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Research paper

# True colors: A literature review on the spatial distribution of eye and hair pigmentation

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ABSTRACT

DNA-based prediction of externally visible characteristics has become an established approach in forensic genetics, with the aim of tracing individuals who are potentially unknown to the investigating authorities but without using this prediction as evidence in court. While a number of prediction models have been proposed, use of prior probabilities in those models has largely been absent. Here, we aim at compiling information on the spatial distribution of eye and hair coloration in order to use this as prior knowledge to improve prediction accuracy. To this end, we conducted a detailed literature review and created maps showing the eye and hair pigmentation prevalence both by countries with available information and by interpolation in order to obtain prior estimates for populations without available data. Furthermore, we assessed the association between these two traits in a very large data set. A strong limitation was the quite low amount of available data, especially outside Europe. We hope that our results will facilitate the improvement of already existing and of novel prediction methods for pigmentation traits and induce further studies on the spatial distribution of these traits.

## 1. Introduction

Prediction of externally visible characteristics (EVC's) based on genetic data, often referred to as Forensic DNA Phenotyping (FDP), has become a major focus in forensic genetic research in the past years. The prime motivation behind this approach is to narrow down the group of potential trace donors in cases where standard genetic fingerprinting, such as short-tandem repeat (STR) profiling, could not provide any matching information with *a priori* known profiles [1,2]. FDP may thereby help focusing police investigations on a (limited) group of suspects, although the legal and ethical framework for such approaches is currently subject to intensive debate (see, for example, [3–7]).

Pigmentation traits, including eye, hair and skin coloration, have been subject of scientific studies for more than 130 years [8,9] and a primary focus of FDP in the past decade. Recent genome-wide association studies have identified numerous genetic variants that contribute to pigmentation [10–18] while others have subsequently used them to predict these traits [19–22]. Prominent and widely used approaches include IrisPlex [23,24] for eye color prediction and its extensions HIrisPlex [25,26] for combined eye and hair color prediction and HIrisPlex-S [27] for predicting the three pigmentation traits eye, hair and skin color. These models are based on multinomial logistic regression models where probabilities for each color category are presented for each trait. IrisPlex uses a total of 6 SNPs for eye color prediction while HIrisPlex includes a set of 24 SNPs and the lastest extension of HIrisPlex-S includes the already 24 established SNPs and additionally 17 related with the skin color prediction. Another established tool for eye color is Snipper [28] which is a Bayesian classifier and uses likelihood ratios to present the outcome of the prediction. All possible likelihoods are calculated and sorted in descending order and the final prediction is the ratio of the two largest likelihoods. Some alternative models are the ones developed by Söchtig et al. [29] and Maroñas et al. [30] for hair and skin color, respectively. These approaches are using iterative naïve Bayesian classification for pairwise phenotype differentiation. Lastly, classification tree approaches were also used for prediction, such as the model by Allwood et al. [31] for eye color prediction and 7-Plex and 8- Plex [32] for both eye and skin color.

In contrast to eye and hair color, which can often be predicted with high accuracy from relatively small sets of DNA markers, skin color prediction is frequently less powerful. Besides the few established tools for skin color prediction mentioned above, numerous studies in the past have already tried to identify genetic variation that underlies human skin coloration which can be, among other causes, a result of the exposure of UV radiation or natural selection [33–38]. Other studies indicated markers that are informative about skin pigmentation,

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**Table 1**
Eye color prevalence across Europe and Central Asia.

| Country | 'Blue' | 'Intermediate' | 'Brown' | References |
|---|---|---|---|---|
| Armenia | 3.05 (0.84-7.63) | 16.78 (10.83-24.31) | 80.15 (72.29-86.61) | [19] |
| Azerbaijan | 6.34 (1.76-15.47) | 22.21 (12.72-34.46) | 71.42 (58.65-82.11) | [19] |
| Denmark | 59.60 (56.67-63.22) | 23.70 (21.02-26.73) | 16.10 (13.87-18.83) | [43,50,53] |
| | 66.20 (57.89-73.84) | 27.60 (20.49-35.61) | 6.20 (2.87-11.45) | |
| | 69.50 (62.12-76.28) | 23.60 (17.47-30.58) | 6.90 (3.61-11.74) | |
| | 64.90 (57.15-72.07) | 25.00 (18.65-32.25) | 10.10 (6.00-15.70) | |
| | 58.50 (50.87-65.89) | 27.30 (20.84-34.48) | 14.20 (9.41-20.25) | |
| | 70.15 (65.29-74.70) | 11.78 (8.72-15.44) | 18.06 (14.33- 22.29) | |
| *average* | 64.84 | 20.45 | 14.50 | |
| Great Britain | 37.59 (29.34-46.40) | 18.79 (12.55-26.48) | 43.60 (35.03-52.47) | [51,53,54] |
| | 44.7 (42.38-47.13) | 29.9 (27.73-32.11) | 25.40 (23.32-27.49) | |
| | 46.1 (44.23-47.92) | 27.7 (26.03-29.35) | 26.30 (24.65-27.92) | |
| *average* | 42.80 | 25.46 | 31.77 | [51,53,54,72] |
| France | 22.00 | 44.00 | 34.00 | [65] |
| Georgia | 7.51(3.66-13.40) | 18.79 (12.55-26.48) | 73.68 (65.35-80.94) | [19] |
| Germany | 39.6 (39.58-39.65) | 33.2 (33.17-33.24) | 27.2 (27.15-27.22) | [9] |
| Iceland | 75.15 (74.93-78.03) | 12.95 (11.99-14.47) | 10.1 (9.22-11.45) | [12] |
| | 73.90 (74.05-77.35) | 15.35 (14.35-17.16) | 8.35 (7.52-9.69) | |
| *average* | 74.52 | 14.15 | 9.22 | |
| Kazakhstan | 3.33 (0.41-11.53) | 11.65 (4.82-22.57) | 85.00 (73.43-92.90) | [19] |
| Netherlands | 60.90 (61.97-67.59) | 11.40 (10.27-14.14) | 21.70 (20.65-25.63) | [12] |
| Poland | 52.50 (49.33-55.55) | 12.50 (10.49-14.64) | 35.10 (32.17-38.12) | [52] |
| Slovenia | 44.70 (35.05-54.78) | 25.70 (17.68-35.17) | 29.60 (21.02-39.22) | [55] |
| Tajikistan | 6.83 (3.00-13.03) | 7.67 (3.58-14.10) | 85.47 (77.76-91.30) | [19] |
| Ukraine (Crimea) | 25.00 (16.55-35.11) | 24.99 (16.55-35.11) | 50.00 (39.39-60.61) | [19] |
| Uzbekistan | 3.44 (0.95-8.59) | 6.02 (2.46-12.04) | 90.51 (83.66-95.17) | [19] |

