



Inferring patterns of folktale diffusion using genomic data

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Observable patterns of cultural variation are consistently intertwined with demic movements, cultural diffusion, and adaptation to different ecological contexts [Cavalli-Sforza and Feldman (1981) *Cultural Transmission and Evolution: A Quantitative Approach*; Boyd and Richerson (1985) *Culture and the Evolutionary Process*]. The quantitative study of gene–culture coevolution has focused in particular on the mechanisms responsible for change in frequency and attributes of cultural traits, the spread of cultural information through demic and cultural diffusion, and detecting relationships between genetic and cultural lineages. Here, we make use of worldwide whole-genome sequences [Pagani et al. (2016) *Nature* 538:238–242] to assess the impact of processes involving population movement and replacement on cultural diversity, focusing on the variability observed in folktale traditions ($n = 596$) [Uther (2004) *The Types of International Folktales: A Classification and Bibliography. Based on the System of Antti Aarne and Stith Thompson*] in Eurasia. We find that a model of cultural diffusion predicted by isolation-by-distance alone is not sufficient to explain the observed patterns, especially at small spatial scales (up to $\sim 4,000$ km). We also provide an empirical approach to infer presence and impact of ethnolinguistic barriers preventing the unbiased transmission of both genetic and cultural information. After correcting for the effect of ethnolinguistic boundaries, we show that, of the alternative models that we propose, the one entailing cultural diffusion biased by linguistic differences is the most plausible. Additionally, we identify 15 tales that are more likely to be predominantly transmitted through population movement and replacement and locate putative focal areas for a set of tales that are spread worldwide.

cultural diffusion | demic diffusion | whole-genome sequences | folktales | Eurasia

Advances in DNA sequencing have opened new ways for exploring the demographic histories of human populations and the relationship between patterns of genetic and cultural diversity around the world. Newly available genome-wide evidence enables us to go beyond the use of linguistic relationship as a measure of common ancestry (1–3) and offers unprecedented support for studying the mechanisms underlying the transmission of cultural information over space and time (4–11) as well as the coevolution of genetic and cultural traits (12–18) across populations.

A key question for research in this area concerns the extent to which patterns of cultural diversity documented in the archaeological and ethnographic records have been generated by demic processes (i.e., the movement of people carrying their own cultural traditions with them) or cultural diffusion (i.e., the transfer of information without or with limited population movement/replacement) (6, 19, 20). Before tackling this question, however, it is critical to note that demic processes and cultural

diffusion are not mutually exclusive conditions but rather, are opposite extremes of a continuous gradient, with intermediate and composite positions that more accurately represent empirical reality.

A broadly adopted null model of cultural diffusion draws on the expectation that selectively neutral variants would form geographic clines produced over time by isolation-by-distance (IBD) processes (21). Under an IBD model, individuals or groups that are spatially closer to each other are expected to be more similar than individuals or groups that are located farther apart. A positive correlation between cultural dissimilarity and geographic distance between samples is, therefore, used to infer processes of cultural transmission of nonadaptive information without population replacement (8, 17). However, observed genetic distance is the composite result of serial founder events, long-term IBD, and subsequent migratory events, which imply recent movement and resettling of people (22). A higher correlation between genetic distance and cultural dissimilarity than between culture and geography has, therefore, been proposed as a way to

Significance

This paper presents unprecedented evidence on the transmission mechanism underlying the spread of a broad cross-cultural assemblage of folktales in Eurasia and Africa. State-of-the-art genomic evidence is used to directly assess the relevance of demic diffusion processes, in particular on the distribution of Old World folktales at intermediate geographic scales, and identify individual stories that are more likely to be transmitted through population movement and replacement. The results provide an empirical solution to operate with linguistic barriers and highlight the impossibility of disentangling genetic from geographic relationships at a cross-continental scale, warning against the direct use of extant genetic variability to infer processes of long-range cultural transmission.

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Data deposition: Genetic data used to run SpaceMix are available at www.ebc.ee/free_data. R scripts and related commands used to generate all of the results described in the paper are available at doi.org/10.5281/zenodo.821360.

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Europe. Ross et al. (23) have shown that, at population level, geographic distribution explains more variability than ethnolinguistic grouping. At this scale, when controlling for the effect of geography, linguistic boundaries do not show any residual significant relationship with folktale variant distribution, suggesting a possible temporal mismatch between folktale and linguistic traditions. However, when individual folktales are considered, ethnolinguistic identity is a significant predictor. This fact suggests that demes belonging to different ethnolinguistic affiliations may undergo higher costs for the transmission of individual folktales, even when they are closer in space. The simultaneous effect of shared linguistic ancestry and spatial proximity was also documented on the distributions of folktales recorded among Arctic hunter-gatherers (26).

