The GenoChip: A New Tool for Genetic Anthropology

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Abstract

The Genographic Project is an international effort aimed at charting human migratory history. The project is nonprofit and non-medical, and, through its Legacy Fund, supports locally led efforts to preserve indigenous and traditional cultures. Although the first phase of the project was focused on uniparentally inherited markers on the Y-chromosome and mitochondrial DNA (mtDNA), the current phase focuses on markers from across the entire genome to obtain a more complete understanding of human genetic variation. Although many commercial arrays exist for genome-wide single-nucleotide polymorphism (SNP) genotyping, they were designed for medical genetic studies and contain medically related markers that are inappropriate for global population genetic studies. GenoChip, the Genographic Project’s new genotyping array, was designed to resolve these issues and enable higher resolution research into outstanding questions in genetic anthropology. The GenoChip includes ancestry informative markers obtained for over 450 human populations, an ancient human (Saqqaq), and two archaic hominins (Neanderthal and Denisovan) and was designed to identify all known Y-chromosome and mtDNA haplogroups. The chip was carefully vetted to avoid inclusion of medically relevant markers. To demonstrate its capabilities, we compared the $F_{ST}$ distributions of GenoChip SNPs to those of two commercial arrays. Although all arrays yielded similarly shaped (inverse J) $F_{ST}$ distributions, the GenoChip autosomal and X-chromosomal distributions had the highest mean $F_{ST}$, attesting to its ability to discern subpopulations. The chip performances are illustrated in a principal component analysis for 14 worldwide populations. In summary, the GenoChip is a dedicated genotyping platform for genetic anthropology. With an unprecedented number of approximately 12,000 Y-chromosomal and approximately 3,300 mtDNA SNPs and over 130,000 autosomal and X-chromosomal SNPs without any known health, medical, or phenotypic relevance, the GenoChip is a useful tool for genetic anthropology and population genetics.

Key words: genetic anthropology, GenoChip, Genographic Project, population genetics, AimsFinder, haplogroups.

Introduction

Apportionment of human genetic variation has long established that all living humans are related via recent common ancestors who lived in sub-Saharan Africa some 200,000 years ago (Cann et al. 1987). The world outside Africa was settled over the past 50,000–100,000 years (Henn et al. 2010) when the descendants of our African forebears spread out to populate other continents (Cavalli-Sforza 2007).
This “Out-of-Africa” hypothesis, backed by archeological findings (Klein 2008) and genetic evidence (Stringer and Andrews 1988; Laval et al. 2010), describes a major dispersal of anatomically modern humans that completely replaced local archaic populations outside Africa, although a scenario involving Europeans and West Africans admixing with extinct hominins was also proposed (Plagnol and Wall 2006). Remarkably, recent studies proposed evidence for two such archaic admixture (interbreeding) events, one with Neandertals in Europe and eastern Asia (Green et al. 2010) and the second with Denisovans in Southeast Asia and Oceania (Reich et al. 2011), though the extent of the hybridization remains questionable (Eriksson and Manica 2012). Overall, the recurrent migrations, admixture, and interbreeding events shaped the autosomes of modern populations into mosaics of ancient and recent alleles harbored in haplotypes that vary in size but not in the building blocks themselves. These subtle differences in autosomal allele frequency between populations together with uniparental markers provide genetic data with the potential to obtain evidence of mixing and migration of human populations.

The advent of microarray single-nucleotide polymorphism (SNP) technology that revolutionized human population genetics and broadened our understanding of genetic diversity largely skipped genetic anthropology for three main reasons: first, only a handful of the estimated 5,000–6,000 indigenous population groups (Burger and Strong 1990; Fardon 2012) were genotyped and studied, which may limit the phylogeographic resolution of the findings. Second, the plethora of genetic markers obtained from different genotyping platforms has resurrected the “empty matrix” problem, whereby populations from different studies can barely be compared due to the low overlap of these platforms. Finally, genotyping costs remained prohibitively high and unjustified for genetic anthropology, as the commercial genotyping platforms, by large, do not accommodate ancestry informative markers (AIMs). Furthermore, these arrays are enriched in trait- or disease-related markers, which prompt a host of psychological, social, legal, political, and ethical concerns from the individual to the population and global levels (Royal et al. 2010).

