Sequence alignment of folk song melodies reveals cross-cultural regularities of musical evolution

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Highlights

- Melodic evolution follows regular patterns across Japanese and English folk songs
- Musical notes with stronger rhythmic functions are less likely to change
- Note insertions/deletions (“indels”) are more common than substitutions
- Substitutions tend to occur between neighboring notes

In Brief

Folk song melodies evolve via descent with modification analogous to genetic evolution. Savage et al. show predictable regularities in the way music changes, with mutations more likely when they have a smaller impact on a song’s melody. These trends are consistent across a large cross-cultural sample of Japanese and English folk songs.

SUMMARY

Culture evolves,^{1–5} but the existence of cross-culturally general regularities of cultural evolution is debated.^{6–8} As a diverse but universal cultural phenomenon, music provides a novel domain to test for the existence of such regularities.^{9–12} Folk song melodies can be thought of as culturally transmitted sequences of notes that change over time under the influence of cognitive and acoustic/physical constraints.^{9,11,13–15} Modeling melodies as evolving sequences constructed from an “alphabet” of 12 scale degrees¹⁶ allows us to quantitatively test for the presence of cross-cultural regularities using a sample of 10,062 melodies from musically

divergent Japanese and English (British/American) folk song traditions.^{17,18} Our analysis identifies 328 pairs of highly related melodies, finding that note changes are more likely when they have smaller impacts on a song's melody. Specifically: 1) notes with stronger rhythmic functions are less likely to change, and 2) note substitutions are most likely between neighboring notes. We also find that note insertions/deletions (“indels”) are more common than note substitutions, unlike genetic evolution where the reverse is true. Our results are consistent across English and Japanese samples despite major differences in their scales and tonal systems. These findings demonstrate that even a creative art form such as music is subject to evolutionary constraints analogous to those governing the evolution of genes, languages, and other domains of culture.

Keywords: cultural evolution, cross-cultural, music, sequence alignment

RESULTS

Music is a universal feature of all known human societies, yet is performed in extraordinarily diverse ways both within and between cultures.^{9,10,19–21} Some have proposed that universal cultural evolutionary regularities shape cross-cultural musical diversity,^{11,14,19,22,23} analogous to evolutionary processes that underlie genetic variation.^{1,24–28} However, attempts to test such proposals quantitatively have focused almost exclusively on Western music.^{29–37} Whether such regularities are specific to Western music or more general features of human music remain unknown.

Previous analyses have also focused on population-level macro-scale evolution. For example, analyses of Western popular and classical music have demonstrated changes over time in the overall frequency of certain types of musical intervals^{30,34}, harmonies³⁶, or lyrics³¹, but do not address the micro-scale processes by which individual musical works change as they are transmitted between individuals. Such micro-level processes of oral transmission likely played important roles through most of our evolutionary history before the advent of musical notation and audio recording technology.³⁸ Folk song melodies are amenable to micro-evolutionary analysis in cross-culturally comparable ways¹¹, allowing us to study real micro-level processes of cultural change and how these are shaped by cognitive or physical processes. This is important not only for explaining musical diversity but also as a case study for understanding cultural evolution in other domains.

By representing melodies as sequences constructed from an “alphabet” using the 12 degrees of the chromatic scale, melodies can be aligned to calculate degrees of similarity and rates of substitutions, insertions, and deletions at different sequence positions by adapting automated sequence alignment algorithms originally developed by molecular geneticists (Fig. 1).^{16,39} We have developed and validated this method in case studies using dozens of folk song melodies from English, Japanese, and other traditions.^{16,40,41} We now apply this method to two large samples of folk songs sung in English (British/American; $n=4,125$) and Japanese ($n=5,957$; Fig. 2). We manually digitized these 10,062 melodies from printed staff notation produced during the mid-20th century representing many decades of work by large teams of Japanese and British/American musicologists (see Methods).

