51´N00°11´ W*			
333	*United Kingdom*	*FM211630*		*"*			
334	*United Kingdom*	*FM211629*		*"*			
335	*United Kingdom*	*FM211628*		*"*			
336	*United Kingdom*	*FM211627*		*"*			
337	*United Kingdom*	*FM211626*		*"*			
338	*United Kingdom*	*FM211625*		*"*			
339	*United Kingdom*	*FM211624*		*"*			
340	*United Kingdom*	*FM211623*		*"*			
341	*United Kingdom*	*FM211622*		*"*			
342	*United Kingdom*	*FM211621*		*"*			
343	*United Kingdom*	*FM211620*		*"*			
344	*United Kingdom*	*FM211619*		*"*			
345	*United Kingdom*	*FM211618*		*"*			
346	*United Kingdom*	*FM211617*		*"*			
347	*United Kingdom*	*FM211616*		*"*			
348	*United Kingdom*	*FM211615*		*"*			
349	*United Kingdom*	*FM211614*	[36]	*"*	*28*	*36*	*51˚51´N00˚11´W*
350	*United Kingdom*	*FM211613*		*"*			
351	*United Kingdom*	*FM211612*		*"*			
352	*United Kingdom*	*FM211611*		*"*			
353	*United Kingdom*	*FM211610*		*"*			
354	*United Kingdom*	*FM211609*		*"*			
355	*United Kingdom*	*FM211608*		*"*			
356	*United Kingdom*	*FM211607*		*"*			
357	*United Kingdom*	*FM211606*		*"*			
358	*United Kingdom*	*FM211605*		*"*			
359	*United Kingdom*	*FM211603*		*"*			
360	*United Kingdom*	*FM211604*		*"*			
361	*United Kingdom*	*FM211602*		*"*			
362	*United Kingdom*	*FM211601*		*"*			
363	*United Kingdom*	*FM211600*		*"*			
364	*United Kingdom*	*FM211599*		*"*			
365	*United Kingdom*	*FM211598*		*"*			
366	*United Kingdom*	*FM211597*		*"*			
367	*United Kingdom*	*FM211596*		*"*			
368	*Turkey: Denizli*	*AJ843859*		*37°77´N29°08´ E*			
369	*Turkey: Denizli*	*AJ843858*		*"*			
370	*Turkey: Denizli*	*AJ843857*		*"*			
371	*Turkey: Mu la*	*AJ843870*		*37°04´N27°38´ E*			
372	*Turkey: Manisa*	*AJ843845*		*38°61´N27°42´ E*			
373	*Turkey: Balıkesir*	*AJ843840*		*39°40´N28°13´ E*			
374	*Turkey: Balıkesir*	*AJ843844*	[10]	*39°64´N27°88´ E*	*29*	*20*	*39˚40´N28˚13´E*
375	*Turkey: Balıkesir*	*AJ843853*		*39°69´N27°95´ E*			
376	*Turkey: Balıkesir*	*AJ843841*		*40°35´N27°97´ E*			
377	*Turkey: Bursa*	*AJ843849*		*40°08´N29°51´ E*			
378	*Turkey: Sakarya*	*AJ843835*		*40°77´N30°40´ E*			
379	*Turkey: Zonguldak*	*AJ843868*		*41°17´N31°39´ E*			

Samples					Populations		
No.	**Country: City of Origin**	**GenBank Acc. No.**	**Reference**	**Coordinates**	**Classified as Pop. No.***	**Size**	**Mean Coordinates**
380	*Turkey: Stanbul*	*AJ843824*		*41°17´N29°61´ E*			
381	*Turkey: Stanbul*	*AJ843823*		*"*			
382	*Turkey: Manisa*	*AJ843839*		*38°61´N27°42´ E*			
383	*Turkey: Denizli*	*AJ843843*		*37°77´N29°08´ E*			
384	*Turkey: Denizli*	*AJ843831*		*"*			
385	*Turkey: Balıkesir*	*AJ843830*		*39°64´N27°88´ E*			
386	*Turkey: Balıkesir*	*AJ843829*		*40°35´N27°97´ E*			
387	*Turkey: Bursa*	*AJ843849*		*40°08´N29°51´ E*			

* Population numbers on Fig. 1A.

Table-2: Pairwise F_{ST} distances between 29 *M. m. domesticus* populations from the Middle East and Europe. Above diagonal: the pairwise F_{ST} values based on mtDNA D-loop sequences; and below diagonal: the statistical significance of F_{ST} values (threshold was $p \leq 0.05$)

