Human Y-Chromosome Short Tandem Repeats: A Tale of Acculturation and Migrations as Mechanisms for the Diffusion of Agriculture in the Balkan Peninsula

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ABSTRACT   Southeastern Europe and, particularly, the Balkan Peninsula are especially useful when studying the mechanisms responsible for generating the current distribution of Paleolithic and Neolithic genetic signals observed throughout Europe. In this study, 404 individuals from Montenegro and 179 individuals from Serbia were typed for 17 Y-STR loci and compared across 9 Y-STR loci to geographically targeted previously published collections to ascertain the phylogenetic relationships of populations within the Balkan Peninsula and beyond. We aim to provide information on whether groups in the region represent an amalgamation of Paleolithic and Neolithic genetic substrata, or whether acculturation has played a critical role in the spread of agriculture. We have found genetic markers of Middle Eastern, south Asian and European descent in the area, however, admixture analyses indicate that over 80% of the Balkan gene pool is of European descent. Altogether, our data support the view that the diffusion of agriculture into the Balkan region was mostly a cultural phenomenon although some genetic infiltration from Africa, the Levant, the Caucasus, and the Near East has occurred. Am J Phys Anthropol 142:380–390, 2010.   © 2010 Wiley-Liss, Inc.

Modern humans are believed to have colonized Europe as early as 40,000 years before present (YBP) (Boyd and Silk, 1997; Mellars, 2006; Anikovich et al., 2007). However, the Last Glacial Maximum (LGM), which ended ~10,000 YBP, forced a contraction that forever changed the landscape of the region; most of Europe was then repopulated from a number of refugia in the Iberian Peninsula, present-day Ukraine, and the northern Balkans (Otte, 1990). Along with the Paleolithic inhabitants, the recession of the ice caps allowed Neolithic pastoral agriculturalists (Zvelebil, 1986; Pinhasi et al., 2000) to traverse into Europe from present-day Anatolia, carrying not only the newly developed farming lifestyle but Middle and Near Eastern Y-chromosomal haplogroups as well (Rosser et al., 2000; Chikhi et al., 2002; Zei et al., 2003; Di Giacomo et al., 2004; Semino et al., 2004; Cruciani et al., 2006; Cadenas et al., 2008). East-to-west gradients of these Neolithic patrimonial genetic signals have been detected throughout the continent (Cavalli-Sforza and Piazza, 1993; Comas et al., 1997; Semino et al., 2000; Gusmão et al., 2003; Dupanloup et al., 2004; Currat and Excoffier, 2005), and several studies have revealed that Europeans represent an amalgamation of both Paleolithic and Neolithic influences. Together, these findings suggest that the assimilation of people, and not just culture, has occurred (Richards et al., 2000; Dupanloup et al., 2004; Roewer et al., 2005). Southeastern Europe and specifically the Balkan states are of particular interest when studying the events that led to the current genetic admixture profiles characteristic of European populations, since they are strategically located and likely served as a corridor for the passage of Neolithic agriculturalists into Europe and possibly for the movement of European migrants into the Levant/Anatolia and the Middle East.

The Balkans consist of Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Romania, and Moldova to the north; Greece to the south; and Montenegro, Albania, Macedonia, and Bulgaria, which lay in between. Archaeological studies suggest that repopulation of the Balkan Peninsula occurred early during the Mesolithic and Neolithic periods although the populace during Mesolithic times was scarce (Lahr et al., 2000; Pinhasi et al., 2000; Malyarchuk et al., 2003). During the late-Bronze age, migrants belonging to the Urnfield culture

from central Europe (Coles and Harding, 1979) colonized the entire region from the Baltic to the Adriatic Sea (Pigott, 1965) while around 3,000 YBP, the Illyrians (Wilkes, 1992) and Thracians (Best and DeVries, 1989), both proto-Indo European tribes, are believed to have attained dominion of the West and Southeast of the peninsula, respectively. Slavic tribes from central and southern Europe are thought to have traversed into the area around the Middle Ages (Alekseeva, 1973; Rebala et al. 2007), assimilating both the Illyrian and Thracian peoples and gradually transforming into modern-day Balkan groups (Malyarchuk et al., 2003).

Mitochondrial DNA (mtDNA) studies suggest that the majority of haplogroups present in the Balkans are commonly found in Western Eurasia (Calafell et al., 1996; Richards et al., 1996; Tolk et al., 2000; Malyarchuk et al., 2003), but there also exist minor contributions from Asia and Africa (Tolk et al., 2000; Malyarchuk et al., 2003); however, these signals are present in other southeastern European populations which lay beyond the confines of the Balkan peninsula (Malyarchuk et al., 2006, 2008). Moreover, Malyarchuk et al. (2003) have noted that the differentiation between the two Balkan populations of Bosnia and Slovenia indicates two separate waves of migration from the Slavic domain into the Balkans during the Middle Ages.

Y-chromosomal studies indicate that the Balkans played a pivotal role in the repopulation of Europe following the LGM. Rootsi et al. (2004) and Pericic et al. (2005) have reported that the current distribution of haplogroup I2a1 throughout Europe follows I2a1's diffusion out of the Balkans and into southeastern and eastern Europe. The authors also report that the region may have served as a corridor for the propagation of haplogroup E1b1b1a, which accounts for 98% of haplogroup E chromosomes in Europe (Cruciani et al., 2004; Semino et al., 2004). Frequency gradients of markers within haplogroup J also suggest that the region has served as a migratory bridge between the Levant and Europe (Semino et al., 2004), and yet other data sets indicate that acculturation has played a major role in the current genetic patterns observed throughout the peninsula (Battaglia et al., 2008).