Point estimates and, in parentheses, 95% confidence intervals for the trait prevalence are given in percentages. If more than one study was available per country, the average across those studies is given.

representing various sets of selected SNPs that were used later on for skin color prediction [10,32,39–44].

Bayesian approaches form a major, powerful and versatile class of statistical prediction models. These models combine probability density estimates of the groups to be distinguished with prior probabilities for the occurrence of subjects/objects from these groups, eventually obtaining posterior probabilities that are used to classify a given subject or object [45]. This use of priors represents a major strength of Bayesian models since it allows incorporating prior knowledge in the prediction, which may in turn improve prediction accuracy. Previous studies have already established some DNA based prediction models built upon naïve Bayesian likelihood classification or Bayesian networks [28–30,46–48].

By using priors in the data analysis, all prior information that is available for an unknown parameter can be expressed before any data-based evidence is considered. Priors can be obtained from past or external information, according to similar experiments, or may also express some subjective belief on the topic. In the context of FDP, priors may be obtained from trait prevalence in the general population, in a specific spatial, ethnic, social or religious subgroup, or in another relevant reference group. Inference of the biogeographic ancestry of an individual in particular may help identifying appropriate prior probabilities if prevalence values for the respective groups are available. However, currently existing approaches to FDP barely use prior knowledge of the biogeographic distribution of traits so far [3,23–26,28,32] and the potential advantage of using priors for appearance prediction has yet to be demonstrated. One example for the use of prior information is Snipper's so-called LOCPRIOR information, i.e. a numerical code that denotes shared characteristics between individuals of population groups and frequencies correlated among populations. The LOCPRIOR information indicates and provides information on specific traits within a population, such as linguistic, geographical, phenotypic ones etc [49]. In this case, sampling locations were used as prior information to assist the clustering between the different categories. Among other causes, the lack of prior implementation may be due to a simple lack of reliable data. While, on the other hand, several internet web sites and press articles present colorful maps on pigmentation traits and give impressive numbers for trait prevalence, their virtually always fail to name their data sources and used methods, rendering such information highly questionable.

In the present study, we aimed for compiling reliable prevalence data for two pigmentation traits, namely categorical eye and hair color, in European populations and beyond. To this end, we conducted a country-specific literature review in order to estimate the geographic prevalence distribution and to obtain reasonable prior probabilities that could be used for improving the prediction accuracy of pigmentation traits. Somewhat surprisingly, we found the available amount of reliable scientific data to be quite limited, despite an ongoing interest in this topic for over a century. We therefore report on only a limited set of mostly European countries for which we were able to compile trustworthy population-representative data concerning eye and hair color distribution. Furthermore, we performed spatial interpolation based on these data. Finally, we report on the extent of correlation between eye and hair color based on the largest study to date on this topic.

## 2. Materials and methods

### 2.1. Pigmentation color categories

In this study, we focused on categorical color categories for eye and hair color, motivated by the Bayesian approach of classifying subjects or objects into one of a set of distinct groups and also by the wider availability of such data compared to only recently introduced metric measurements of pigmentation. More specific, we used the categories 'blue', 'brown' and 'intermediate' for eye color description, as a simplification to the categories established in study of Sulem [12], namely blue/gray, green and brown/black. Categories 'blond', 'brown' and 'red' for hair color description were determined, following the studies of Lock-Andersen [43,50] and merging the brown and black coloration into one. A number of publications (both old and recent) deviated from this scheme. In order to keep the three-category classification and to ensure consistency across studies, we mapped 'hazel' eye color to 'brown', whereas 'green' and 'yellow' were mapped to 'intermediate'. The 'gray' color category was merged with 'blue' throughout.

