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Informativeness of the CODIS STR Loci for Admixture Analysis*

ABSTRACT: Population admixture (or ancestry) is used as an approach to gene discovery in complex diseases, particularly when the disease prevalence varies widely across geographic populations. Admixture analysis could be useful for forensics because an indication of a perpetrator's ancestry would narrow the pool of suspects for a particular crime. The purpose of this study was to use Fisher's information to identify informative sets of markers for admixture analysis. Using published founding population allele frequencies we test three marker sets for efficacy for estimating admixture: the FBI CODIS Core STR loci, the HGDP-CEPH Human Genome Diversity Cell Line Panel and the set of 39 ancestry informative SNPS from the Shriver lab at Pennsylvania State University. We conclude that the FBI CODIS Core STR set is valid for admixture analysis, but not the most precise. We recommend using a combination of the most informative markers from the HGDP-CEPH and Shriver loci sets.

KEYWORDS: forensic science, CODIS STR loci, admixture analysis, population admixture, ancestry

The estimation of ancestral contributions to admixed populations has helped geneticists answer questions about human origins and intercontinental migrations (1–6). Admixture analysis is now also being used as an approach to gene discovery for complex diseases where the diseases show wide prevalence variation across ethnic boundaries. An indication of a perpetrator's ancestry could also be useful in a forensic setting because it would narrow the pool of suspects for a particular crime. There are several established methods to infer ancestry at the individual and/or population levels (4,7,8), but criteria for determining how many and what types of markers are necessary for the success of these analyses has only been addressed recently (9,10). Not all markers are equally informative for admixture analysis, and in order to determine a perpetrator's ethnicity, not only the most informative markers would be needed, but also a small enough set of markers so that this type of analysis would be effective with limited DNA samples.

The purpose of this study is to assess different readily available sets of genetic markers for estimating admixture in individuals. We use Fisher's expected information (11) to assess the utility of different marker sets. Fisher's expected information is closely related to maximum likelihood method statistical estimation (11,12), which has been applied to estimating admixture proportions (13). We focus first on testing the FBI CODIS Core STR set for informativeness for admixture analysis (available at http://www.cstl.nist.gov/div831/strbase/fbicore.htm). By testing these loci, we are exploring a resource that is already available to most forensic laboratories. We also tested two other publicly available sets of loci, the 39 ancestry informative SNPs (Single Nucleotide Polymorphisms) from Mark Shriver's laboratory at Pennsylvania State University (14–16) (available at http://www.ncbi.nlm.nih.gov/SNP/) and a subset of 13 loci chosen from the 377 autosomal microsatellite loci from the HGDP-CEPH Human Genome Diversity Cell Line Panel (4,17,18) (available at http://research.marshfieldclinic.org/genetics/). We are able to compare the informativeness of these additional markers sets (i.e. SNPs and microsatellites) and to evaluate their efficiency relative to the CODIS STR loci.

Materials and Methods

Information and Model Populations

The basic question that we will address is "how much information about an individual's ancestry may we anticipate from genotyping that individual for a set of genetic markers?" As we will show, this information depends on how many source populations have contributed ancestors to the individual, which source populations have contributed to the individual, and the fraction of the individual's ancestors that trace to each of the contributing source populations. Our analysis will consider the situation for three source populations: Africans, Europeans, and Native Americans. This will efficiently illustrate important statistical relationships and allow us compare different databases. We recognize that the ancestry of many individuals in the United States also contains contributions from source populations on other continents. For example, it will be desirable in the future to assess the information available for detecting Asian ancestry; however, SNP data are currently unavailable for this important population.