Given the important geographical and historical position of the Balkan states, the current project aims to elucidate the genetic relationships between the region and the surrounding European and Near Eastern populations to better understand the mechanisms that have shaped the current genetic composition of the peninsula. Four hundred and four unrelated male individuals from Montenegro and 179 from Serbia were typed across 17 Y-STR loci and compared across 9 Y-STR loci (DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, and DYS385a/b) to geographically targeted collections from Europe, the Middle East, Anatolia, and the Caucasus. For the first time, we report on the phylogenetic relationships among Balkan populations as well as between neighboring regions (i.e., Europe and the Middle East) based on allelic frequencies of individual Y-STR loci.

MATERIALS AND METHODS
Sample collection and DNA purification

Samples were collected from total of 404 unrelated Montenegrin and 179 Serbian males with informed consent and typed for 17 Y-STR loci. Genealogical information was recorded dating back to a minimum of two generations to establish regional ancestry and a lack of familial ties among the individuals sampled. One hundred and forty-one blood samples on FTA cards were processed according to the manufacturer's specifications (Whatman, Middlesex, UK) and an additional 263 buccal swabs were extracted using the conventional phenol–chloroform method (Novick et al., 1995; Antunez de Mayolo et al., 2002) for Montenegro. The 179 buccal swabs from Serbian individuals were phenol-chloroform extracted. Sample collection and processing were conducted abiding to the guidelines stipulated by the ethical review boards at all the research institutions involved in the project.

Previously published data

A total of 19 geographically targeted reference populations were included for comparison across 9 Y-STR loci (DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, and DYS385a/b), since the rest of the loci typed in this study were not reported for several of the reference collections. The geographical locations, population designations, number of individuals, and references are included in Table 1 and Figure 1.

DNA amplification and STR genotyping

PCR amplification of the 17 Y-STR loci (DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, DYS385a/b, DYS437, DYS438, DYS439, DYS448, DYS456, DYS458, DYS635, and GATA H4) was conducted using the AmpFl/STR Yfiler PCR Amplifcation Kit (Applied Biosystems, Foster City, CA) following the manufacturer's recommendations (Applied Biosystems, 2005). Products were sized on an ABI Prism 310 Genetic Analyzer (Mansfield et al., 1998) using the GeneScan v. 3.7 software (Applied Biosystems). Alleles were named according to nomenclature guidelines established by the International Society for Forensic Genetics (Gusmão et al., 2006) using the Yfiler kit's allelic ladder.

Data analyses

The direct gene-counting method was used to estimate Y-STR allelic frequencies (Li, 1976). Basic diversity statistics were computed using the software package Arlequin v. 3.11 (Schneider et al., 2005), whereas observed gene and haplotype diversities were calculated according to Nei (1987).

A correspondence analysis (CA) and a Neighbor-Joining (NJ) phylogram, both based on Y-STR allelic frequency distributions for loci DYS19, DYS389I, DYS389II, DYS390, DYS391, DYS392, DYS393, and DYS385a/b, were generated with the aid of the NTSYSpc 2.02i (Rohlf, 2002) and PHYLIP 3.52c (Felsenstein, 2002) programs, respectively. The bootstrap values for the NJ tree were calculated performing 1,000 replications and using Nei's genetic distance (Saiton and Nei, 1987).

Admixture estimates based on Y-STR allelic frequency distributions were performed using the SPSS 14.0 statistical software package (Long et al., 1991; Perez-Miranda et al., 2006). The first set of analyses consisted of populations grouped based on geographical and phylogenetic relationships (Table 1) as parents while using the Balkan states as hybrids or offspring. The selection of populations to include in each group was based on the co-segregation of collections in the CA and NJ