The first phase of The Genographic Project focused on reconstructing human migratory paths through the analysis of uniparentally inherited markers on the Y-chromosome and mitochondrial DNA (mtDNA). The success of the project in both inferring details of human migratory history (e.g., Balanovsky et al. 2011; Schurr et al. 2012) and attracting over half a million public participants interested in tracing their genetic ancestry has prompted entrepreneurs to offer multiple self-test kits that provide information ranging from disease risk and life-style choices (e.g., diet) to genetic ancestry (Wolinsky 2006). Some of these solutions have been criticized for making deceptive health-related claims and providing limited and imprecise answers regarding ancestry (Royal et al. 2010). The concerns about ancestry reporting were not unjustified, as these entrepreneurs adopted the commercial genotyping platforms that were fraught with medically informative markers, depleted of AIMs, and overall yielded biased measures of genetic diversity (Albrechtsen et al. 2010).

Although uniparental arrays do not suffer from the aforementioned predicaments, they are limited in that they represent only a smaller and more ancient portion of our history and ignore our remaining ancestors whose contribution to our genome was more recent and substantial. In contrast, assessment of the spatial and temporal patterns of genetic variation in the rest of the genome coupled with data obtained from other disciplines can provide more information of our ancestors. However, autosomal-driven studies attempting to discern markers informative to genetic anthropology from those having medical relevance often met with legal or ethical obstacles and failed to attract participants who remained concerned about the sharing and potential exploitation of their medical information (Royal et al. 2010). These constraints render all commercial genotyping arrays unsuitable for genetic anthropology, including the Human Origins array (Lu et al. 2011) that contains coding and medically related markers.

To facilitate high-quality research in genetic anthropology without obtaining health, trait, or medical information, we resolved to develop a novel genotyping array—which we call the GenoChip. Our goals were to 1) design a state of the art SNP array dedicated solely to genetic anthropology, 2) validate its accuracy, 3) evaluate its abilities to discern populations compared with alternative arrays, and 4) demonstrate its performances on worldwide populations.

Materials and Methods

Genotype Data Retrieval


SNP Validation

To cross-validate the GenoChip’s autosomal genotypes, we genotyped 168 samples from 14 worldwide populations of the 1000 Genomes Project including Americans of African
Comparing Population Genetic Summary Statistics between Genotyping Arrays

To compare the performances of the validated approximately 130,000 autosomal and X-chromosomal SNPs of the GenoChip array to commercial arrays, we obtained the list of SNPs for the Illumina Human660W-Quad BeadChip (544,366 SNPs) from Illumina and the Affymetrix Axiom Human Origins array (627,719 SNPs) available at ftp://ftp.cephb.fr/hgdp_supp10/Harvard_HGDP-CEPH/all_snp.map.gz (last accessed May 19, 2013). Because of the lack of overlap between these genotyping arrays, we used subsets of data calculated for HapMap III populations. Minor allele frequency (MAF) and $F_{ST}$ estimates for African, European, and Asians were obtained from the “continental” HapMap data set, as described in Elhaik (2012). Briefly, genotype data of 602 unrelated individuals from eight populations (YRI, LWK, Maasai in Kinyawa, Kenya [MKK], CEU, TSI, CHB, Chinese from metropolitan Denver, Colorado [CHD], and JPT) were downloaded from the International HapMap Project web site (phase 3, second draft) (Altschuler et al. 2010), passed through rigorous filtering criteria, and finally merged into continental populations (African [288], European [144], and Asian [170]). The final continental data set consisted of 3 million SNPs genotyped in at least one population from each continent.

The MAF and $F_{ST}$ values of the continental data set for autosomal (2,823,367) and X-chromosomal (86,449) SNPs were compared with those obtained from GenoChip (126,425 and 2,421 SNPs, respectively), Illumina Human660W (541,104 and 12,916 SNPs, respectively), and Affymetrix Axiom Human Origins Array (308,949 and 2,984 SNPs, respectively).