With three ancestral populations, the expected frequency of the kth allele at the gth locus in the admixed individual is given by

$$E(p_{gAk}) = m_1 p_{g1k} + m_2 p_{g2k} + m_3 p_{g3k}$$
$$= p_{g3k} + m_1 \delta_{g1k} + m_2 \delta_{g2k} \quad (1)$$

where the ancestral contributions, m_i $(i = 1, 2, 3)$ sum to 1.0, the three ancestral populations are denoted by $A = 1, 2, 3$ and

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the δ coefficients are defined as $\delta_{g1k} = p_{g1k} - p_{g3k}$ and $\delta_{g2k} = p_{g2k} - p_{g3k}$. The constraint $\sum_i m_i = 1.0$ ensures that the outcome of analysis is unaffected by the way parental populations are numbered, or which population was subtracted from the others. The log-likelihood function for the individual is,

$$\ln L = \sum_g \sum_k n_{gk} \ln(p_{gAk}) = \sum_g \sum_k n_{gk} \ln(p_{g3k} + m_1\delta_{g1k} + m_2\delta_{g2k}) \quad (2)$$

where n_{gk} ($k = 0, 1, 2$) is the number of copies of the kth allele in the genotype at the gth locus of the admixed individual. Maximum likelihood estimates $\widehat{m}_i (i = 1, 2)$ for the ancestral contributions are obtained from the log likelihood function by setting the partial derivatives,

$$\frac{\partial \ln L}{\partial m_i} = \sum_g \sum_k n_{gk} \frac{\delta_{gik}}{E(p_{gAk})} \quad (3)$$

equal to zero, and solving simultaneously. The maximum likelihood estimate of the contribution from the third source population is obtained by subtraction, i.e., $\widehat{m}_3 = 1 - \widehat{m}_1 - \widehat{m}_2$.

The expected information with respect to the set of individual admixture proportions is obtained from a matrix *(INF)* with elements equal to the negative expected second partial derivatives of the log likelihood function

$$INF(m_i, m_j) = -E\left[\frac{\partial^2 \ln L}{\partial m_i \partial m_j}\right] = 2\sum_g \sum_k \frac{\delta_{gik}\delta_{gjk}}{E(p_{gAk})} \quad (4)$$

where i and j are equal to 1 or 2. For individuals formed by admixture among three or more parental populations, the most informative marker loci are those that simultaneously add to the diagonal elements of the information matrix without greatly increasing the off diagonal elements. The determinant of the information matrix is a useful criterion for assessing the degree to which a particular genetic marker increases the information for all ancestry proportions. For a 2 by 2 matrix (as used for three ancestral populations) the determinant is defined as,

$$D = \det[INF(m_i, m_j)] = INF(m_1, m_1)INF(m_2, m_2) - INF(m_1, m_2)^2 \quad (5)$$

where $INF(m_1, m_2)$ is the expected shared information for the estimates of m_1 and m_2, $INF(m_1, m_1)$ is the expected information for the estimate of m_1 (i.e. ancestral proportion of population 1), $INF(m_2, m_2)$ is the expected information for the estimate of m_2 (i.e. ancestral proportion of population 2).

The expected variances of the first two estimated proportions ($V_{\hat{m}_1}$ and $V_{\hat{m}_2}$) are obtained from the diagonal elements of the inverse of the information matrix, $V = INF^{-1}$. The variance of the third estimated proportion is obtained $V_{\hat{m}_3} = V_{\hat{m}_1} + V_{\hat{m}_2} + 2V_{\hat{m}_1\hat{m}_2}$, where $2V_{\hat{m}_1,\hat{m}_2}$ is the off-diagonal element of V. The expected standard error, $s_{\hat{m}_i}$, for each fraction of ancestry from each source population is found by taking the square root of the respective variance. The information for $\widehat{m}_3$ is $INF(m_3, m_3) = 1/V_{\hat{m}_3}$. The maximum likelihood estimates of admixture proportions and their standard errors are asymptotically unbiased with an increasing number of marker loci[11]. The rate of approach to the asymptote also depends on factors such as the expected heterozygosity and dominance relationships among alleles. Codominant loci including SNPs and STRs approach the asymptote more rapidly, all other factors being equal.