TABLE 1. Populations analyzed using Y-STR data

| Population	Abbreviation	N	References
Balkans			
Albanians (Kosovo)	ALBK	117	Pericić et al., 2004
Bosnia and Herzegovina	BOH	181	Klarić et al., 2005
Croatia	CRO	166	Ljubković et al., 2008
Greece	GRE	39	Bosch et al., 2006
Macedonia	MAC	150	Spiroski et al., 2005
Montenegro	MON	400	Present
Serbia	SER	179	Present
Serbia (Vojvodina)	SERV	185	Veselinović et al., 2008
Slovenia	SLO	121	Sterlinko et al., 2001
West Croatia	WCR	101	Lovrecic et al., 2005
Europe			
Germany (Hamburg)	HAM	49	Rodig et al., 2007
Italy	ITA	155	Turrina et al., 2006
Lithuania	LIT	127	Pepinski et al., 2004
Russia (Lipezkaja)	LIP	47	Roewer et al., 2008
Russia (Penzenskaya)	PEN	81	Roewer et al., 2008
Romania (Poiesti)	ROM	37	Bosch et al., 2006
Caucasus			
Armenia	ARM	100	Nasidze et al., 2003
Azerbaijan	AZE	72	Nasidze et al., 2003
Georgia	GEO	77	Nasidze et al., 2003
Middle East/Anatolia			
Iran	IRA	80	Nasidze et al., 2003
Turkey	TUR	39	Nasidze et al., 2003
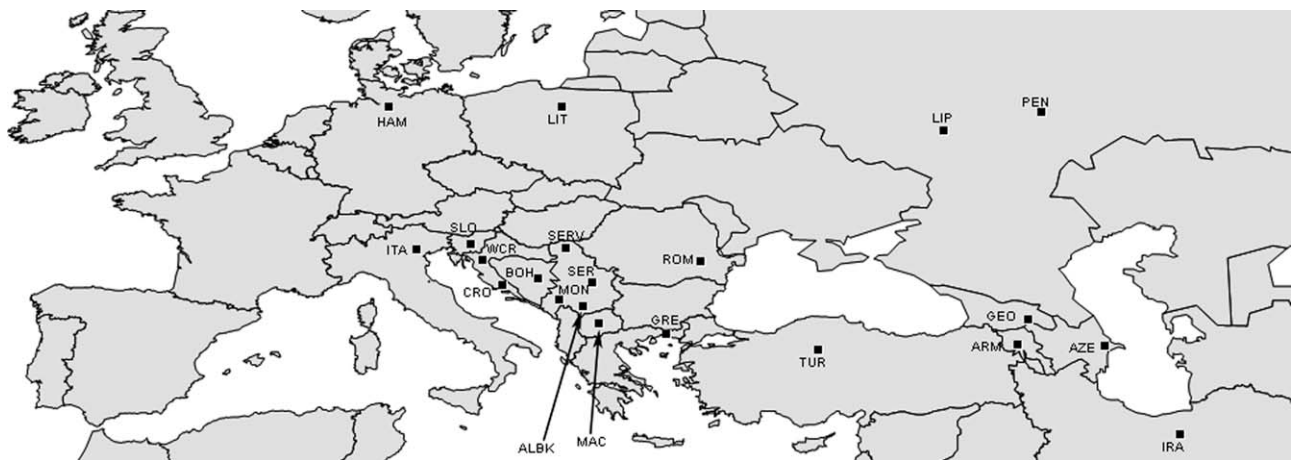
Fig. 1.   Populations analyzed using Y-STR allelic frequency data. Population denominations are provided in Table 1.

dendrograms, defining biogeographical regions with genetic affinities. A second set of analyses consisted of using individual Balkan collections as parental populations to each Balkan data set in order to ascertain gene-flow throughout the region.

Y-chromosomal haplogroup predictions were generated using Whit Athey's haplogroup predictor (Athey, 2006) on the web (http://www.hprg.com/hapest5/). A network projection was produced with the aid of the program NETWORK 4.2.00 (Rohl, 1997); bifurcations were assigned based on predicted haplogroup distributions (Supporting Information Fig. 1). Gradient maps based on the frequencies of haplogroups I2a, R1b, R1a, and E1b1b were generated with the aid of the Surfer 9 package from Golden Software (www.goldensoftware.com). Precise latitudes and longitudes for all populations included in these projections can be found in Supporting Information Table 1.

RESULTS
Y-STR intrapopulation diversity

A total of 318 and 171 different haplotypes were detected in the Montenegro and Serbian populations, respectively; haplotypes, and their frequencies are presented in Supporting Information Tables 2 and 3 for Montenegro and Serbia respectively. Y-STR allelic frequencies for Montenegro can be found in Table 2 on a locus-by-locus basis, whereas Table 3 presents similar data for Serbia. The most common haplotype observed is found at a frequency of 2.72% for Montenegro. In the Serbian collection, the most notable haplotype is observed at a frequency of 1.12%. A total of 270 unique haplotypes are represented in Montenegro, whereas 163 are found in Serbia.

The most abundant Y-chromosomal haplogroup based on Athey's haplogroup predictor for the Montenegro

TABLE 2. Allelic frequencies for 17 Y-STR loci in Montenegro (n = 404)

Allele	DYS19	DYS385a	DYS385b	DYS389I	DYS389II	DYS390	DYS391	DYS392	DYS393	DYS437	DYS438	DYS439	DYS448	DYS456	DYS458	DYS635	Y GATA H4
7																	
9							0.0050				0.0025	0.0099					0.0025
10		0.0099					0.5520				0.0767	0.0371					0.0371
11		0.1683	0.0668				0.4307	0.8292	0.0074		0.7153	0.3045					0.4530
12		0.0173		0.1523			0.0099	0.0297	0.1361		0.1114	0.4035		0.0025	0.0050		0.4653
12.2											0.0941				0.0074		
13	0.2896	0.1139	0.0223	0.6485	0.0025		0.0025	0.0941	0.7970	0.0025		0.2252		0.0371	0.0025		0.0336
14	0.2277	0.3366	0.1312	0.1906				0.0124	0.0520	0.4554		0.0173		0.1089	0.0099		0.0025
15	0.1733	0.0842	0.2970	0.0074	0.0198			0.0297	0.0074	0.4208		0.0025		0.5050	0.2401		
16	0.2599	0.2327	0.1188		0.3366			0.0050		0.1015				0.1832	0.2450		
16.2			0.0050														
17	0.0495	0.0371	0.1411		0.2995					0.0198			0.0025	0.1460	0.3045		
17.2			0.0025												0.0025		
18			0.1782										0.0594	0.0143	0.1337		
19			0.0272		0.3094								0.3639		0.0322		
20			0.0099		0.0322								0.4802	0.0025	0.0099	0.0025	
21						0.0074							0.0842		0.0050	0.0347	
22						0.0891							0.0099		0.0025	0.1733	
23						0.1337										0.2748	
24						0.6485										0.4629	
24.3						0.0124											
25						0.0990										0.0520	
26						0.0099											

TABLE 3. Allelic frequencies for 17 Y-STR loci in Serbia (n = 179)