Overview of This Study

In this study, we focus on 596 folktales comprising “animal tales” and “tales of magic” (27) typed as present (one) or absent (zero) in 33 populations (dataset MAIN), for which whole-genome sequences are available and exhibiting presence of at least five folktales (Fig. 1B, *SI Appendix*, and *Dataset S1 Tables S1-2.1, S1-2.2, S1-2.3, and S1-2.4*). Following previous examples (8), we test for deviations from a null model of pure cultural diffusion without population replacement (IBD), in which geographic distance alone is the best predictor of the decreasing number of shared folktales between pairs of populations. We measure and compare the fit of a number of alternative models comprising (i) a clinal model, in which populations belonging to different ethnolinguistic groups are less likely to share folktales as predicted by IBD (cultural diffusion with linguistic barriers); (ii) population movement and admixture between demes (demic process) as a substantial additional driver of folktale transmission; and (iii) a demic process constrained by linguistic barriers.

We test our hypothesis first by visualizing possible mismatches between actual geographic location of each population and the location inferred by applying explicit models accounting for genetic and cultural admixture (population movement with replacement) (28). We quantify the impact of linguistic barriers on both genetic and folktale variability using analysis of molecular variance (AMOVA) (29). We further investigate this by looking for the set of linguistic barrier parameters (intensity and geographic buffer) that maximizes the fit between genetic distance and geographic distance on the one hand and folktale distance and geographic distance on the other hand. We use this parameter combination to generate alternative models, with fitness that is formally assessed at both a global scale and over cumulative geographic distance. Following the assumptions of previous works (8), we develop a method to identify those folktales that—in the whole corpus—may be more likely to have been transmitted through population movement and replacement, supporting the idea that individual tales may have undergone different processes. To provide a starting point for this additional analysis on the diffusion of individual or smaller packages of tales, we infer potential focal areas—intended as a putative proxy for center of origin—of the most popular tales in the dataset.

Results

Effects of Ethnolinguistic Boundaries. We use AMOVA (29) to formally assess the impact of ethnolinguistic boundaries on both genetic and folktale variability, focusing only on Eurasian populations (dataset Eurasia; $n = 30$) to control for the effect of the Out of Africa expansion on genetic distance (*SI Appendix* and *Dataset S1, Tables S1-3.1, S1-3.2, S1-3.3, and S1-3.4*). We assign each population to an ethnolinguistic group (*Materials and Methods, SI Appendix*, and *Dataset S1, Tables S1-4.1 and S1-4.2*). Our analysis yielded $\Phi_{ST} = 0.036$ ($P < 0.001$) for genetic distance matrix, whereas $\Phi_{ST} = 0.1$ ($P < 0.001$) for distances based on folktale distributions. These results confirm the expected differ-

ential impact of intergroup boundaries between genetic and cultural variability and are consistent with previous results obtained for population structure on the transmission of cultural traits (23, 30).

We use this evidence to further investigate the separate effects of linguistic barriers on the flow of genetic and cultural information by focusing on two parameters (i.e., intensity and geographic buffer of the cultural barrier) (details are in *Materials and Methods*). We find that the parameter combinations that resulted in the highest correlation between genetic–geographic distances (intensity = 0.1; radius = 1,500 km) and between folktale–geographic distances (intensity = 0.3; radius = 3,000 km) imply that linguistic barriers have a differential impact of these two kinds of information, and we use this parameter setting to generate two corrected distance matrices for genetics (geneticL) (*Dataset S1, Table S1-5.1*) and folktales (folktaleL) (*Dataset S1, Table S1-5.2*), respectively. By using raw and corrected distance matrices, we define alternative models as (i) biased cultural diffusion (folktaleL ~ geographic), (ii) demic diffusion (folktale ~ genetic), and (iii) biased demic diffusion (folktaleL ~ geneticL).

Assessing Models of Folktale Transmission. We set out to test for deviations from the null model of cultural diffusion caused by IBD. We explore the relationship between our genetic, folktale, and geographic distance matrices using SpaceMix (28) (*SI Appendix*). We note that, when transformed into pseudospacial coordinates, folktale distances tend to match actual geographic coordinates better than genetic distances (Fig. 1C and *SI Appendix, Fig. S1-3.1*). The role of geography and ethnolinguistic barriers is also confirmed by a NeighborNet (31) based on folktale distances, showing a broad spatial clustering and proximity/reticulation between demes belonging to the same ethnolinguistic group (*SI Appendix*).