Fisher's expected information for an individual depends on the actual fractions of ancestry contributed by the source populations to the individual (i.e., m_1, m_2, and m_3). Therefore, we must evaluate the expected information relative to a specified set of ancestry coefficients. We will loosely refer to a set of ancestry coefficients, e.g. ($m_1 = 0.500$, $m_2 = 0.375$, and $m_3 = 0.125$), as a 'model population' because the expected information is the same for all people with the same ancestry fractions. We created 16 model populations that run the gamut from individuals with 100% ancestry from one source population, to individuals ancestry combined from any two of the populations, to individuals with ancestry combined from all 3 populations.

Marker Evaluation Strategy

For each combination of proportionate admixture for three founding populations, African, European and Native American, we first tested the informativeness of the CODIS STR loci, and subsequently considered two other publicly available marker sets in order to evaluate the informativeness of alternative sets of loci that could also be useful in the forensic setting. In Tables 1 and 2 we show the population specific information, the joint information, the determinant of the information matrix and the population specific standard deviations for the FBI CODIS set of 13 STRs and the set of 39 Shriver SNPs, respectively. In Table 3 we show the population specific information, the joint information, the determinant of the information matrix and the population specific standard deviations for the best set of 13 markers from the 377 marker HGDP-CEPH panel for each model population, in order to directly compare these to the 13 CODIS STR loci.

Results

Tables 1–3 present the results for the FBI CODIS STR, Shriver SNP, and CEPH STR genetic marker sets, respectively. The informativeness of each of these three sets of genetic markers was evaluated for individuals with 16 different combinations of African, European, and Native American admixture because the information supplied by a set of genetic markers depends on the ancestral mix of the individual.

This analysis shows that the FBI CODIS STR loci are not the most informative set of loci that can be used for admixture analysis. Although the amount of information supplied by a marker set varies by model population. The information and determinants of the information matrix for each of the 16 model populations tested is significantly lower for the CODIS STR set of loci compared to the other sets of loci being tested (Tables 1–3). In fact, the standard deviations for each of the model populations for the set of 13 loci from the HGDP-CEPH panel and the 39 Shriver SNPs was generally much lower compared to what it was for the same model population using the CODIS STR loci. Ironically, the poor performance of the CODIS STR loci for ancestry estimation is probably a consequence of the fact that this set of loci is optimal for establishing the uniqueness of individuals. CODIS STR allele frequencies have low correlations between different populations and ethic groups.

The population specific information and determinants of the information matrix tended to be higher for the set of 39 Shriver SNPs (Table 2) than for the set of 13 microsatellites from the HGDP-CEPH panel (Table 3), although the HGDP-CEPH selected markers were more informative than the Shriver SNP markers for some model populations. For all model population combinations the expected population specific standard deviation was reasonably similar for the Shriver set and the 13 HGDP-CEPH loci. The

TABLE 1—*Information and population standard deviations for the CODIS STR loci.*

Population Model	Proportionate Admixture			$INF(m_1, m_1)$	$INF(m_2, m_2)$	$INF(m_1, m_2)$	D	s_{m_1}	s_{m_2}	s_{m_3}
	African	European	Native American							
1	0.00	0.00	1.00	40.36	27.88	8.22	1057.67	0.16	0.20	0.22
2	0.00	0.25	0.75	39.63	12.01	7.01	426.82	0.17	0.30	0.30
3	0.00	0.50	0.50	46.54	11.55	6.82	490.75	0.15	0.31	0.30
4	0.00	0.75	0.25	74.08	14.31	8.07	995.29	0.12	0.27	0.27
5	0.00	1.00	0.00	17.46	13.66	6.66	194.17	0.27	0.30	0.30
6	0.25	0.00	0.75	17.82	32.38	5.88	542.51	0.24	0.18	0.27
7	0.25	0.25	0.50	17.67	12.29	6.58	173.73	0.27	0.32	0.31
8	0.25	0.50	0.25	19.44	13.55	8.74	186.86	0.27	0.32	0.29
9	0.25	0.75	0.00	54.12	52.15	45.17	781.66	0.26	0.26	0.14
10	0.50	0.00	0.50	15.67	43.82	5.66	654.46	0.26	0.15	0.27
11	0.50	0.25	0.25	17.52	14.54	8.43	183.79	0.28	0.31	0.29
12	0.50	0.50	0.00	34.03	31.55	25.84	406.44	0.28	0.29	0.19
13	0.75	0.00	0.25	18.34	79.18	6.89	1404.35	0.24	0.11	0.24
14	0.75	0.25	0.00	29.10	26.38	19.61	383.29	0.26	0.28	0.21
15	1.00	0.00	0.00	29.14	22.81	14.67	449.47	0.23	0.25	0.22
16	0.33	0.33	0.33	17.41	12.84	7.53	166.76	0.28	0.32	0.30