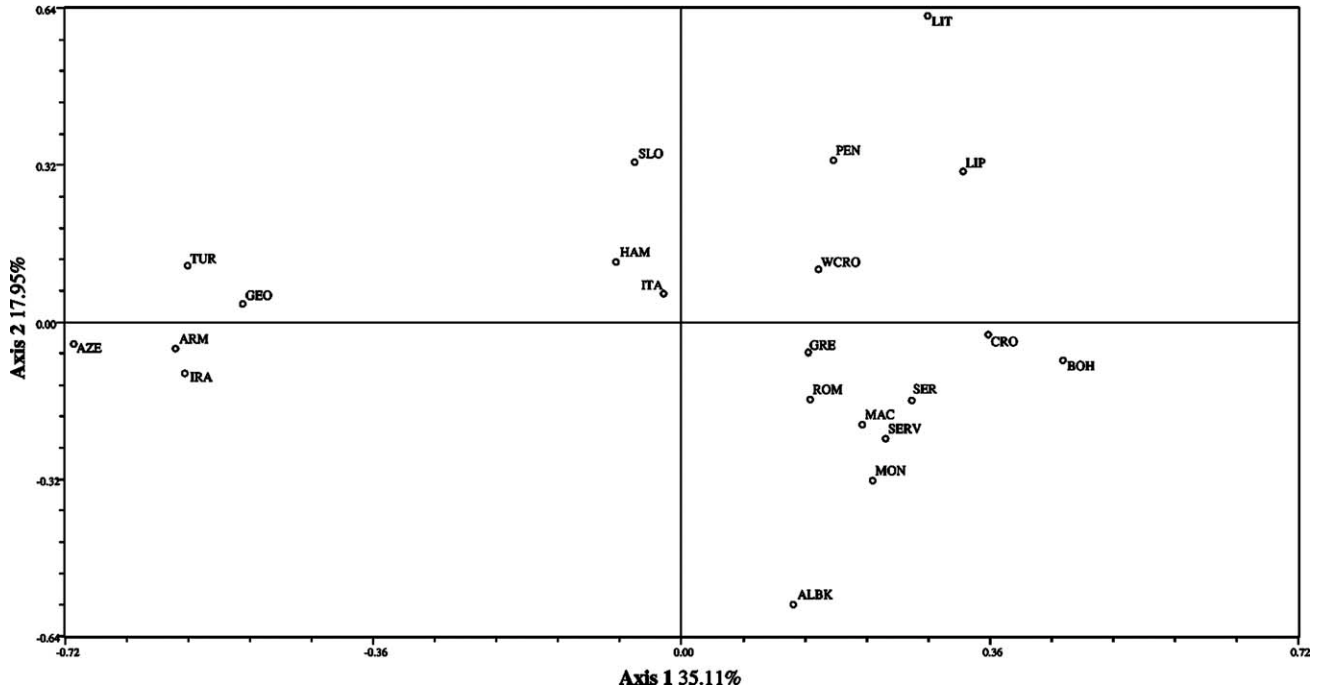| Allele	DYS19	DYS385a	DYS385b	DYS389I	DYS389II	DYS390	DYS391	DYS392	DYS393	DYS437	DYS438	DYS439	DYS448	DYS456	DYS458	DYS635	Y GATA H4
9							0.0112				0.0670	0.0056					0.0056
10		0.0112	0.0056				0.5642				0.7151	0.1006					0.0335
11		0.1173	0.0168				0.4022	0.8492			0.1676	0.2346					0.5307
12		0.0335		0.1453			0.0223	0.0391	0.0782		0.0503	0.3910					0.3575
13	0.1742	0.1285	0.0391	0.7263				0.0559	0.8492	0.0056		0.2570		0.0053	0.0168		0.0670
14	0.1854	0.3651	0.2235	0.1285	0.0112			0.0335	0.0559	0.4525		0.0056		0.1453	0.0168		0.0056
15	0.2247	0.1788	0.3520		0.0335			0.0168	0.0168	0.4413		0.0056		0.5475	0.2235		
16	0.3258	0.1453	0.1061		0.2849			0.0056		0.0894				0.1391	0.1899		
17	0.0899	0.0168	0.0670		0.3408					0.0112				0.1453	0.3855		
17.2															0.0056		
18		0.0056	0.1453		0.2905								0.0223	0.0224	0.1453		
19			0.0447		0.0335								0.3911		0.0168		
20					0.0056								0.5084			0.0447	
21						0.1006							0.0615			0.2123	
22						0.1341							0.0168			0.2235	
23						0.5530										0.4413	
24						0.0279										0.0615	
24.3																	
25						0.1676										0.0168	
26						0.0168											

Fig. 2. Correspondence analysis based on allelic frequencies of individual Y-STR loci. Population denominations are provided in Table 1.

group was found to be I2a (P37.2) at a frequency of 29.2%. Other abundant haplogroups detected at considerable frequencies are E1b1b-M215 (27.0%), R1b-M343 (9.2%), and R1a-L62,L63 (7.4%). For the Serbian population, I2a (P37.2) is also present at very high frequencies (38.5%), and haplogroups E1b1b-M215 (17.3%), R1b-M343 (4.5%), and R1a-L62,L63 (14.5%) are also observed at considerable levels. The Bayesian probabilities for the vast majority of the predicted haplogroups yielded confidence estimates of 100.00%. These values are reported in Supporting Information Tables 2 and 3 along with the predicted haplogroup for each Y-STR profile encountered.