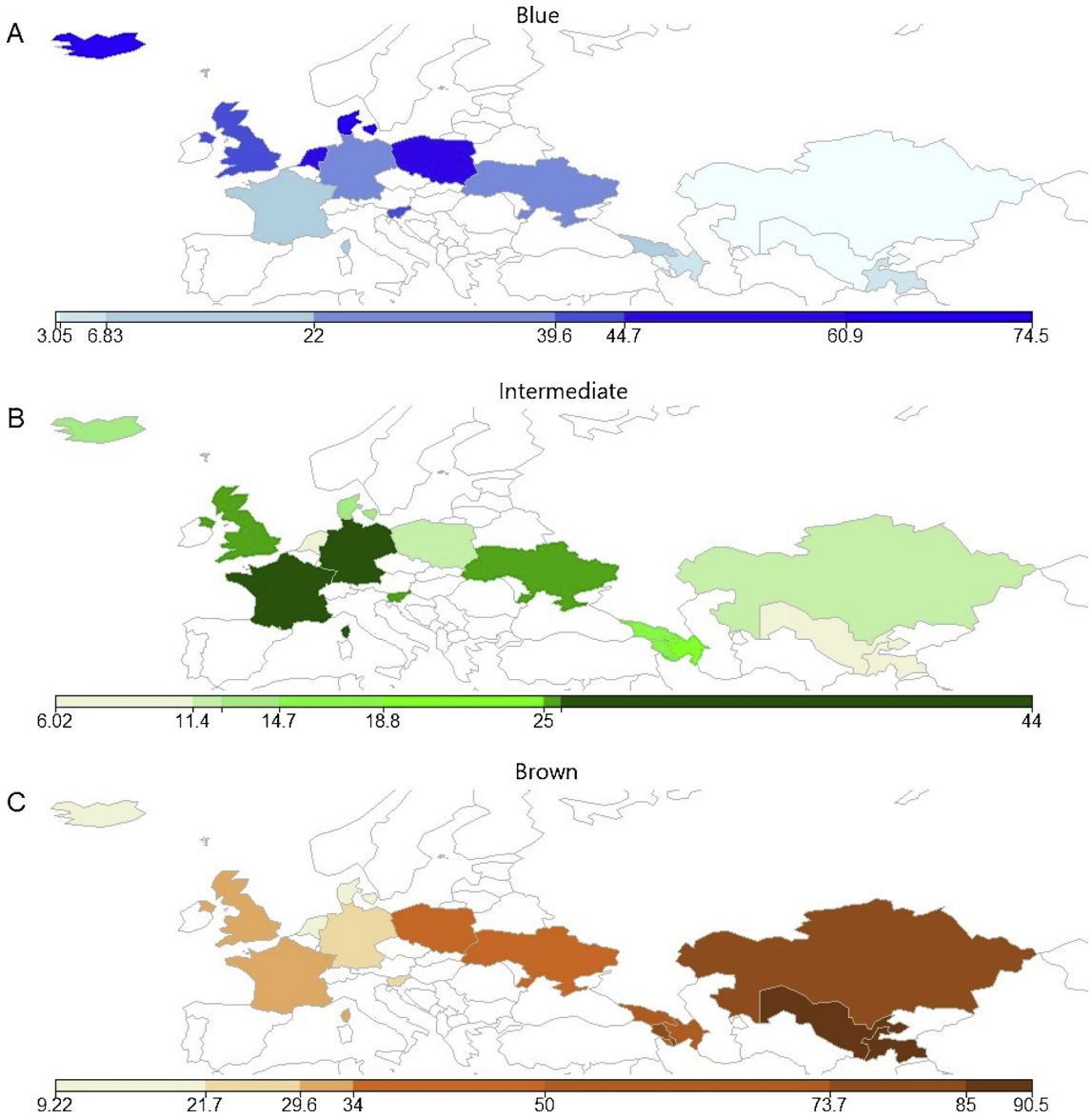


**Fig. 1.** Spatial distribution of categorical eye color prevalence across Europe and Central Asia. (A) 'Blue'; (B) 'Intermediate'; (C) 'Brown'. Numbers are given in percentages. Countries without available data are shown blank. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Correspondingly, 'black' and 'brown' hair color were amalgamated into a single category 'brown', whereas 'dark blond',' fair' and 'light brown' were merged with 'blond'. Shades such as 'auburn' or 'reddish' were already referred by a number of studies included, as one merged category with red hair. Separations such as 'light blue', 'dark blue' or 'grey' were aggregated into 'blue'.

### 2.2. Literature search and criteria for inclusion

We performed extensive literature searches (see Table S1 for a list of used terms) through PubMed (www.ncbi.nlm.nih.gov/pubmed) as well as through Google (www.google.com), and subsequently followed up references from publications obtained from these searches. Results fell into two distinct classes, namely comparatively recent human genetic studies and comparatively aged anthropological studies (see below). In order to assure reliable and population-representative data, we applied the following criteria to any source under consideration:

- *Population-based sampling*: We included only those studies where data sets were sampled in a population-based study or without respect to a specific pigmentation trait. In this way, we tried to avoid biases in the prevalence estimation that, for example, may occur with oversampling of individuals belonging to a certain category in retrospective association studies.
- *Sample size*: In order to protect against sporadic reports and strong chance deviations of the prevalence estimates from the population mean, we required each included study to have a minimum size. In particular, we chose a minimum size of 60 for eye color and of 130 for hair color. Uncertainty of the derived prevalence estimates was assessed by 95% confidence intervals. Studies whose total sample size failed the thresholds stated above were excluded.
- *Plausibility*: Studies had to be consistent in their presentation to be considered trustworthy. We encountered numerous studies where pigmentation category proportions did not sum up to unity (with totals both substantially below and above 100%) or inconsistent naming of categories. We therefore required studies to actually yield pigmentation category totals of 100% (or close) for consistently named categories in order to be included; otherwise they were

**Table 2**
Hair color prevalence across Europe.

| Country | 'Brown' | 'Blond' | 'Red' | References |
|---|---|---|---|---|
| Denmark | 29.00 (26.07-32.14) | 67.30 (64.07-70.33) | 3.60 (2.47-5.03) | [43,50,53] |
| | 11.10 (6.44-17.3) | 83.40 (76.38-89.10) | 5.50 (2.41-10.58) | |
| | 12.60 (8.14-18.61) | 79.30 (73.00-85.49) | 7.50 (4.06-12.51) | |
| | 9.50 (5.68-15.36) | 76.80 (71.59-84.66) | 11.30 (7.12-17.50) | |
| | 19.80 (14.34-26.70) | 76.10 (69.59-82.63) | 3.40 (1.27-7.31) | |
| | 49.73 (44.61-54.87) | 45.81 (40.73-50.95) | 4.45 (2.61-7.03) | |
| *average* | 30.66 | 64.00 | 4.99 | |
| Great Britain | 64.65 (55.91-72.75) | 20.30 (13.83-28.14) | 15.03 (9.43-22.26) | [51,53,54] |
| | 38.3 (36.10-40.75) | 56.40 (54.04-58.78) | 5.20 (4.17-6.33) | |
| | 47.5 (45.64-49.34) | 47.40 (45.54-49.24) | 5.10 (4.34-5.99) | |
| *average* | 50.15 | 41.36 | 8.44 | |
| Estonia | 43.00 | 56.00 | 1.00 | [65] |
| France | 84.00 | 12.00 | 4.00 | [65] |
| Germany | 31.40 (31.34-31.41) | 68.40 (68.36-68.43) | 0.20 (0.23-0.23) | [9] |
| Iceland | 26.20 (25.12-28.37) | 64.70 (64.28-67.75) | 7.10 (6.33-8.25) | [12] |
| | 26.00 (24.79-28.18) | 65.55 (64.87-68.48) | 6.75 (5.92-7.87) | |
| Netherlands | 25.90 (23.44-28.45) | 71.45 (68.84-74.00) | 2.60 (1.81-3.70) | [12] |

Point estimates and, in parentheses, 95% confidence intervals for the trait prevalence are given in percentage. If more than one study was available per country, the average across those studies is given.

excluded.