TABLE 2—*Information and population standard deviations for the 39 Shriver SNP loci.*

Population Model	Proportionate Admixture			$INF(m_1, m_1)$	$INF(m_2, m_2)$	$INF(m_1, m_2)$	D	s_{m_1}	s_{m_2}	s_{m_3}
	African	European	Native American							
1	0.00	0.00	1.00	274.27	116.66	68.59	27290.85	0.07	0.10	0.10
2	0.00	0.25	0.75	4181.62	62.23	51.23	257613.81	0.02	0.13	0.13
3	0.00	0.50	0.50	2155.00	55.00	41.69	116785.45	0.02	0.14	0.13
4	0.00	0.75	0.25	1478.75	62.05	43.62	89846.41	0.03	0.13	0.13
5	0.00	1.00	0.00	1257.09	263.01	192.82	293453.30	0.03	0.07	0.06
6	0.25	0.00	0.75	98.39	93.96	36.35	7922.99	0.11	0.11	0.12
7	0.25	0.25	0.50	93.62	58.48	32.84	4396.81	0.12	0.15	0.14
8	0.25	0.50	0.25	95.91	58.70	36.65	4286.42	0.12	0.15	0.14
9	0.25	0.75	0.00	119.12	93.03	64.36	6939.03	0.12	0.13	0.11
10	0.50	0.00	0.50	84.78	94.79	31.06	7071.45	0.12	0.11	0.13
11	0.50	0.25	0.25	87.63	62.07	35.64	4168.71	0.12	0.14	0.14
12	0.50	0.50	0.00	107.05	79.94	56.00	5421.55	0.12	0.14	0.12
13	0.75	0.00	0.25	98.75	118.18	31.83	10657.32	0.11	0.10	0.12
14	0.75	0.25	0.00	120.08	82.12	56.17	6706.57	0.11	0.13	0.12
15	1.00	0.00	0.00	2181.35	159.11	66.53	342658.07	0.02	0.08	0.08
16	0.33	0.33	0.33	88.87	57.89	34.02	3987.03	0.12	0.15	0.14

TABLE 3—*Information and population standard deviations for the HGDP-CEPH panel of loci (Best set of 13 for each model population).*

Population Model	Proportionate Admixture			$INF(m_1, m_1)$	$INF(m_2, m_2)$	$INF(m_1, m_2)$	D	s_{m_1}	s_{m_2}	s_{m_3}
	African	European	Native American							
1	0.00	0.00	1.00	452.94	266.98	201.30	80404.23	0.06	0.08	0.06
2	0.00	0.25	0.75	675.82	50.98	49.24	32028.73	0.04	0.15	0.14
3	0.00	0.50	0.50	495.08	42.04	34.48	19624.29	0.05	0.16	0.15
4	0.00	0.75	0.25	621.60	54.36	39.68	32215.67	0.04	0.14	0.14
5	0.00	1.00	0.00	515.78	289.90	257.16	83393.36	0.06	0.08	0.06
6	0.25	0.00	0.75	75.72	171.28	36.44	11641.45	0.12	0.08	0.12
7	0.25	0.25	0.50	77.98	45.08	33.90	2366.13	0.14	0.18	0.15
8	0.25	0.50	0.25	84.80	46.24	40.92	2246.71	0.14	0.19	0.15
9	0.25	0.75	0.00	248.58	217.16	209.14	10242.09	0.15	0.16	0.07
10	0.50	0.00	0.50	60.12	137.24	29.16	7400.56	0.14	0.09	0.14
11	0.50	0.25	0.25	69.90	52.66	42.02	1915.25	0.17	0.19	0.14
12	0.50	0.50	0.00	202.22	170.76	168.40	6172.53	0.17	0.18	0.08
13	0.75	0.00	0.25	71.14	176.72	35.64	11301.65	0.13	0.08	0.12
14	0.75	0.25	0.00	224.74	178.40	181.26	7238.43	0.16	0.18	0.07
15	1.00	0.00	0.00	650.14	402.20	390.86	108714.77	0.06	0.08	0.05
16	0.33	0.33	0.33	72.08	46.60	37.64	1942.16	0.15	0.19	0.15