In molecular evolution, substitution rates vary due to chemical processes involved in DNA replication (e.g., transitions are chemically more likely than transversions) and selective constraints (e.g., purifying selection removing deleterious mutations).⁴² We can draw analogies between melodic and molecular evolution to predict likely changes, while still recognizing that the specific mechanisms of musical change will be different.¹¹ In particular, neutral, or nearly neutral genetic mutations are more likely to be retained than those subject to purifying selection.^{43,44} Similarly, we hypothesized that musical “mutations” (note changes) that have a smaller impact on the melody are more likely to occur and/or be retained than those that have a larger impact. Such changes should be more likely to occur due to cognitive and motor constraints on singing production, and/or because they are less likely to be noticed and corrected/selected against by the performer/audience.^{11,15,45–48} We made the following two predictions regarding specific regularities of melodic evolution:

1) **Rhythmic function:** Some notes are more important than others in conveying the overall tune and lyrics. We predicted that notes with stronger rhythmic functions (e.g., final notes; rhythmically stressed notes) should be more stable than functionally less important ones (e.g., brief ornamental notes that are added to a main sequence of notes; unstressed notes). Changes in these positions could interfere with the sense of melodic closure by failing to end on the tonic (the most stable note of the scale), or by interfering with the meaning of the lyrics (e.g., by deleting stressed notes carrying important syllables).^{14,46,49} For example, only one of the five changes shown in Fig. 1 - the first syllable of “Scarborough” - occurs at functionally stronger rhythmic downbeats or final positions (cf. Methods regarding controlling for different base rates of stronger and weaker positions).

2) **Substitution distance:** Substitutions between small melodic distances should be more common than between large ones, either because smaller distances require smaller physical deviations in vocal production (making them more likely to occur) or are less perceptually noticeable (increasing the probability that “mutations” will not be “corrected” by purifying selection),^{15,45,47,50} or both. For instance, singers should be more likely to substitute the note “G” with neighboring notes such as “F” or “A” (two semitones below or above), rather than substituting distant notes such as “C” (5 semitones above, or seven semitones below). In the example in Fig. 1, the first two syllables of the word “Scarborough” are sung using the notes “E^b” and “F” in the top version, while in the bottom version they are sung to the notes “D” and “E^b”, respectively. These represent small changes of 1 semitone (minor 2nd) and 2 semitones (major 2nd), respectively.

Automatic analysis identifies 328 independent pairs of highly related melodies

To assess these predictions, we first analyzed our samples of 10,062 folk songs (Fig. 2) to identify related melodic variants we could compare to examine what kinds of differences in musical notes are more common, and where these differences occur. Alignment of the millions of possible pairs of melodic sequences was performed automatically (STAR Methods). Most pairs showed less than 60% similarity (Fig. S2) reflecting the fact that many unrelated “tune families”^{51,52} are represented in these samples. Our analyses focus on highly related melodies (defined as at least 85% identical, following similar studies of protein evolution⁵³) in order to optimally balance sample size, alignment quality, and independence of samples. We identified 328 highly

related pairs containing a total of 2,604 non-matching sites (1,798 indels and 806 substitutions).

A potential drawback of this sampling approach is that focusing only on pairs of highly similar melodies limits the degree of deviation that can be expected in our subsequent analysis of substitutions and indels. Sensitivity analysis suggests that our results are not an artifact of this sampling decision (Fig. S4A, STAR Methods). In the Discussion section we describe possible challenges in generalizing our findings to more distantly related melodies or repertoires.