#### 2.2.1. Recent human genetic studies

A number of human genetic studies have been published in recent years. Perhaps not surprising given the higher levels of variety in Europe compared to other continents, most of these publications used European samples or those of European descent. These studies include genome-wide association studies or smaller studies on eye color [12,19,43,50–55] and on hair color [12,43,50,51,53,54,56]. Notably, some eye color data outside Europe were available for Central Asia for populations along the "Silk Road", namely from Armenia, Azerbaijan, Tajikistan, Kazakhstan, Georgia, Ukraine (Crimea) and Uzbekistan [19] (Supplementary Table S3).

Despite this apparent wealth of studies, at least on Europe, we had to exclude a number of them [57–64] for the potentially biased collection of their data, for comprising too small of a sample size, for lack of information on the data sources or for being not population-representative. In total, twelve studies met our quality criteria for population representativeness and were used for the subsequent analysis.

#### 2.2.2. Anthropological studies

Externally visible pigmentation traits have been subject to anthropological studies for over a century. It should be noted, however, that the interest was not in eye and hair color, or cranial and morphological measurements and other features in this respect, *per se*, but as means to define postulated basic human types, or "races", which would then be used to explain human appearance as a potential mixture of such types to varying degrees. While this originally scientific working hypothesis has long been dropped, and rightly so, and despite later or even contemporary distortions and misuses of this concept, best known from the race ideologies of the 19$^{th}$ and 20$^{th}$ century, those early publications may potentially inform on the prevalence of pigmentation traits in a number of different populations. We found a few studies that promised to serve this purpose, namely studies by Virchow [9], Galton [8] and Coon [65]. The impressive (and apparently largely forgotten) anthropological survey by the famous German physician Rudolf Virchow from the second half of the 19$^{th}$ century [9] represents by far the largest study on pigmentation traits ever conducted. An enormous sample of 6,758,827 children aged between 6 and 14 years old from different schools across all German provinces was collected, with schoolteachers assessing their pigmentation. This study also gave separate information on the German Jewish population, likely to be representative of the Ashkenazim, and provided evidence for less than one third of Germans being fair skinned with blond hair and blue eyes, for significant numbers of Prussians showing dark pigmentation and for a large proportion of German Jews being blond. Notably, Virchow arrived at the conclusion that there were no specific patterns in the pigmentation of any "race" under study. Within the framework of our analyses, we considered Virchow's data as being representative for today's Germany pigmentation distribution. However, some caution is required regarding the representativeness of the hair color prevalence values given the young age of the children in the survey and age-related hair color darkening in adulthood [1,66–71], rendering the estimate for blond hair an upper limit. Another, apparently useful, source was a book by Carleton S. Coon on "The Races of Europe" [65] and their physical anthropology. This book focused on the origin and the admixtures of purported human types, such as Upper Paleolithic, Caucasoid and Mediterraneans, and also aimed at compiling and synthesizing information from a vast number of different sources on features such as eye, hair and skin color, beard rufosity in males, cranial and nasal indexes and height, and more, covering an area that stretched from Northern Europe through Middle East, Central and West Europe, Mediterranean countries to North Africa and Western Asia. While at first apparently representing a comprehensive and reliable source, the variety of cited literature led to inconsistent, incomplete and frequently missing data. We finally considered only information on eye and hair color from France and on hair color from Estonia trustworthy and included it in our study. An early article by Francis Galton [8] provided some data on eye color in England, but they were not included due to unclear population representativeness.

#### 2.2.3. Web sites

We found a surprisingly large number of web sites, during the period from November through December 2017 that would apparently provide trait prevalence values for many populations and even interpolated colored geographic maps (see Table S2 for a list of such web sites). However, none of these sites provided information on the source of the presented data. We therefore excluded these web sites from further consideration based on their undocumented and therefore highly questionable data basis. The substantial number of web sites may reflect a strong interest of the general public in these traits, which thereby would be promising means to attract traffic to these sites.

### 2.3. Final data sets

Based on our selection criteria described above, we compiled two data sets from sources considered trustworthy, namely one for categorical eye color and one for categorical hair color. The eye color set