Because of the large number of $F_{ST}$ values in each data set, their length distributions are very noisy. We thus adopted a simple smoothing approach in which $F_{ST}$ values are sorted and divided to 1,000 equally sized subsets. The distribution of the mean $F_{ST}$ value is then calculated using a histogram with 40 equally sized bins ranging from 0 to 1. To test whether two such $F_{ST}$ distributions obtained by different arrays are different, we used the Kolmogorov–Smirnov goodness-of-fit test and the false discovery rate correction for multiple tests (Benjamini and Hochberg 1995). Because the differences between the distributions were highly significant due to the large sample sizes, we also calculated the effect size, first by using the nonoverlapping percentage of the two distributions, and then by using Hedges’ $g$ estimator of Cohen’s $d$ (Hedges 1981). If the area overlap is larger than 98% and Cohen’s $d$ is smaller than 0.05, we consider the magnitude of the difference between the two distributions to be too small to be biologically meaningful.

Principal components analysis (PCA) calculations were carried out using smartpca of the EIGENSOFT package (Patterson et al. 2006). Polygons were drawn manually around populations clustered separately from one another.

Results and Discussion

Choosing the Markers

The GenoChip was designed as an Illumina iSelect HD custom genotyping bead array that offers the ability to interrogate almost any SNP. In designing the chip, we endeavored to identify the fewest possible SNPs that offer an increased power for ancestry inference in comparison to random markers (Royall et al. 2010). SNPs that discern and identify populations are termed AIMs and are considered invaluable tools in population genetics and genetic anthropology. Half of our AIMs were culled from the literature, and the remaining were calculated using our novel AIMsFinder based on an approach described by Elhaik (2013) and infocalc (Rosenberg 2005). The GenoChip consists of 80,000 autosomal and X-chromosomal AIMs from over 450 worldwide populations (fig. 1).

To facilitate studies on the extent of gene flow from Neanderthal and Denisovan to modern humans, we collected from the literature SNPs and haplotypes from genomic regions bearing evidence of interbreeding (Noonan et al. 2006; Green et al. 2010; Yotova et al. 2011). In addition, we used a
modified version of IsoPlotter+ (Elhaik et al. 2010; Elhaik and Graur 2013) to identify regions in which modern humans and Neanderthals share the derived allele and chimpanzees and Denisovans share the ancestral allele (supplementary text S1, Supplementary Material online). Using the same approach, we identified SNPs within regions enriched for the Denisovan shared derived alleles with humans. Overall, we included nearly 26,000 autosomal and X-chromosomal SNPs from potential interbreeding hotspots with extinct hominins. To support studies of more recent gene flow from ancient to modern humans, we included approximately 10,400 high-confidence Paleo-Eskimo Saqqaq SNPs (Rasmussen et al. 2010). In addition, we included approximately 12,000 high-confidence Aboriginal SNPs (Rasmussen et al. 2011). High-linkage disequilibrium (LD) SNPs ($r^2 > 0.4$) were excluded in all populations, by choosing a random SNP of the high-LD pair, except for hunter gatherers such as the Hadza and Sandawe of Tanzania (Tishkoff and Williams 2002) and Melanesian populations (Conrad et al. 2006) that are used to infer interbreeding with extinct hominins (Reich et al. 2010; Lachance et al. 2012).

To support potential imputation efforts, we supplemented regions of low SNP density (<1 SNP over 100,000 bases) with random common SNPs from HapMap III (1,000 SNPs with MAF > 20%) and the 1000 Genomes Project (3,500 SNPs with MAF > 10% in at least one continental population). To prevent false positives, we included mostly SNPs observed in both the HapMap III and 1000 Genome Project data sets (Altshuler et al. 2010; Durbin et al. 2010). We further eliminated A/T and C/G SNPs to minimize strand misidentification.