HGDP-CEPH loci or the Shriver SNP set, or combinations of them, would allow for the most precise estimates of an individual's ancestry to be estimated, which could be a step in the right direction to solving a crime when absolutely no prior information was known about the perpetrator.

Discussion

Identifying sets of loci that are useful for admixture analysis has become a topic of interest again for population geneticists, geneticists and epidemiologists, in order to better understand underlying population substructure and its affect on disease associations (4,9,10,14,15,19–22). We believe that admixture is important to the field of forensics and there is a need to identify a set of loci that would be cost effective and time efficient to genotype that would be useful across many different mixtures of individual ancestry. For some crimes, a photograph, sketch or eyewitness description of the perpetrator is available, but for people with mixed ancestry it is difficult to simply look at them and know their ancestry with accuracy. For many crimes, the perpetrator is completely unknown and proper assignment of ancestry and subsequently ethnicity could be useful for solving the crime.

We found that the FBI Core CODIS set of 13 STRs, which is used on a regular basis for forensic investigations, is neither the most informative nor precise set of loci for estimating individual ancestry. We argue that one of the reasons for this result was that these loci were specifically chosen to be applicable for individual identification in all populations (i.e., minimizing coincidental match probability; 23). It is not surprising that these loci are less informative for identifying admixture. They are more variable within populations (with respect to gene diversity and the number of segregating alleles) and yield smaller levels of gene differentiation as measured by F_{ST} (or G_{ST}) (24).

The method used in this study to evaluate informativeness for admixture analysis was based on the maximum likelihood method for estimation of admixture proportions (13,25). The underlying ancestral population distribution can be quite vague in the case of a perpetrator and the method used here does not require prior information about the ancestry of the individual under suspicion, as the Bayesian techniques would require (4,6,9). Hence, we believe a method based on the maximum likelihood method for estimation of admixture proportions is most appropriate for forensic science applications.

In order to make a recommendation of an appropriate alternative set of loci that can be used for admixture analysis in forensic studies, two other sets of publicly available loci were tested for informativeness for admixture, the 39 Shriver SNPs and the set of 377 microsatellites in the HGDP-CEPH panel. The set of the 13 best microsatellites from the HGDP-CEPH panel and the Shriver set of 39 SNPs are much more informative for individual admixture compared to the CODIS STR loci, therefore a recommendation for a useful set of best markers for individual admixture analysis should be derived from these sets of loci. The best loci from the HGDP-CEPH panel and the best loci from the Shriver set vary according to the model population, the proportions of admixture from the mixing populations in each model population and δ (the founding population allele frequency differential). Therefore, it is not necessarily a straightforward process to make a global recommendation of a proper panel of markers for all populations. Although, for forensic applications, we believe the panel with the lowest average expected standard deviation for admixture would be the optimal set to use, because the sets with lower standard deviations would give one more confidence in the ethnicity assignment for an individual using these methods. We found that the standard errors of the best sets of markers found here could be reduced significantly (i.e. cut in half) if the set of the 56 most informative loci from the HGDP-CEPH panel for each of the model populations was used. However this may still not be the most cost effective set of loci to use, hence we recommend using a combination of the 13 best markers from the HGDP-CEPH panel and the most informative SNPs from the Shriver panel.

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