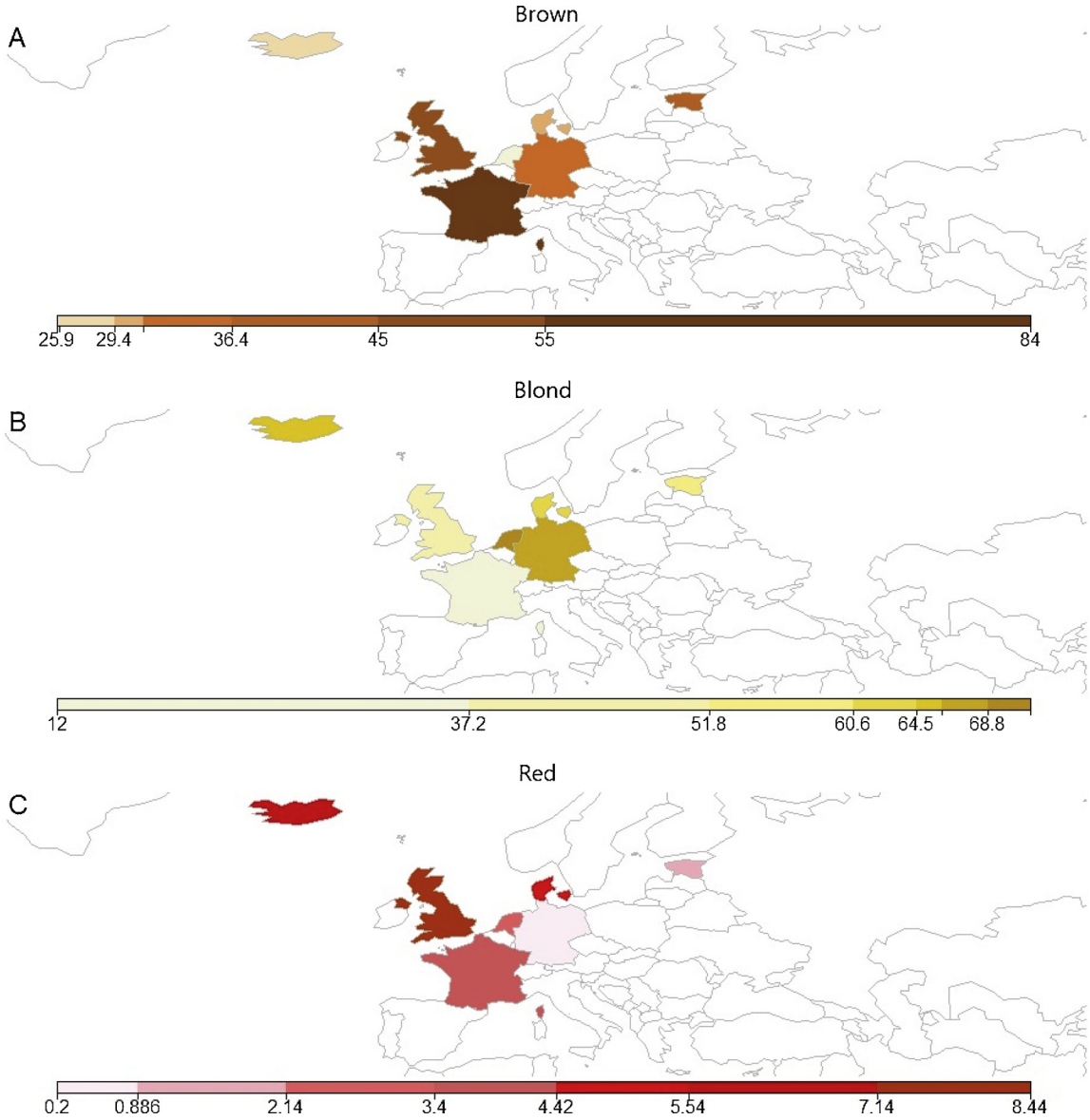


**Fig. 2.** Spatial distribution of categorical hair color prevalence across Europe. (A) 'Brown'; (B) 'Blond'; (C) 'Red'. Numbers are given in percentages. Countries without available data are shown blank. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

contained data from 16 European countries as well as from Central Asian countries along the "Silk Road" [9,12,19,43,50–55,65,72] (see Table S3 for the data summary). The hair color set was restricted to seven European countries, namely Denmark [43,50,53], Estonia [65], Great Britain [51,53,54], France [65], Germany [9] (see Table S4 for the overall data summary), Iceland [12] and The Netherlands [12]. If more than one study was available for a particular country, such as Denmark, we used the average prevalence for each category.

## 3. Statistical analysis

All analyses were performed in R version 3.4.3 [73]. Association between eye and hair color was assessed by Cramer's V on the 3 × 3 table of eye and hair color categories, while independence was tested by use of a chi-squared test where a P-value < 0.05 was deemed significant, as implemented in package lsr [74]. Uncertainty of proportion estimates for each category was assessed by binomial 95% confidence intervals, except for hair color in France and Estonia where information on the total sample size was lacking. Maps for visualization were created separately for eye and hair color and for each category, using packages vcd [75] and rworldmap [76]. Cut-offs were defined by use of quantiles. Spatial interpolation was performed to obtain trait prevalence estimates for geographic regions, or countries, for which no data were available. We employed inverse distance weighted (IDW) interpolation which estimates the value of an unmeasured location by using the values of the neighboring measured data points. Each of the values has a weight which is proportional to the inverse of the distance raised to a power function p. P can be any positive real number although in our case the default value of 2 was used. Since we do not have any directional influences in our data, the Shepard method was used which assumes equally influenced points in all directions. The general inverse distance weighted (IDW) interpolating function for finding an interpolated value $u$ at a given point $x$ based on the given points $u_i = u(x_i)$ for $i = 1,2, \ldots, N$ is of the form:

$$u(x) = \begin{cases} \frac{\sum_{i=1}^{N} w_i(x) u_i}{\sum_{i=1}^{N} w_i(x)} & : \quad if\ d(x, x_i) \neq 0\ for\ all\ i \\ u_i & : \quad if\ d(x, x_i) = 0\ for\ some\ i \end{cases}$$