The resulting chip has a SNP density of at least 1/100 kilobases over 92% of the assembled human genome (hg19) (fig. 2), including regions uncharted by the HapMap (I-III) and HGDP projects (Conrad et al. 2006; Altshuler et al. 2010). This high density of the chip and the excess inclusion of AIMs make it suitable for imputation, particularly for common markers (Pasaniuc et al. 2012).
SNPs, we excluded SNPs that were in high LD (tation efforts toward inferring potential medical-relevant associated with phenotypic traits. Finally, to circumvent impu-
plex (MHC) region. We also excluded SNPs reported to be
2008), GWAS Central (Thorisson et al. 2009), and SNPedia,
(2009 ), The Genetic Association Database
2007), the National Human Genome Research Institute
Genome-Wide Association Studies (GWAS) Catalog
ments without any known functional association (Graur et al.
 SNPs) and the GenoChip in-
cluded the most comprehensive collection of uniparental
markers.

Vetting the Chip for Health, Trait, or Medical Markers
Several steps were taken to ensure that the genetic results
would not be exploited for pharmaceutical, medical, and
biotechnological purposes. First, participant samples were
maintained in complete anonymity during GenoChip analysis.
Second, no phenotypic or medical data were collected from
the participants. Third, we included only SNPs in noncoding
regions without any known functional association (Graur et al.
2013), as reported in dbSNP build 132. Last, we filtered our
SNP collection against a 1.5 million SNP data set (Pheno SNPs)
containing all variants that have potential, known, or sus-
ppected associations with diseases.

To construct the Pheno SNPs data set, we extracted SNPs
from multiple open-access databases including the Online
lnm.nih.gov/omim/, last accessed May 19, 2013), the Cancer
Genome Atlas (Hudson et al. 2010), PhenCode (Giardine et al.
2007), the National Human Genome Research Institute
(NHGRI) Genome-Wide Association Studies (GWAS) Catalog
(Hindorff et al. 2009), The Genetic Association Database
(Becker et al. 2004), MutaGeneSys (Stoyanovich and Pe’er
2008), GWAS Central (Thorisson et al. 2009), and SNPedia,
as well as SNPs identified in the major histocompatibility com-
plex (MHC) region. We also excluded SNPs reported to be
associated with phenotypic traits. Finally, to circumvent imput-
tation efforts toward inferring potential medical-relevant
SNPs, we excluded SNPs that were in high LD ($r^2 > 0.8$) with
the Pheno SNPs.

We thus designed the first genotyping array dedicated
for genetic anthropological and genealogical research that
is suitable for detecting gene flow from archaic hominins
and ancient humans into modern humans as well as between
worldwide populations. The final GenoChip has over 130,000
highly informative autosomal and X-chromosomal markers,
approximately 12,000 Y-chromosomal markers, and approxi-
mately 3,300 mtDNA markers without any known health,
medical, or phenotypic relevance (supplementary table S2,
Supplementary Material online).

Validating the GenoChip Results
The accuracy of the autosomal genotypes obtained by
the GenoChip was assessed by genotyping 168 worldwide
samples from the 1000 Genomes Project and cross-validating
the results. The concordance rate per sample was over 99.5%.
We did not observe any position with mismatching homozy-
gote alleles. The marginal error rate was expected due to the
low coverage of the 1000 Genomes Project data, particularly
for rare alleles (Durbin et al. 2010). We thus confirmed that
genotypes reported by the GenoChip are accurate.

The ability of the GenoChip to infer uniparental hap-
logroups was similarly assessed by genotyping 400 additional
samples with known haplogroups. The haplotypes of these
samples were confirmed by Sanger sequencing of the full
mitochondrial genome and all relevant Y chromosome SNP
locations that determined the exact haplogroup down to
the last branch of the published Y-chromosomal tree (supplemen-
tary text S2 , Supplementary Material online). The average
success rates for the paternal and maternal haplogroups
were 82% and 90%, respectively (fig. 3). The reasons for
our inability to validate the remaining haplogroups are the
unavailability of control samples to identify deeper splits in
the tree. Moreover, some haplogroups cannot be measured
with the Illumina bead chip technology because they are not
represented by a real SNP but rather by large-scale variations
of repetitive elements. We note that some of the failed
markers for particular haplogroups can be substituted by
phylogenetically equivalent markers and rescue these hap-
logroups, although formally they were counted as missing.
Our experience with the tens of thousands of GenoChip
participants indicates that most samples (>99%) are classified
on haplogroup branches that are perfectly captured by the
GenoChip. The remaining users for which the exact position
along the tree cannot be assigned (e.g., R-P312*) are classified
to a higher level haplogroup (e.g., R-P310). A large-scale
genotyping effort to validate the remaining haplogroups is
undergoing. We thus confirmed that GenoChip produces
highly accurate results and has broad coverage for markers
defining Y-chromosome and mtDNA haplogroups.