The English (n=242 pairs) and Japanese (n=86 pairs) subsets of these highly related melodies displayed contrasting tonal systems (Fig. 3; STAR Methods), reflecting their independent histories, and demonstrating that our approach can be applied outside of Western music traditions. Some scales (e.g., the anhemitonic pentatonic scale CDFGA) were found in both samples, but most scales were found only in one or the other sample (e.g., the 陰 “in” scale CD^bFGA^b only in Japanese songs, the major scale CDEFGAB only in English songs). We observed 23 unique English scales, 12 unique Japanese scales, and 4 scales found in both samples (Fig. 3A). Overall, most Japanese melodies used a small number of pentatonic scales (5-note scales such as CDFGA or CD^bFGA^b), while English melodies used a more diverse set of scales, with heptatonic scales predominant (i.e., 7-note scales like CDEFGAB; Fig. 3B). Consequently, the English sample displayed a more diverse spread of note substitutions than the Japanese (Fig. 3C). Despite these differences, our approach allows us to test the same general ideas about rhythmic function and substitution distance in both samples.

Musical notes with stronger rhythmic functions are less likely to change

To test the effect of rhythmic function, we estimated relative stability of stronger vs. weaker rhythmic positions by calculating the degree of similarity at stronger vs. weaker functional positions (Fig. 4A). We calculated similarities for stronger and weaker functional positions separately for each pair of highly related melodies, and this paired comparison means that each song acts as its own control.

Notes with stronger rhythmic functions are more stable than notes with weaker functions (English: paired $t = 15.2$, Cohen’s $d = 0.98$, $df = 241$, $p < .001$; Japanese: paired $t = 6.8$, $d = 0.73$, $df = 85$, $p = <.001$). In both English and Japanese samples, final notes were most stable, followed by stressed notes, unstressed notes, and ornamental notes (Fig. S3A). This reflects the fact that singers are free to add, remove, or alter ornamental embellishments and unaccented notes while minimally affecting the lyrics or overall melodic shape (e.g., deleting the extra ornamental notes after “sage” and “and” in the top melody of Fig. 1 does not change these lyrics). These results are consistent regardless of where we draw the line between “stronger” vs. “weaker” rhythmic functions (cf. STAR Methods). Fig. S4A also shows that more similar pairs of melodies do not show greater differences between stronger and weaker function, ensuring that our results are not driven by our choice to focus only on highly related pairs of melodies. Results are also consistent when controlling for tonal function, as operationalized by note frequency (Table S3).

Musical substitutions tend to occur between neighboring notes

Our preceding analysis of functional position shows *where* changes tend to occur. We now examine *how* such changes tend to happen when they occur. First, exploratory analysis found that the majority of musical changes in both English and Japanese samples tended to involve insertion/deletion of notes rather than substitution of different notes (English: 1053 indels vs. 641 substitutions; Japanese: 745 vs. 165, respectively).

Turning to our prediction that focused only on substitutions, the number of substitutions between pairs of notes was strongly negatively correlated with the distance between the two notes (English: $r_{\text{Spearman}} = -.81$, $r_{\text{Pearson}} = -.74$; Japanese: $r_{\text{Spearman}} = -.82$, $r_{\text{Pearson}} = -.72$; all $df = 9$, all $P < .01$; Fig. 4B). This general pattern interacts with the tonal relationships between notes, such that substitutions almost always occurred between notes within the same scale. For example, using the C major scale for reference, a single semi-tone change could either be between two notes in the same scale (e.g., B-C, E-F), or could lead to a note in a different scale (e.g. C to Db). Because most scales contain few or no possible 1-semitone intervals between scale degrees,⁵⁴⁻⁵⁶ 1-semitone substitutions are rarer than 2-semitone substitutions despite being a smaller substitution distance (see STAR Methods for an exploratory analysis quantifying such interactions between substitution distance and tonal relationships).