where

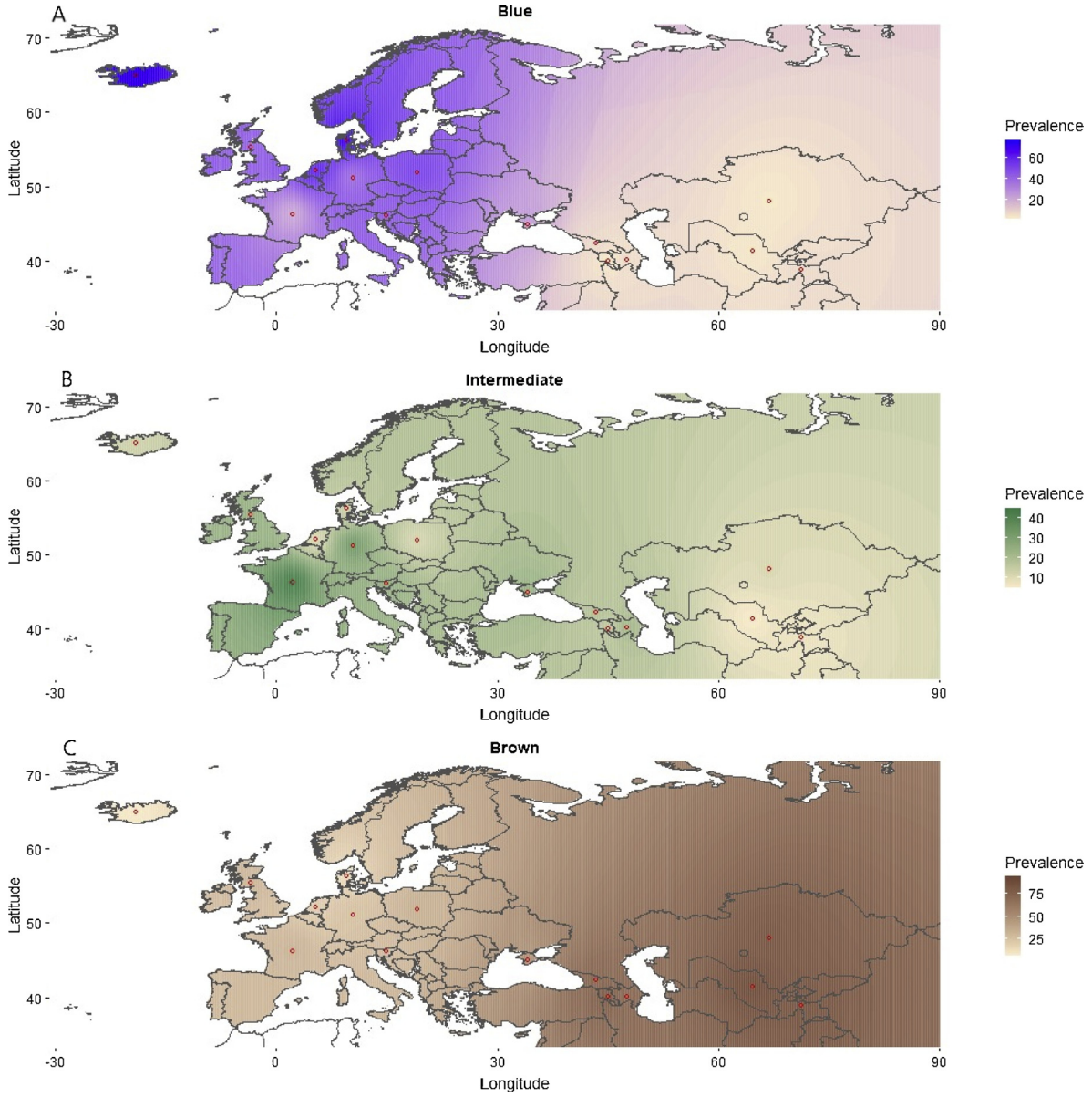


**Fig. 3.** Spatial interpolation of categorical eye color prevalence. (A) 'Blue'; (B) 'Intermediate'; (C) 'Brown'. Numbers are given in percentages. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

$$w_i(x) = \frac{1}{d(x, x_i)^p}$$

is the inverse distance weighting function as defined by Shepard [77]. Variable $x$ represents an arbitrary interpolated point, $x_i$ a known interpolating point while $d$ is the distance between the known point $x_i$ and the unknown point $x$. $N$ denotes the number of the known data points. Due to the limited amount of data available for mapping, no specified number of neighbors was considered. The interpolation was performed by use of the gstat package [78,79], while ggplot2 [80] was used for creating graphs.

## 4. Results

### 4.1. Eye color prevalence

The prevalence estimates for 'blue', 'brown' and 'intermediate' eye color differed considerably between the countries for which reliable data were available, ranging from 3.05 to 90.51 (Table 1). The highest prevalence of any of the eye color traits was observed in Uzbekistan (> 90% for 'brown'), while Iceland followed closely with a prevalence of 74.52% for 'blue' eyes. 'Intermediate' color occurred less frequently compared to the other two categories and reached its maximum of 44% in France (Table 1). Prevalence of 'blue' eyes was smallest in Armenia (3.05%) among all countries with available data, whereas Iceland comprised the smallest prevalence (9.22%) of 'brown' eyes. In our study set, 'intermediate' eye color showed the lowest prevalence in Uzbekistan (6.02%). Overall, blue eye color dominated in Northern Europe, whereas brown eye color was highly prevalent in Central Asia (Fig. 1). Interestingly, France and Germany appeared to present the largest proportion of carriers of intermediately colored eyes among all countries with available data.

### 4.2. Hair color prevalence

Despite the limited amount of scientific data available, we were able to compile some trustworthy outcomes regarding the hair color prevalence for a small number of countries, mostly for the Northwestern part of Europe. Due to this fact, the results below present a preliminary