testing the GenoChip’s Abilities to Discern Populations

MAF Distribution
Before comparing the ability of the GenoChip SNPs to discern
populations, we compared the similarity of their MAF distri-
bution with those of the Illumina Human660W and Affymetrix
Human Origins SNP arrays. Because of the low overlap of
these three arrays, we obtained and analyzed genotype data
from eight HapMap populations. The results of the complete
set of HapMap markers were compared with three subsets of
markers that overlapped with those of each array.
A comparison of the MAF distributions of the three arrays revealed gross differences in allele frequencies (fig. 4, supplementary fig. S1, Supplementary Material online). In the HapMap data set, over 82% of the SNPs are common (MAF > 0.05) and less than 5% are considered rare (MAF < 0.01). The proportion of common SNPs in all the arrays is similar (96–98%), but the GenoChip is enriched for the most common SNPs (MAF > 0.25). Because of the high frequency of the rare ENCODE SNPs in the HapMap data set, none of the arrays resembled the shape of the HapMap’s MAF distribution. Nonetheless, both the Human660W (0.07%) and Human Origins (0.36%) arrays are enriched in rare SNPs compared with the GenoChip (0.008%). Similar trends were observed for X-chromosomal SNPs. Here, the HapMap data set consisted of 83% common SNPs, compared with 93% for the GenoChip and 96% for the commercial arrays. The GenoChip array exhibits similar enrichment in the most common SNPs (MAF > 0.3), but unlike the commercial arrays, it also consists of 1% extremely rare SNPs due to the inclusion of rare haplotypes speculated to indicate interbreeding with archaic hominins. Altogether, the MAF distributions of the three arrays differ from the HapMap MAF distribution and
correspond to the choices of SNP ascertainment made in the design of each array.

**Genomewide $F_{ST}$ Distribution**

To assess the extent of genetic diversity that can be inferred among human subpopulations by the different arrays, we next compared their $F_{ST}$ distributions (Wright 1951). $F_{ST}$ measures the differentiation of a subpopulation relative to the total population and is directly related to the variance in allele frequency between subpopulations, such that a high $F_{ST}$ corresponds to a larger difference between subpopulations (Holsinger and Weir 2009). Elhaik (2012) used 1 million markers that were genotyped in 602 HapMap samples from eight populations to carry out a two-level hierarchical $F_{ST}$ analysis. He showed that the greatest proportion of genetic variation occurred within individuals residing in the same populations, with only a small amount (12%) of the total genetic variation being distributed between continental populations and even a lesser amount (1%) between intracontinental populations. An $F_{ST}$ distribution for three continental populations employing 3 million HapMap SNPs yielded an even lower estimate (8%) to the proportion of genetic variation distributed between continental populations due to the large number of rare alleles (Elhaik 2012).

In a similar manner to (Elhaik 2012) later analysis, we used the $F_{ST}$ values calculated for eight HapMap populations grouped into three continental populations to create three subsets for the markers that overlap with each array. Although all $F_{ST}$ distributions were similar in shape to the HapMap $F_{ST}$ distribution, they differed in their means (fig. S2, Supplementary Material online). The autosomes and X-chromosomal SNPs of the commercial arrays have significantly lower $F_{ST}$ values ($P < 0.05$) than that of the GenoChip due to the high fraction of rare uninformative SNPs in these arrays. The magnitude of the differences between the $F_{ST}$ values of the GenoChip to those of the commercial arrays were also large for autosomal (area overlap 86–91%, Cohen’s $d$ 0.09–0.13) and X-chromosomal SNPs (area overlap 93%, Cohen’s $d$ 0.09–0.11). These results suggest a reduced ability of the commercial arrays to elucidate ancient demographic processes (Kimura and Ota 1973; Watterson and Guess 1977).