We then assess the goodness of fit of all of the alternative models at a global scale by comparing Pearson’s product–moment correlation (32), bias-corrected distance correlation (33), and partial distance correlation (34, 35) (Tables 1 and 2; details are in *Materials and Methods* and *SI Appendix*). It is evident how, after Bonferroni correction, all alternative models accounting for ethnolinguistic boundaries perform better than the models that do not consider them. With both product–moment correlation coefficient and bias-corrected distance correlation, the best model is the one representing cultural diffusion with linguistic barriers followed by demic processes constrained by linguistic barriers. With distance correlation, however, the difference between the two models is smaller than with standard correlation coefficient. When the dependence between variables is assessed controlling for a third variable through partial distance correlation, linguistic-biased cultural diffusion remains as good a predictor of folktale variability as IBD. This phenomenon could be due

Table 1. Variable association at a global level

Model	cor	P	bcdCor	P
Folktale ~ genetic	0.20	<0.001	0.20	<0.001
Folktale ~ geographic	0.19	<0.001	0.31	<0.001
Genetic ~ geographic	0.71	<0.001	0.84	<0.001
FolktaleL ~ geneticL	0.55	<0.001	0.55	<0.001
FolktaleL ~ geographic	0.64	<0.001	0.57	<0.001
GeneticL ~ geographic	0.76	<0.001	0.83	<0.001

Comparison between null model of cultural diffusion predicted by IBD (folktale ~ geographic) and alternative models [i.e., demic diffusion (folktale ~ genetic), cultural diffusion biased by linguistic barriers (folktaleL ~ geographic), and demic diffusion biased by linguistic barriers (folktaleL ~ geneticL)]. Values refer to Pearson’s product–moment correlation (cor) and bias-corrected distance correlation (bcdCor) after Bonferroni correction.

Table 2. Partial distance correlation at a global scale

Model	pdCor	P
Folktale ~ genetic, geographic	-0.11	1.00
Folktale ~ geographic, genetic	0.26	<0.001
FolktaleL ~ geneticL, geographic	0.17	<0.001
FolktaleL ~ geographic, geneticL	0.25	<0.001

Results of partial distance correlation for null (folktale ~ geographic, genetic) and alternative models [i.e., demic diffusion (folktale ~ genetic, geographic), cultural diffusion biased by linguistic barriers (folktaleL ~ geographic, geneticL), and demic diffusion biased by linguistic barriers (folktaleL ~ geneticL, geographic)] after Bonferroni correction.

to the fact that, at a global scale, correlation between language-corrected genetic distance and geographic distance is higher (Fig. 1) and lowers the residual signal.

Significant deviations from the null model of cultural diffusion predicted by IBD are further investigated over cumulative geographic distance by comparing Pearson's correlation coefficients (Fig. 2 and *SI Appendix*, Table S1-7.1). Above 4,000 km, language-biased cultural diffusion presents with the highest fit at all bins followed by language-biased demic diffusion. Under 4,000 km, folktale distance exhibits stronger dependence from genetic distance than from geographic distance. This relationship is particularly visible under 2,000 km, where the effect of linguistic barriers is the same for genetic and cultural variability.

All results allow us to reject the null model of plain cultural diffusion predicted by IBD and suggest instead that, of all alternative models, the one involving cultural diffusion mitigated by linguistic barriers could be the most plausible one. In addition, as previously pointed out (Fig. 1), results consistently confirm that small geographic scale offers a more efficient disentanglement between possible uncoupled effects of genetic and geographic distances over cultural variables—even after correcting for potential ethnolinguistic barriers.

Uniform Body of Knowledge or Individual Units? Our results show that, when considering the folktales contained in our dataset as a uniform corpus, the null model dictated by IBD could be rejected. Previous results (23), however, have shown that individual tales or smaller groups of tales may be transmitted across populations as partially independent evolutionary units. If a given cultural trait is not transmitted through population movement and replacement, populations that share it should not exhibit significantly lower genetic distance than populations that do not exhibit it (8). To single out folktales that markedly contradict such null hypothesis, we compare the distribution of pairwise genetic distances corrected for ethnolinguistic boundaries among populations sharing a given tale against distances of the remaining pairs of populations using the Mann–Whitney–Wilcoxon test. We focus on 308 folktales that are present in at least five populations and run two separate tests, the first considering all pairs of populations (*Dataset S1*, Table S1-6.1) and a second considering only those within a conservative geographic range of 6,000 km (Fig. 1*A* and *Dataset S1*, Table S1-6.2). After Bonferroni correction, 15 of 308 analyzed folktales (4.9%) (*Dataset S1*, Tables S1-7.1 and S1-7.2) present with significantly lower than expected pairwise genetic distance, hence allowing us to reject our null hypothesis and suggesting that these tales may indeed have spread during events of demic diffusion biased by ethnolinguistic barriers.

Folktale Dispersal and Focal Areas. For a subset of the analyzed folktales, we identify focal areas, representing potential areas of origin and defined as locations that maximize the decay of a given folktale abundance over geographic distance measured with Pearson's correlation coefficient (*Dataset S1*, Table S1-8.1).