### Y-STR interpopulation diversity

Phylogenetic relationships among the populations studied were assessed using CA, NJ analysis and admixture profiles. A general collection from Serbia (Lauc et al., 2005) and another from Albania (Bosch et al., 2006) were also included in the analyses, however, because they both overlapped with the other Serbian and Albanian populations currently in the phylogenetic projections, they were removed to reduce redundancies (Data not shown). Overall, geographical relationships are mirrored in both the CA and NJ projections with all the Balkan states partitioning loosely in the lower right portion of the plot within the CA (see Fig. 2) and sharing a clade in the tree (see Fig. 3). West Croatia is found in the upper right quadrant instead of with the other Balkan states, and a similar pattern is observed in the NJ phylogram, however, close genetic ties are still discernable based on Axis 1 correlations among the groups. Slovenia is the only Balkan population that departs considerably from this grouping and is found instead in the upper left-quadrant by itself. The European populations (not found within the Balkan Peninsula) map mostly to the

upper right quadrant of the graph (with the exemption of Hamburg and Italy found in the center of the chart instead), and intermediate between the Balkan branches and a Middle Eastern/Caucasian branch in the NJ projection. The Middle Eastern and Caucasian populations cluster to the left of the chart, midway along the *y*-axis. It should be noted that relationship between the Balkan populations and the group of other Europeans are stronger than the relationship between the Balkan collections and the Middle Eastern/Caucasus groups. In addition, Axis I (over which the Balkan and other European collections are related) exhibits 35.11% of the total variance, while Axis II only possesses 17.91%. The total variance displayed by these two dimensions of the CA is of 53.02%.

When admixture analyses are performed using the non-Balkan Europeans, the Caucasus, and the Middle East/Anatolia as parents, the European group is the major contributor to every Balkan population analyzed (Table 4). European influences range from 100% in Croatia, and Bosnia and Herzegovina to as low as 69% in the Albanians. Middle Eastern influences are null in most Balkan collections with the exemptions of Montenegro (3.8%) and Albania (31.0%). Influences from Caucasia range from 0.0% in Albania, Croatia and Bosnia and Herzegovina to 14.7% in Slovenia. Geneflow, throughout the Balkans, appears mostly guided by geographical relationships as populations found proximal to each other are the main contributors to each other. For example, neighbors Bosnia and Herzegovina, and Croatia contribute 83.0% and 97.7% to each other, respectively (for a detailed report, see Table 5).

Contour maps

Haplogroups I2a and E1b1b (Fig 4a,d) both exhibit high densities within the Balkan states. These haplogroups are also observed at high levels throughout
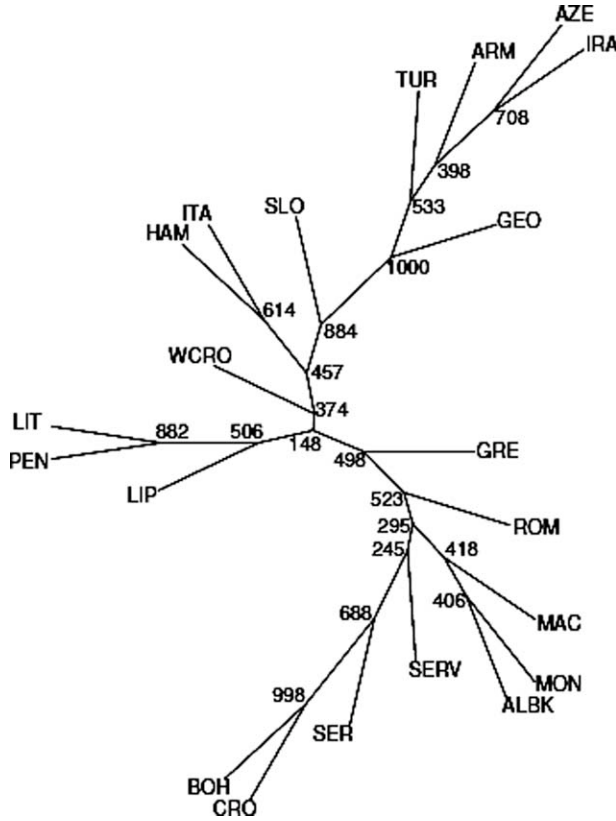
Fig. 3. Neighbor Joining phylogram based on allelic frequencies of individual Y-STR loci. Population denominations are provided in Table 1.

Eastern Europe but are found at considerably lower concentrations in western European regions. Haplogroup R1b (Fig. 4b), on the other hand, is found at high densities throughout Western Europe but dwindles steadily toward the east. R1a (Fig. 4c) reaches its frequency peak in western Russia (from the populations included in this report) and attains high levels in central Europe as well.

DISCUSSION

The Montenegro population is highly diverse with an observed haplotype diversity of 99.78% ± 0.03%; similarly, high-variance was detected in the Serbian collection (95.5% ± 0.04%). These high-diversity values are also present throughout the rest of the Balkan Peninsula with values ranging from 74.3% ± 7.2% in the Andon Poci, an ethnic group within Albania, to 99.8% ± 0.4% in Macedonians (Bosch et al., 2006). Nevertheless, despite the widespread high variance, the region is highly homogenous with little stratification on a population-by-population basis (Bosch et al., 2006), both at the Y-chromosome and mtDNA levels. Phylogenetic analyses in this study suggest a tight-knit genetic relationship between the Balkan states that follows a primarily geographical cline (see Fig. 3), a finding also reflected in the admixture analyses between the Balkan groups (Table 5). The northernmost populations from Croatia, and Bosnia and Herzegovina are the main contributors to each other, whereas Montenegro and Serbia exhibit similarities in their admixture profiles, expected given their

TABLE 4. *Admixture analysis of the Balkan states using regional groups of populations as parentals*