DISCUSSION

Our analyses supported our predictions of cross-cultural regularities in melodic evolution. Across divergent samples of Japanese and English folk songs, we observed the same tendencies for melodies to change at weaker functional positions and for changes to happen between neighboring scale degrees. These cross-cultural regularities coexisted and interacted with substantial cross-cultural differences. For example, the set of available note substitutions was reduced in the Japanese sample, which was dominated by 5-note (pentatonic) scales while the English sample was dominated by 7-note (heptatonic) scales. Likewise, while both samples showed a predominance of note insertion/deletions over substitutions, this tendency was substantially stronger in the Japanese sample (4.5:1) than in the English sample (1.6:1), consistent with the tradition of relatively greater freedom of ornamentation (小節 “*kobushi*” - literally, little melody) in Japanese folk song performance tradition.^{19,57} The coexistence of cross-cultural differences and regularities suggests a flexible cultural system that is nevertheless subject to various constraints that can give rise to convergent cultural evolution of similar patterns in diverse cultures.⁵⁸

Substitution distance and rhythmic function alone will not explain all aspects of musical evolution, just as similar constraints do not explain all aspects of biological evolution.⁵⁹ For example, cognitive and motor constraints on singing likely play a major role in our samples of primarily unaccompanied folk songs, but the cultural evolution of other repertoires (e.g., instrumental music, dance accompaniment) may reflect different constraints specific to the instrumentation and performance context.^{10,48} Our choice to focus on highly related folk song variants where there is strong selection for the preservation of traditional melodies excludes genres or situations where different evolutionary forces may apply. However, case studies applying this methodology to popular music copyright disputes, more distantly related folk songs, and art music genres have shown intriguing parallels, suggesting that our findings may apply more generally beyond highly related folk songs.^{41,60,61}

Our predictions were loosely inspired by general mechanisms governing genetic evolution and other domains of cultural evolution.^{1,24–28} However, the precise mechanisms differ for each domain. For example, we found that indels were substantially more common than substitutions in both English and Japanese musical samples, despite being rare in coding regions of DNA because they tend to cause “frame shifts” that change large sections of coded proteins.⁴² We propose that indels are more frequent in musical evolution because singers can lengthen or shorten note rhythms to preserve the overall meter and avoid musical “frame shifts”. For example, in the melodies in Figure 1 the word “and” is sung across two eighth notes (half a beat each) in the top version, while in the bottom version it is sung to a single quarter note (one beat in the meter). This means the overall meter has not been changed even though a note in the sequence has been deleted.

Cultural transmission experiments^{48,62–66} may help to clarify the precise mechanisms underlying the cross-cultural regularities we have identified. Mechanisms might include the role of motor vs. perceptual constraints or unconscious mistakes vs. conscious innovation. For example, most of the changes in our analysis represented small, isolated changes at functionally unimportant sites that could easily be the result of unconscious copy-errors, especially through the error-prone process of oral transmission. However, a few changes, such as major insertions, deletions, or substitutions of entire phrases, seem likely to have been intentional.

Our finding that substitutions tend to occur between neighboring notes is consistent with the well-established phenomenon of melodic proximity (i.e., most melodic intervals tend to be small).^{9,20,45,56} Thus, if a pair of melodies show a note substitution preceded by an identical sequence of notes, the substituted notes are likely to fall within a narrow range of the preceding note (e.g., in Fig. S1A, the red “C” in the top melody is at the same pitch as the preceding note, while the red “B^b” in the bottom melody is only 2 semitones lower). However, the mechanism underlying pitch proximity effects remains debated. The “motor constraint hypothesis” for musical structure proposes that small melodic intervals are common “because large jumps require sudden contraction or relaxation in the muscles controlling vocal fold tension”.¹⁵ Alternatively, they could instead be due to cognitive constraints on pitch production and perception, with smaller differences between melodies also less likely to be noticed and transmitted.

Similar alternative mechanisms might explain our finding that notes with stronger rhythmic function are more stable. We proposed that interactions between musical and linguistic rhythm may underlie this effect: stressed syllables more crucial to the meaning of the lyrics tend to fall on musically stressed rhythmic positions, and such syllables may be less likely to change due to their importance to the narrative. An alternative explanation is that rhythmically stressed positions tend to have more tonally stable notes,⁶⁷ and thus the effect may be explained due to intra-musical interactions between rhythm and pitch, rather than cross-domain interactions between musical and linguistic rhythm. Observational corpus studies such as ours are unlikely to conclusively resolve such mechanisms, but could provide a fruitful basis for designing future controlled experiments.