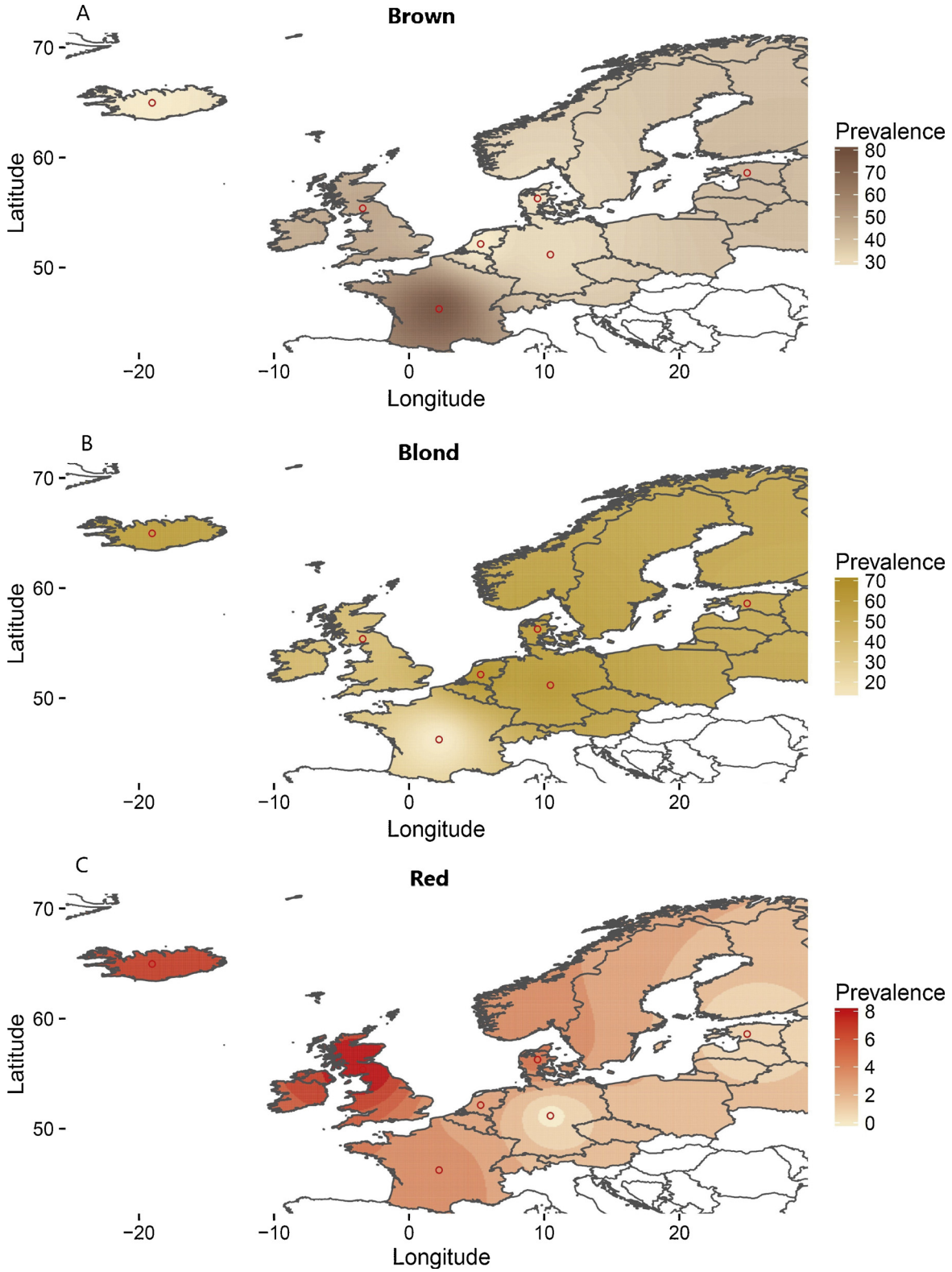


**Fig. 4.** Spatial interpolation of categorical hair color prevalence. (A) 'Brown'; (B) 'Blond'; (C) 'Red'. Numbers are given in percentages. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

overview of the hair color hair frequency that should be considered with caution. Prevalence for all three color categories ('blond', 'brown' and 'red') ranged from 0.2 to 84% (Table 2). The highest prevalence was observed for 'brown' hair in France, simultaneously the smallest frequency of 'blond' hair (12%). The Netherlands showed the largest share of blond hair (71.45%) and the smallest prevalence of brown-haired people (25.9%). Red hair color prevalence was comparatively small throughout, being highest in Great Britain (8.44%) and quite low in Germany (0.2%; Table 2). Overall, we noticed that blond hair dominated in Germany and the Netherlands, while the red hair trait reached its most frequent occurrence in Iceland and Great Britain (Fig. 2). Great Britain also appeared to have, together with France, a

**Table 3**
Joint occurrence of eye and hair color in Germany.

| | | Hair color 'Blond' | 'Brown' | 'Red' | Total |
|---|---|---|---|---|---|
| **Eye color** | **'Blue'** | 2,149,027 | 514,628 | 6657 | 2,670,312 |
| | **'Intermediate'** | 1,582,339 | 650,468 | 5066 | 2,237,873 |
| | **'Brown'** | 878,488 | 949,822 | 3864 | 1,832,174 |
| | **Total** | 4,609,854 | 2,114,918 | 15,587 | 6,740,359 |

Data were compiled from [9]. Numbers are given in counts.

**Table 4**
Hair color probability conditional on eye color category in Germany.

| | | Hair color 'Blond' | 'Brown' | 'Red' | Total |
|---|---|---|---|---|---|
| **Eye color** | **'Blue'** | 80.4 | 19.2 | 0.24 | 99.84 |
| | **'Intermediate'** | 70.7 | 29 | 0.22 | 99.92 |
| | **'Brown'** | 47.9 | 51.8 | 0.21 | 99.91 |

Data were compiled from [9]. Numbers are given in percentage.

**Table 5**
Eye color probability conditional on hair color category in Germany.

| | | Eye color 'Blue' | 'Intermediate' | 'Brown' | Total |
|---|---|---|---|---|---|
| **Hair color** | **'Blond'** | 46.6 | 34.3 | 19.05 | 99.95 |
| | **'Brown'** | 24.3 | 30.7 | 44.9 | 99.9 |
| | **'Red'** | 42.7 | 32.5 | 24.7 | 99.9 |

Data were compiled from [9]. Numbers are given in percentage.

high percentage of brown haired people. Denmark and Estonia had higher proportion of blond hair carriers compared to the other two hair color categories.

### 4.3. Prevalence interpolation

Interpolated maps, based on already collected information for the specific set of countries described above, may assist in the estimation of the eye and hair color prevalence for countries where no measurements were available. As one may notice, the blue eye color is predicted to dominate in Northern Europe compared to the Southeastern countries where the percentage resembles less than 10% (Fig. 3). The intermediate coloration was interpolated to be of higher prevalence in Western Europe and to spread almost uniformly across the Balkan countries. Carriers of brown eyes were interpolated with high frequency in the Eastern countries in contrast to Western Europe where we observed the smallest prevalence values. In Northern Europe, brown hair pigmentation occurs at minimum prevalence in contrast to blond hair which dominates there (Fig. 4). Red hair prevalence is predicted to be higher in Western compared to Eastern Europe.

### 4.4. Binomial confidence intervals

We also calculated, separately for each category, the 95% Binomial confidence intervals in order to assess the uncertainty of our prevalence estimates for each trait (Tables 1 and 2). It should be noted, however, that for countries with more than one study available, such as Denmark, confidence intervals were not always overlapping between studies.