Parental populations	Hybrid populations									
	Montenegro	Serbia	Serbia (V)	Greece	Albanians (Kosovo)	Macedonia	West Croatia	Croatia	Bosnia and Herzegovina	Slovenia
Caucasus	0.116 ± 0.279	0.044 ± 0.261	0.118 ± 0.243	0.128 ± 0.202	0.000 ± 0.349	0.122 ± 0.246	0.017 ± 0.124	0.000 ± 0.339	0.000 ± 0.382	0.147 ± 0.068
Europe	0.846 ± 0.084	0.956 ± 0.079	0.882 ± 0.073	0.872 ± 0.061	0.690 ± 0.105	0.878 ± 0.074	0.983 ± 0.037	1.000 ± 0.103	1.000 ± 0.115	0.853 ± 0.064
Middle East/Anatolian	0.038 ± 0.277	0.000 ± 0.258	0.000 ± 0.241	0.000 ± 0.200	0.310 ± 0.346	0.000 ± 0.244	0.000 ± 0.123	0.000 ± 0.336	0.000 ± 0.382	0.000 ± 0.000

TABLE 5. Geneflow between the Balkan states

| Parental populations	Hybrid populations									
	Montenegro	Serbia	Serbia (V)	Greece	Albanians (Kosovo)	Macedonia	West Croatia	Croatia	Bosnia and Herzegovina	Slovenia
Montenegro		0.289 ± 0.103	0.226 ± 0.176	0.000 ± 0.214	0.577 ± 0.363	0.168 ± 0.105	0.000 ± 0.170	0.000 ± 0.154	0.000 ± 0.186	0.000 ± 0.449
Serbia	0.416 ± 0.145		0.528 ± 0.209	0.000 ± 0.249	0.000 ± 0.489	0.354 ± 0.124	0.263 ± 0.185	0.029 ± 0.192	0.000 ± 0.231	0.000 ± 0.529
Serbia (V)	0.133 ± 0.092	0.201 ± 0.078		0.000 ± 0.145	0.000 ± 0.290	0.038 ± 0.072	0.000 ± 0.129	0.000 ± 0.104	0.000 ± 0.126	0.000 ± 0.324
Greece	0.000 ± 0.085	0.000 ± 0.070	0.052 ± 0.110		0.000 ± 0.265	0.237 ± 0.058	0.458 ± 0.096	0.030 ± 0.095	0.000 ± 0.116	0.000 ± 0.290
Albanians (Kosovo)	0.229 ± 0.048	0.000 ± 0.046	0.028 ± 0.073	0.000 ± 0.087		0.155 ± 0.040	0.000 ± 0.076	0.000 ± 0.061	0.023 ± 0.076	0.000 ± 0.183
Macedonia	0.130 ± 0.152	0.157 ± 0.127	0.091 ± 0.198	0.518 ± 0.212	0.423 ± 0.435		0.000 ± 0.214	0.000 ± 0.172	0.000 ± 0.207	0.000 ± 0.547
West Croatia	0.000 ± 0.096	0.163 ± 0.074	0.000 ± 0.139	0.469 ± 0.137	0.000 ± 0.327	0.000 ± 0.084		0.023 ± 0.121	0.000 ± 0.144	1.000 ± 0.258
Croatia	0.055 ± 0.116	0.050 ± 0.103	0.000 ± 0.149	0.013 ± 0.180	0.000 ± 0.349	0.000 ± 0.090	0.000 ± 0.162		0.977 ± 0.075	0.000 ± 1.542
Bosnia and Herzegovina	0.035 ± 0.103	0.140 ± 0.091	0.000 ± 0.133	0.000 ± 0.162	0.000 ± 0.321	0.048 ± 0.080	0.000 ± 0.141	0.830 ± 0.055		0.000 ± 0.172
Slovenia	0.002 ± 0.040	0.000 ± 0.033	0.075 ± 0.054	0.000 ± 0.063	0.000 ± 0.129	0.000 ± 0.033	0.279 ± 0.041	0.088 ± 0.047	0.000 ± 0.058	

close geographical quarters and historical ties. A close relationship, also seemingly based on geographical ties, is observed between Greece and Macedonia, although the two populations are also extensively linked historically (Shea, 1997).

The most common minimal haplotype for 7 Y-STR loci (DYS19-DYS389I-DYS389II-DYS390-DYS391-DYS392-DYS393) in Europe according to Gusmão et al. (2003) is 14-13-29-24-11-13-13 at an average frequency of 4.5% across 197 European collections (Willuweit and Roewer, 2007). In the Montenegro population, this haplotype is found at a frequency of 5.45%, and the same is present at 2.23% in Serbia. The profile is found at similar frequencies throughout the Peninsula [Macedonia (3.9%), Greece (2.6%), Albania (2.9%) and Serbia (2.6%)]; however, there is no clear pattern in the distribution of this Y-STR profile throughout the Balkans.

The Y-chromosomal haplogroups most frequently encountered in the Montenegro and Serbia populations are I2a, R1b, R1a, and E1b1b, altogether encompassing 73.8% and 74.8% of all Y-chromosomes in the two countries, respectively. Haplogroup I2a, found at 29.2% in Montenegro and at 38.5% in Serbia, is believed to be autochthonous to Europe, specifically to the Balkan region (Semino et al., 2000; Barac et al., 2003; Rootsi et al., 2004; Pericić et al., 2005), where it may have arisen during the LGM. Frequencies of the haplogroup in neighboring populations range from 8.4% in Greece to 63.8% in Herzegovina within the Balkans (Pericić et al., 2005) and dwindle outside the peninsula where, as close as in Italy, it is only found at frequencies ranging from 0.7% to 1.3% in different provinces (Rootsi et al., 2004). The haplogroup is also found at frequencies as high as 15.0% in Belarus and 16.7% in Adygea (Russia), and a gradient (Fig. 4a) is observed in its levels throughout the region (Balanovski et al., 2008; Mirabal et al., 2009). These frequency gradients suggest that haplogroup carriers took a northeastern route through the Balkan territories into northwestern Russia rather than toward western Europe supporting previous claims by Pericić et al. (2005).