Cultural evolution can take many forms and act on different scales, and our approach in this study provides an important complement to analyses that have examined musical evolution at the scale of broader musical styles or traditions. Future studies might

examine the interplay between the micro-level and macro-level processes of change to assess when, where, and why different processes may be more influential. Several authors of this study (PES and GC) have experience performing the repertoires studied in casual and competitive contexts. We are excited to quantify and test factors of substitution distance and rhythmic function that we have found relevant to our own performance experience, while also recognizing that future studies will be necessary to explore other factors that we know are important but were unable to test with the current sample (e.g., lyrics³¹, visual aspects of performance^{68,69}).

A cross-cultural understanding of the evolution of creative arts such as music represents a difficult but important challenge.^{70–74} While cultural relativists argue that musical evolution does not follow cross-culturally general rules,^{7,75} our analysis suggests instead specific, cross-culturally general regularities that limit some boundaries of musical creativity. Such regularities are relevant not only for understanding the evolution of traditional folk songs but also for art music⁶⁰ and popular music^{33,76,77} around the world, with applications to areas such as copyright law and cover song detection.^{11,12,41,61,78} Our general approach of investigating the microevolutionary mechanisms of melodic evolution could also be applied to investigate other aspects of cultural change and the creative arts. Such processes may be most directly relevant to situations where something is communicated to an audience who then in turn reproduce it. Such candidates include folk tales/myths,^{79,80} dances,^{81–83} religious rituals,^{84,85} and written manuscripts.^{86,87} Evolutionary approaches to these domains have tended to focus on reconstructing historical relationships between traditions, yet the approach taken here could test for general regularities shaping human cultural diversity. Our findings suggest that even an art form as malleable as music can be understood as an evolutionary process with cross-cultural regularities.

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AUTHOR CONTRIBUTIONS

Conceptualization: PES, QDA, TEC; Methodology: PES, SP, HS; Analysis: PES, SP, GC; Investigation/ Resources/ Visualization/ Writing original draft: PES. Writing – review & editing: TEC, QDA, SP, HS, GC.

INCLUSION AND DIVERSITY

-We worked to ensure ethnic or other types of diversity in the recruitment of human subjects.

-One or more of the authors of this paper self-identifies as an underrepresented ethnic minority in science.

-While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list.

-The author list of this paper includes contributors from the location where the research was conducted who participated in the data collection, design, analysis, and/or interpretation of the work.

DECLARATIONS OF INTERESTS

The authors declare no competing interests.

MAIN-TEXT FIGURE/TABLE LEGENDS

Figure 1. An example of coding, aligning, and analysing melodic evolution. An excerpt from "Scarborough Fair" (Child ballad #2) shown as sung by Martin Carthy (1965, top melody; <https://open.spotify.com/track/4IPMSVOF9a726iwKtC0K1T?si=c6cc60050a8546fa>) and by Simon & Garfunkel (1966, bottom melody; <https://open.spotify.com/track/3g2fYZW5v2od8KIF7VktT0?si=8378941812a24d7d>).^{11,88} Using an "alphabet" of 12 scale degrees (i.e., pitch-classes in relation to a tonal center), melodies are transposed to a common tonic ("C") and converted from staff notation (**A**) to aligned sequences (**B**) by adapting sequence alignment methods from molecular genetics. Gaps due to insertion/deletion (blue) are represented by dashes ("-"), bold indicates notes with stronger rhythmic functions (i.e., metrically accented and/or final notes). See STAR Methods for details about the process of documenting and analyzing melodies, and Fig. S1 for analogous examples using English and Japanese folk songs included in the analysis.