### 4.5. Correlation between eye and hair color

Correlated traits may facilitate an improved prediction by borrowing strength from an already observed trait, although this is subject to ongoing investigation (not shown). We therefore investigated the degree of association between eye and hair color in the large German data set compiled by Virchow [9] (see Table S4 for an excerpt of the main results table). Based on the joint occurrence of eye and hair color categories in these data (Table 3), these pigmentation traits showed a modest association (Cramer's V = 0.20) that was nevertheless highly significantly different from zero ($p = 2.2 \times 10^{-16}$). We also estimated conditional probabilities for the presence of particular color categories in one trait given the presence of a category in the other trait, namely the probability of hair color given the eye color (Table 4) and eye color given the hair color (Table 5). Notably, as seen in Table 4, the 'blond' hair trait has a high conditional probability for 'blue' eye color (80.4%) but also for 'intermediate' eyes (70.7%). On the other hand, 'blond' and 'brown' hair colors are almost equally likely (47.9% *vs* 51.8%) given the presence of 'brown' eyes. The 'red' hair trait did not show a substantial conditional probability for any of the eye colors, which is not surprising giving the comparatively low prevalence of this trait in the population. More specifically, the conditional probability ranged between 0.21% and 0.24% but no significant difference occurred among the three eye categories. Given hair color, we observed a high conditional probability of 'blue' eyes with 'blond' hair, reaching the level of 46.6% (Table 5). This is followed by the 'intermediate' trait and lastly is the 'brown' eyes, which have only the 19% of our sample.

## 5. Discussion

In the present study, we aimed at assessing the spatial distribution of eye and hair pigmentation, separately for different countries. The basic motivation for this approach was the compilation of prior knowledge on this distribution for subsequent use in potentially enhancing the prediction accuracy of those two traits. To this end, we conducted a detailed literature review in order to collect information on the geographic prevalence distribution for eye and hair color. However, the lack of available data for many populations, especially outside of Europe, and the limited amount of reliable data were two significant obstacles to our analysis. Despite the fact that the distribution of human pigmentation has been a topic of major interest for decades, only few studies could be considered to provide trustworthy information concerning the origin of their data used and the representativeness of the sample. The majority of these studies were focused on the pigmentation of European populations, which immediately limited the scope of our research, evidencing the need for future studies with a worldwide research focus. In this way, it will be possible to estimate small prevalence values of exceptional pigmentations in populations which do not show large variability overall. Reports on blue-eyed people in the African and Chinese populations which, despite the low prevalence of their trait, may serve as an example; those occurrences should not be neglected from pigmentation distribution studies (see Supplementary Table S5).

Data on eye and hair pigmentation were provided by a number of studies, which focused on different topics such as genetic markers responsible for pigmentation [12,19,51–54], interdependence between pigmentation and incidence of diseases [50], prevalence of the distribution of hair and eye color in specific populations [43], anthropological studies on different populations [65] and prediction of eye color [55]. Here, we concentrated on the association between eye and hair coloration and also the pigmentation prevalence across different countries, mostly inside of Europe. It should be noted, however, that the obtained estimates are based on studies with usually quite limited sample sizes, as expressed by the considerable range of the corresponding confidence intervals which at times did not even overlap for the same country.

With respect to the eye and hair color in the data set on the German population by Virchow we noticed that the highest association was obtained between blond hair and blue eyes while brown hair was associated with brown eyes. The extremely high percentage of blond-haired individuals compared to the other two categories was remarkable in this data set but may be explicable not only by the fact that Germans predominantly feature light pigmentation, but also that the

sample set included only children aged between 6 and 14 years, whose pigmentation tends to be lighter than that of adults. Due to age-related hair color change, larger proportions of adults in future studies of Germany are likely to lead to smaller prevalence estimates for this pigmentation trait. Thus, hair color prevalence values in the adult German population will likely be slightly different from the ones reported in this study.

The generally lighter pigmentation in North Europeans compared to individuals from Eastern countries was to be expected. However, there were a few surprising cases where the frequency of a trait deviated from this expectation. This includes the highest percentage of intermediate eye color in France comprising almost the half of the population (44%) and also the extremely low percentage of red hair in Germany (0.2%). Furthermore, brown hair color was observed with higher frequency in France (84%) and also in the British population (50.15%). These discrepancies are explicable in terms of the size of the population data set, the age of the individuals included or the non-standardized way that these data were collected.

Throughout our study, we interpolated the pigmentation distribution for countries where no data were available. In the resulting maps we presented the estimations only for those countries that were considered trustworthy in our limited data set, especially for hair color. For eye color, some predictive errors are also likely to occur. In Italy, higher frequency of blue eyes compared to the other two categories was predicted. We could consider these values valid at least for the Northern part of Italy since data of neighboring countries such as France and Slovenia were available and included in our analyses, but not necessarily for Italy as a whole. It is therefore important to note that conclusions from our interpolation results should be drawn with caution. Thus, this study should be considered to be of preliminary nature and the information assembled here should be considered approximate for the definition of priors. More studies on pigmentation traits with a unified color category definition and larger sample sizes on a worldwide level will be required in order to arrive at a more accurate and comprehensive picture of pigmentation trait prevalence. This would allow to expand our results and provide prevalence estimates for continents and regions not yet covered. To be used in future prediction models, priors may be obtained by suitable averaging of prevalence values across countries, regions or even continents, depending on the degree of differentiation and the required accuracy. Given Europe's large internal variability, some applications may require prior values specific to Northern and Southern Europe or the continent as a whole. For this reason, we hope that studies on the topic that have been published in languages other than English or German and that unfortunately escaped our attention could be included in our data set in the future. This is likely to be of particular importance for the completion of the spatial picture of pigmentation trait prevalence for geographic regions outside Europe. Given the importance of data variation for the framework of this study, we surmise that the computational strategy followed here and the pigmentation maps presented will provide some assistance in different scientific fields and in future forensic application related to the EVC prediction.

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## Conflict of interest

The authors declare that they have no competing interests.

## Authors' contributions

All authors read and approved the final manuscript.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fsigen.2019.01.001.

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