29	28	27	26	25	24	23	22	21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	Pop.
.206	.287	.152	.149	.207	.178	.137	.364	.148	.182	.131	.428	.243	.597	.420	.261	.147	.626	.515	.433	.430	.321	.160	.181	.226	.212	.235	.221	.000	**1**
.131	.251	.210	.171	- .01	.253	.202	.240	.155	.169	.044	.312	.217	.599	.361	.243	.180	.549	.530	.375	.304	.403	.152	.166	.155	.128	-.05	.000	+	**2**
.092	.233	.204	.218	.063	.265	.158	.253	.123	.139	.097	.291	.145	.688	.374	.200	.148	.778	.600	.365	.466	.737	.228	.170	.149	.088	.000	−	+	**3**
.030	.248	.160	.114	.114	.208	.159	.087	.089	.104	.138	.297	.215	.554	.347	.218	.163	.511	.503	.342	.073	.335	.204	.168	.119	.000	−	+	+	**4**
.108	.234	.204	.195	.151	.237	.170	.215	.143	.170	.110	.362	.236	.616	.413	.251	.171	.623	.553	.403	.230	.425	.246	.151	.000	+	−	+	+	**5**
.105	.238	.162	.158	.161	.045	.166	.273	.101	.093	.155	.359	.197	.572	.368	.231	.143	.591	.472	.381	.343	.370	.187	.000	+	+	+	+	+	**6**
.199	.311	.208	.136	.109	.327	.249	.348	.226	.269	.127	.407	.267	.699	.434	.302	.198	.700	.645	.465	.473	.481	.000	+	+	+	+	+	+	**7**
.366	.429	.185	.286	.411	.509	.417	.492	.403	.446	.464	.477	.409	.817	.602	.450	.252	.939	.767	.631	.728	.000	+	+	+	+	+	+	+	**8**
.107	.353	.367	.395	.323	.481	.332	.134	.237	.284	.370	.478	.401	.754	.566	.431	.316	.806	.701	.568	.000	+	+	+	+	+	+	+	+	**9**
.363	.349	.429	.452	.348	.403	.310	.452	.318	.313	.409	.505	.087	.534	.067	.035	.313	.108	.539	.000	+	+	+	+	+	+	+	+	+	**10**
.449	.528	.546	.628	.514	.422	.330	.588	.282	.284	.595	.602	.425	.485	.614	.490	.464	.783	.000	+	+	+	+	+	+	+	+	+	+	**11**
.526	.456	.597	.704	.564	.747	.524	.629	.560	.592	.679	.634	.251	.809	.108	.186	.454	.000	+	+	+	+	+	+	+	+	+	+	+	**12**
.169	.137	.098	.105	.170	.116	.178	.287	.142	.179	.121	.358	.150	.522	.290	.179	.000	+	+	+	+	+	+	+	+	+	−	+	+	**13**
.248	.237	.232	.289	.226	.268	.178	.344	.203	.188	.241	.403	.008	.523	.011	.000	+	+	+	−	+	+	+	+	+	+	−	+	+	**14**
.372	.319	.383	.434	.346	.465	.342	.463	.364	.368	.403	.503	.077	.630	.000	−	+	+	+	−	+	+	+	+	+	+	+	+	+	**15**
.533	.598	.603	.676	.583	.539	.437	.626	.453	.467	.650	.630	.492	.000	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**16**
.217	.233	.231	.256	.184	.208	.179	.331	.146	.151	.211	.402	.000	+	+	−	+	+	+	−	+	+	+	+	+	+	+	+	+	**17**
.355	.441	.339	.352	.28	.365	.354	.411	.366	.364	.326	.000	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**18**
.145	.24	.158	.120	.051	.211	.190	.287	.137	.190	.000	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	−	+	**19**
.031	.295	.196	.215	.147	.021	.053	.191	-.05	.000	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	**20**
.031	.273	.182	.190	.119	.042	.050	.182	.000	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	**21**
.091	.359	.302	.286	.245	.312	.257	.000	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**22**
.127	.277	.190	.256	.175	.102	.000	+	−	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**23**
.127	.310	.180	.231	.218	.000	−	+	−	−	+	+	+	+	+	+	−	+	+	+	+	+	+	−	+	+	+	+	+	**24**
.110	.263	.200	.176	.000	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	−	+	**25**
.154	.263	.090	0.000	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**26**
.168	.291	.000	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**27**
.268	.000	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	**28**
.000	+	+	+	+	+	+	+	−	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	−	+	+	**29**