The Illumina Human660W array had the highest fraction of low-$F_{ST}$ alleles, suggesting it is the least suitable for population genetic studies compared with the GenoChip and Human Origins. As only half of the Human Origins SNPs could be tested, it is difficult to evaluate its performance. However, we speculate that the large number of rare alleles reflect the private alleles of the dozen populations used for its ascertainment. Because the MAF and $F_{ST}$ were not used as filtering criteria for the GenoChip SNPs, we can conclude that its enrichment toward high-$F_{ST}$ SNPs mirrors the success of the ascertainment process and its potential for population genetic studies.

**Genetic Diversity in Worldwide Populations**

Last, PCA (Price et al. 2006) was used to explore the extent of population differentiation between 14 worldwide populations that were genotyped on the GenoChip in the validation stage (fig. 6A). The samples aligned along the two well-established geographic axes of global genetic variation: PC1 (sub-Saharan Africa vs. the rest of the Old World) and PC2 (east vs. west Eurasia) (e.g., Li et al. 2008; Elhaik 2013). GenoChip results reveal geographically refined groupings of Eastern (Luhya) and Western (Yoruba) Africans, Eastern (Chinese and Japanese) and South Eastern (Vietnamese) Asians, Amerindian (Peruvians Mexicans) and Indian populations, and finally...
Northern (Finnish), Southern (Italian and Iberians), and Western (British and CEU) Europeans. As expected, the Amerindian populations form a gradient along the diagonal line between European and East Asians based on their dominant ancestry as did the African Americans along the diagonal line between Africans and Europeans. These patterns are similar to those observed in worldwide populations using commercial arrays (e.g., Teo et al. 2009; Xing et al. 2010).

When we consider only the East Asian populations (comprising CHB, JPT, and KHV), the first and second axes of variation completely separated the three populations (fig. 6B), in agreement with Teo et al. (2009). In a similar manner, we were able to differentiate Gujarati Indians and Americans of Mexican ancestry (fig. 6C), as well as Italians, Iberians, and Western European populations (fig. 6D), with the exception of one TSI outlier. As expected, some overlap

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**Fig. 6.—** PCA plots of genetic diversity across 14 worldwide populations. Each figure represents the genetic diversity seen across the populations considered, with each sample mapped onto a spectrum of genetic variation represented by two axes of variations corresponding to two eigenvectors of the PCA. Individuals from each population are represented by a unique color. (A) Analysis of all populations. The insets magnify European, Asian, and the cluster of Amerindian and Indian individuals. (B) Analysis of East Asian individuals. (C) Analysis of European individuals. (D) Analysis of Amerindian and Indian individuals. A polygon surrounding all or most of the individuals belonging to a group designation highlights the population groups.
was observed between individuals of Northern and Western European ancestry (CEU) and British (GBR).

Conclusions
To summarize, we designed, developed, validated, and tested the GenoChip, the first genotyping chip completely dedicated to genetic anthropology. The GenoChip will help to clarify the genetic relationships between archaic hominins such as Neanderthal and Denisovan, extinct humans, and modern humans as well as to provide a more detailed understanding of human migratory history. We compared the MAF and \( F_{ST} \) distributions of the GenoChip SNPs to those of HapMap and two commercially available arrays and demonstrated the ability of the GenoChip to differentiate subpopulations within global data sets. We expect that the expanded use of the GenoChip in genetic anthropology research will expand our knowledge of the history of our species.

Supplementary Material
Supplementary text S1 and S2, tables S1 and S2, and figures S1–S4, and are available at Genome Biology and Evolution online (http://www.gbe.oxfordjournals.org/).

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Literature Cited


Wolinsky H. 2006. Genetic genealogy goes global. Although useful in investigating ancestry, the application of genetics to traditional genealogy could be abused. EMBO Rep. 7:1072–1074.
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