The frequency of haplogroup R1b in Montenegro is similar (9.4%) to those found in the rest of southeastern Europe (around 9%), whereas in Serbia, it is present at 4.5% (Pericić et al., 2005). The haplogroup is widespread throughout western Europe at levels as high as 88.1% in the Basque from Spain and France (Semino et al., 2000). Its presence in the Balkans is thought to mark a post-LGM migration from the refugium in Iberia, a claim supported by a decline in marker levels in a west to east fashion (Fig. 4b), although the haplogroup is thought to have originated in West Asia and traversed into Europe before the glaciations (Semino et al., 2000; Unherhill et al., 2001; Wells et al., 2001). A more polemic marker, R1a, is found at frequencies of 7.4% in Montenegro and at 14.5% in Serbia. The haplogroup has been found to possess similarly high levels of accumulated Y-STR variance in both European and Asian populations (Mirabal et al., 2009), making it difficult to elucidate its migratory patterns (Semino et al., 2000; Wells et al., 2001; Sengupta et al., 2006), although most investigators now agree that the haplogroup arose in the Central Asian steppes and marks the migration of the Kurgan horse culture (Wells et al., 2001; Sengupta et al., 2006) thought to have divulged the Indo-European languages (Semino et al., 2000; Wells et al., 2001; Sengupta et al.,
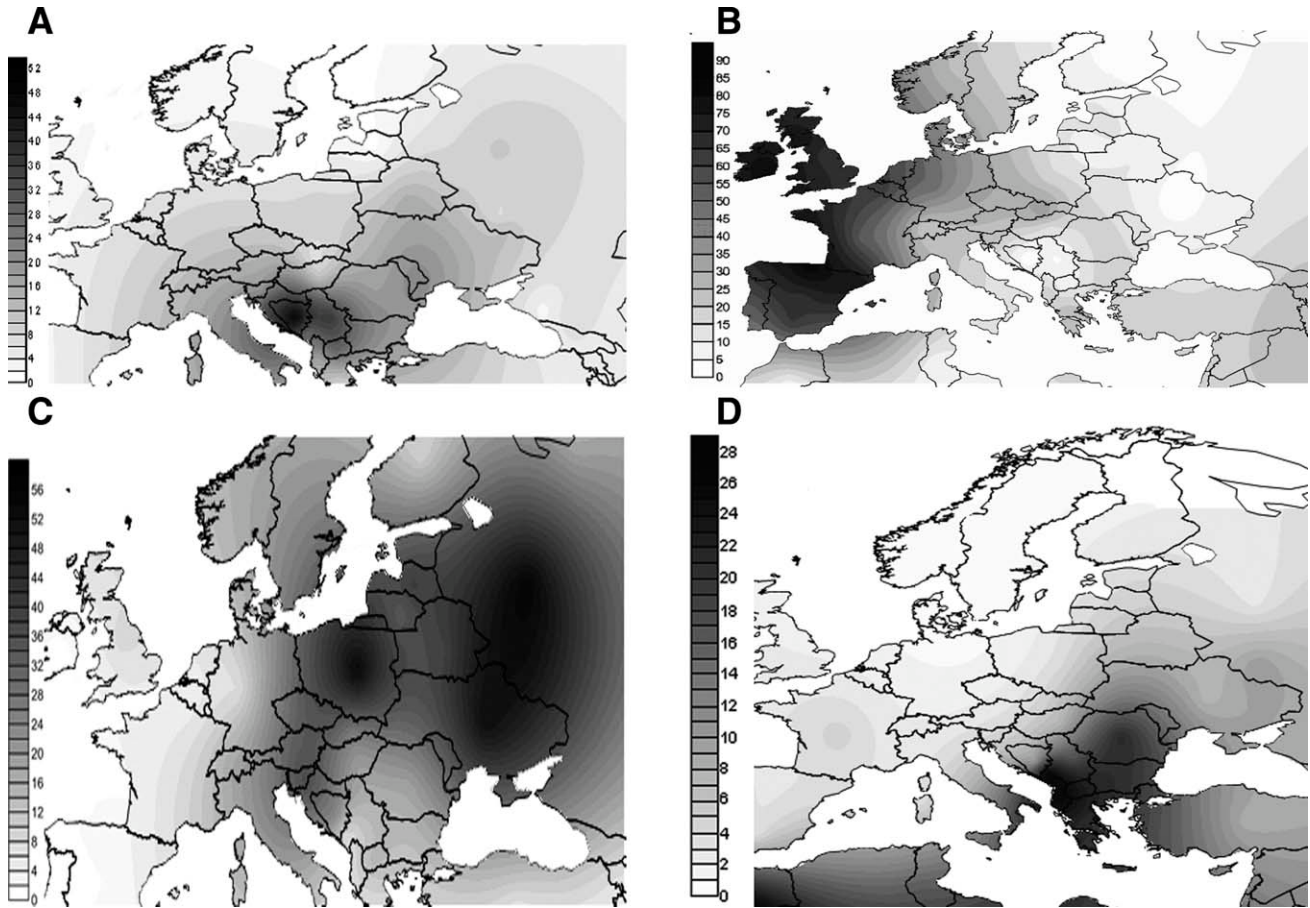
Fig. 4. Geographical representations of frequency gradients for haplogroups I2a (**A**), R1b (**B**), R1a (**C**) and E1b1b (**D**). Contour maps were generated from data reported in Supporting Information Table 1 by using the program Surfer v.9.0.343 (http://www. goldensoftware.com).