Focal areas were generated for the 19 most widespread folktales, which follow four main trends (*SI Appendix*). Some of these tales possibly started to be diffused mostly via cultural transmission from Eastern Europe, with subsequent radial diffusion across Eurasia and Africa [such as Aarne Thompson Uther catalog 155 (ATU155): “The Ungrateful Snake Returned to Captivity” in *SI Appendix*, Fig. S1-8-I 1 or ATU313: “The Magic Flight” in Fig. 3], whereas others probably started their journey from Caucasus (*SI Appendix*, Fig. S1-8-I 6–8). Examples of the latter are ATU400: “The Man on a Quest for His Lost Wife,” ATU480: “The Kind and Unkind Girls,” ATU531: “The Clever Horse,” and ATU560: “The Magic Ring.” Some narrative plots might have originated in northern Asia—such as the famous “Thumbling” (Tom Thumb) (*SI Appendix*, Fig. S1-8-I 18)—whereas a last group could have spread from Africa (*SI Appendix*, Fig. S1-8-I 17), such as in the case of ATU670: “The Man Who Understands Animal Language.”

Discussion

Using Genetic Evidence to Infer Processes of Cultural Transmission.

Our results resonate with broader questions in cultural evolutionary studies, particularly those concerning the mechanisms of cultural transmission over time and space. They show that the use of newly generated, whole-genome sequences offers a unique opportunity for an unbiased assessment of patterns of cultural variation in the ethnographic and archaeological records. Genetic variability has been already interpreted in the past as a direct proxy of the movement of human groups over time and space, and as such, it has been used as a potential marker of demic mechanisms (8, 17).

We show the effect of ethnolinguistic barriers on both genetic and cultural population structure. By introducing an empirical approach, we find that ethnolinguistic identity has a potentially independent and differential impact on genetic and cultural information. More specifically, our results suggest that linguistic

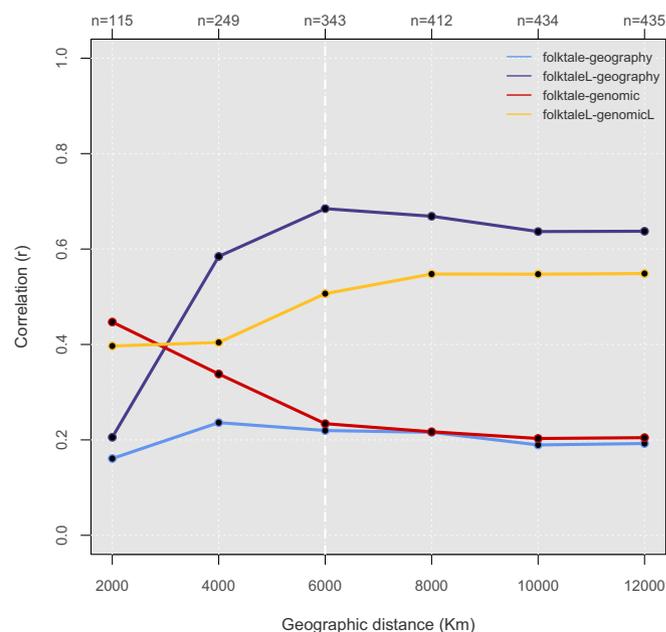


Fig. 2. Comparison of the null model of cultural diffusion dictated by IBD (folktale ~ geographic; light blue) against all alternative models: demic diffusion (folktale ~ genetic; red), language-biased cultural diffusion (folktaleL ~ geographic; purple), and language-biased demic diffusion (folktaleL ~ geneticL; yellow) over cumulative geographic distance. Product-moment correlation coefficients are calculated at each geographic bin (size = 2,000 km), with original distance matrices up to 12,000 km.

of (d_G, f_G) and (d_F, f_F) those that maximized the above-mentioned correlations. Notably, $f_G = 0$ or $f_F = 0$ (i.e., absence of linguistic barriers) had an equal chance of being picked up as the best values for our parameters. We instead reported (1,500, 0.1) and (3,000, 0.3) as best pairs of genetic and folktale parameters, respectively. To obtain unbiased genetic ($Dgen'$) and folktale ($Dfolk'$) distances, we, therefore, corrected for the effect of linguistic barriers, so that, for populations (i, j), $Dgen'_{ij} = Dgen_{ij} \times (1 - f_G)$ if $d_{ij} \leq d_G$ and $Dfolk'_{ij} = Dfolk_{ij} \times (1 - f_F)$ if $d_{ij} \leq d_F$.

Data Availability and Codes. R scripts and related commands used to generate all of the results described in the paper are available at doi.org/10.5281/zenodo.821360.

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