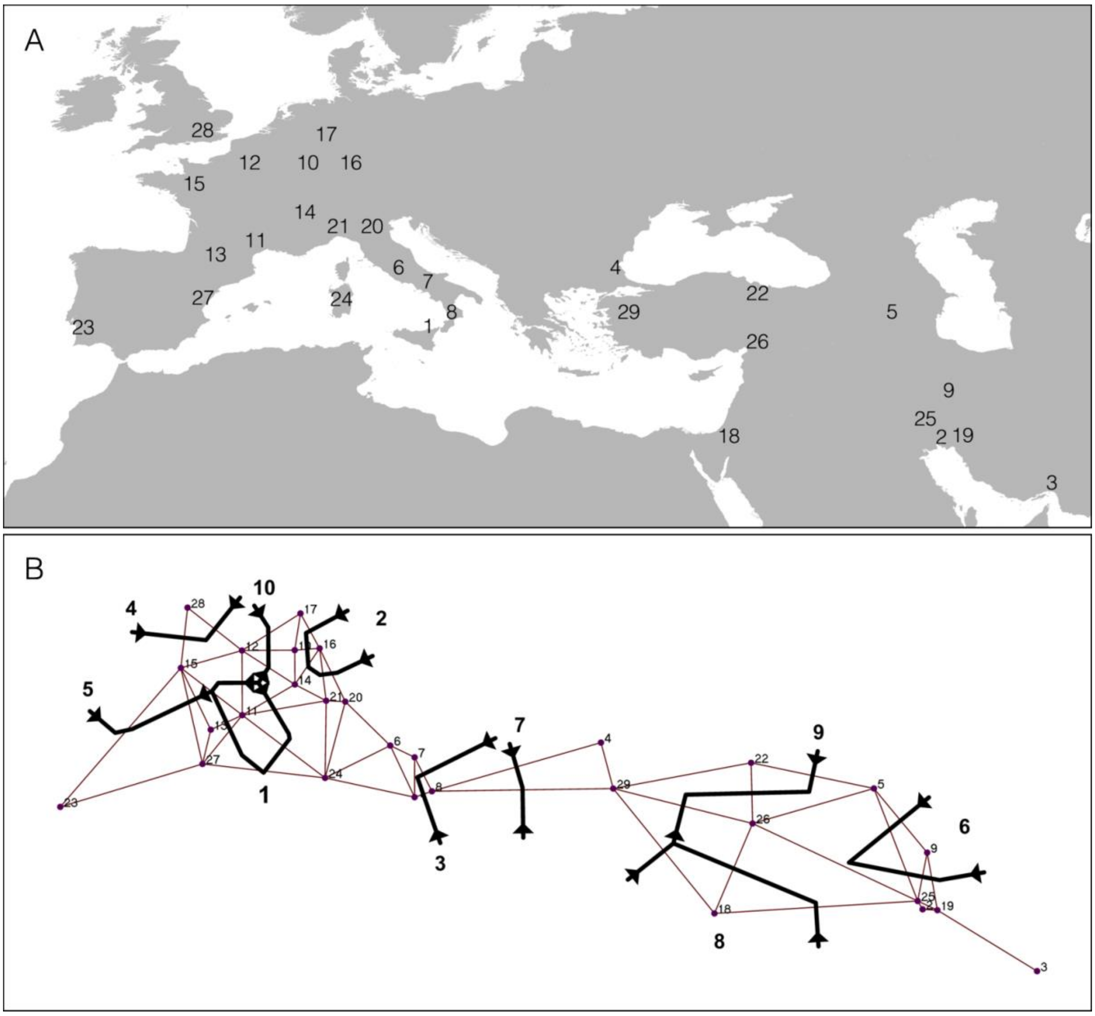

Figure-1: (A) Map of populations; and (B) genetic boundaries obtained with Monmonier's algorithm. Genetic discontinuity zones are represented by numbered thick black lines and localities are connected by a Delaunay triangulation network (thin lines).

Table-3: AMOVA among *M. m. domesticus* populations, according to the BARRIER analysis

Source of variation	d.f.	Variance components	% variation	Fixation indices	p-values
Among groups	*10*	*0.912*	*21.57*	$F_{CT} = 0.2157$	*0.0000*
Among populations within groups	*18*	*0.5595*	*13.23*	$F_{SC} = 0.1687$	*0.0000*
Within populations	*353*	*2.7563*	*65.19*	$F_{ST} = 0.348$	*0.0000*
Total	*381*	*4.2278*	*100*		

Note: Genetic partition was tested among groups across the identified barriers: [Group I: 9]; [Group II: 2, 3, 5, 19, 25, 26]; [Group III: 18]; [Group IV: 4, 22, 29]; [Group V: 8]; [Group VI: 1, 6, 7, 10, 14, 17, 20, 21, 24]; [Group VII: 16]; [Group VIII: 11]; [Group IX: 12, 15]; [Group X: 28]; [Group XI: 13, 23, 27].

As previously reported [21], owing to man-promoted colonization demographical events, western house mouse populations genetically fell into three degree s of differentiation— the lower one in south Europe, an medium degree between south Europeans and North European populations, and a higher degree between European and the Middle Eastern populations— which has proposed a two-stage process of population expansion [5-8, 21] : the first one (Neolithic stage; starting 10,000 BC) restricted to the eastern Mediterranean basin close to starting location of its commensalism with man, and the second one (Iron Age stage; starting 1,000 BC) continues westwards along the Mediterranean by sea transportation and then to north and western continent through overland routes. Regardless of geographic distance, these historical demographic events have resulted in the multiple simultaneous founding of populations indwelling the region [21-23]. Monmonier's algorithm in BARRIER analysis identified more barriers in Western Europe region (in comparison to the Middle East) which imply the high genetic heterogeneity resulted from multiple simultaneous founding of populations.

Conclusion

The Monmonier's maximum difference algorithm, a computational geometry method in BARRIER analysis, graphically represented a discontinuity pattern in the western house mouse genetic landscape, which its formation process have been attributed to man-promoted historical migrations since the Neolithic transition.

References

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