2006). In the Balkan states, the haplogroup likely represents the Slavic substrata of the region brought into the area from central Europe during the Middle Ages (Rebala et al., 2007). It is readily apparent from the contour maps generated in this study that two separate foci exist for this haplogroup within Europe, in Western Russia and Central Europe; both areas are likely key expansion points for the marker throughout the region (Fig. 4c).

The presence of haplogroup E1b1b in the peninsula at frequencies ranging from 5.6% in Croatia to 45.6% in Albania (Pericić et al., 2005) has been interpreted as signals of the genetic admixture experienced by European populations with Neolithic farmers (Semino et al., 2004). This North African marker is present in the Balkan region at considerably higher levels (i.e., 45.6% in Albania) than in Tunisian or Moroccan individuals (15.5% and 27.9%, respectively), and comparisons in the frequencies of the haplogroup throughout these areas are suggestive of alternative theories as to the haplogroup's origin (possibly a Balkan ancestry). Nevertheless, deeper analyses indicate a marked bifurcation between individuals from these localities as samples from the Balkan states belong to the subclade E1b1a2-V13, a mutation considerably more recent in age (13.7 ± 2.3 kya for E1b1b vs. 8.7 ± 2.6 kya for E1b1a2) than that denoted by E1b1b-M35 (Cruciani et al., 2007) in North Africa. The frequency of E1b1b in Montenegro is intermediate within the range in the Balkans at 27.0%,

whereas, in Serbia, it is observed at 17.3%. The gradients of the haplogroup throughout Europe (Fig. 4d) exhibit similar clinal patterns to the ones observed for I2a (Fig. 4a) and also suggest that migrants may have taken a northeastern route into Russia rather than traversing toward western Europe (Pericić et al., 2005). These patterns have also been interpreted as remnants of the Bronze Age expansion throughout southeastern Europe (Cruciani et al., 2007).

Middle Eastern indicators such as J1 (0.5% in Montenegro, 0.6% in Serbia), J2a (4.7% in Montenegro, 3.3% in Serbia), J2b (4.5% in Montenegro, 1.7% in Serbia) and G2a (2.5% in Montenegro, 2.2% in Serbia) (Semino et al., 2004; Cadenas et al., 2008) as well as markers generally considered specific to the Indian subcontinent such as haplogroups L (1.2% in Montenegro, 0.6% in Serbia) and H (1.5% in Montenegro, 2.2% in Serbia) (Cordeaux et al., 2004; Sengupta et al., 2006; Thamseem et al., 2006), and haplogroups N (1.5% in Montenegro, 3.3% in Serbia) and Q (2.0% in Montenegro, 1.7% in Serbia) of Central Asian/Siberian ancestry (Wells et al., 2001; Zegura et al., 2004; Rootsi et al., 2007) were also detected in the Montenegro population but at frequencies lower than 5% and as such may represent minor migratory events. The presence of haplogroups L and H may in turn be a remnant of the Romani populations in the area (of south Asian descent), signals which have also been detected in mtDNA (Malyarchuk et al., 2008).

Phylogenetic relationships between the Balkan states and the rest of Europe, along with admixture profiles, indicate a mostly European genetic component for the Balkan populations. In both the CA (see Fig. 2) and NJ (see Fig. 3) projections, the European populations map closer to the Balkan groups than do the Middle Eastern or Caucasian populations. European groups contribute over 80% of each Balkan population's Y-chromosomal component with the exemption of Albanians, which exhibit a 31.0% Middle Eastern/Anatolian contribution. The Middle Eastern/Anatolian and Caucasus groups make considerably lower, and at times null, contributions to the Balkan populations (Table 4) with no clear trend as to which factors (genetic, cultural, or ethnolinguistic) are affecting the observed admixture patterns. Nevertheless, the overwhelming presence of haplogroups autochthonous to Europe within the Montenegro and Serbian populations and the other Balkan states used for comparison in this study along with the lack of a cline from the southern Balkans toward Central Europe of Middle Eastern/Anatolian contributions suggest that although some admixture between the Paleolithic inhabitants of the European terrain and Neolithic migrants has occurred, the dissemination of agriculture occurred predominantly due to acculturation (Battaglia et al., 2009) rather than via genetic amalgamation as previously suggested (Richards et al., 2000; Dupanloup et al., 2004; Roewer et al., 2005).

Contributions from the Caucasus can be observed in all the southern and central Balkan populations at similar levels (ranging from 4.4% in Serbia to 12.8% in Greece) with the exemption of the Albanian minority within Kosovo (Table 4). Of the northernmost Balkan populations included in this study, the only populations that display any influences from the Caucasus are West Croatia (1.7%) and Slovenia (14.7%). It is possible that these signals from Caucasia are reflections of common genetic patrimonies (i.e., both Balkan and Caucasus populations being affected by the same/similar source populations), given the lack of genetic influences from the Middle Eastern/Anatolian groups, which are more geographically proximal to the Balkan peninsula than the groups from the Caucasus. Alternatively, the similarities may have arisen from backflow from the Balkans into the Caucasus.

ACKNOWLEDGMENTS

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