Figure 2. Geographic distributions of the full sample of 10,062 traditional folk song melodies sung in English (British/American; n=4,125) and Japanese (n=5,937). North America, British Isles, and Japan are plotted separately using different scales, and within each the two sub-regions with the largest sample sizes are indicated.

Figure 3. Differences in tonal systems for highly related pairs of English (n=242 pairs) and Japanese (n=86 pairs) melodies.

(A) Distributions of individual scales. Each letter combination represents a unique scale using those notes (scales found in both English and Japanese songs are highlighted with red boxes).

(B) Distribution of numbers of scale degrees.

(C) Substitutions among the 12 scale degrees. Arrow widths are proportional to the number of substitutions. The scale degrees of the most common scale in each repertoire are highlighted using white circles. Insertions/deletions and notes that are not substituted in a given repertoire are not shown. Directionality is also not visualized (e.g., whether a C-G substitution is going up 7 semitones or down 5 semitones). Substitutions

in both samples tend to occur at small distances (i.e., around the outside of the circle)
 but the specific patterns differ, in part due to the different scales used.

Figure 4. Substitution distance and rhythmic function predict rates of musical evolution.

Left-hand side represents English folk songs (n=242 highly related pairs), right-hand side represents Japanese folk songs (n=86 highly related pairs). See Figure S3 for alternative methods of quantifying substitution distance and rhythmic function and STAR Methods for discussion of our choice to function on rhythmic function as opposed to tonal function.

(A) Notes with stronger rhythmic functions (final or stressed) are more stable than those with weaker functions (unstressed or ornamental). Dots represent stability for each functional type for each highly related pair. Red dots represent means, red bars represent 95% confidence intervals.

(B) Substitutions are more common between smaller distances. Error bars represent bootstrapped 95% confidence intervals (cf. STAR Methods for details).

STAR METHODS:

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Melodic sequences	This paper	https://github.com/pesavage/melodic-evolution/blob/master/data/MelodicEvoSeq.xlsx
Pre-calculated matrices of pairwise melodic similarities	This paper	https://osf.io/nhvzw/
Software and algorithms		
R 4.1.0	R Foundation	https://www.r-project.org
Analysis code	This paper	https://github.com/pesavage/melodic-evolution

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Patrick E. Savage (psavage@sfc.keio.ac.jp).

Materials availability

All melodic sequences, metadata, and analysis code are publicly available at <http://github.com/pesavage/melodic-evolution>. The original musical notations cannot be shared digitally due to copyright restrictions, but are all published in refs.^{17,18}

Data and code availability

All melodic sequences, metadata, and analysis code are publicly available at <http://github.com/pesavage/melodic-evolution>.

METHOD DETAILS

Sample. For our sample, we chose two comprehensive collections of traditional English and Japanese folk songs transcribed into staff notation, totaling 10,062 melodies (Fig. 2). **1) *The traditional tunes of the Child ballads***¹⁸ contained 4,125 melodies from North America and the British Isles, comprising all known pre-20th century Child ballad melodies and most known traditional melodies from 1900-1968. The “Child ballads” are a set of 305 families of traditional folk song texts (“text families”) identified by Francis Child as the oldest and most traditional folk song narratives in the English language.⁸⁹

During the early 20th century, researchers such as Cecil Sharp, Maud Karpeles, and Alan Lomax developed an interest in English folk songs and their trans-Atlantic evolutionary relationships after discovering that many ballads thought to have gone extinct in the British Isles were in fact flourishing in altered form on the other side of the Atlantic in the US Appalachian mountains.^{22,90–92} With the recently invented phonograph allowing songs to be recorded in detail, the number of recordings of these songs expanded rapidly, leading eventually to these songs being re-popularized by artists such as Joan Baez, Bob Dylan, and Simon & Garfunkel.^{52,93}

Because Child's classifications are based on lyrics, not melodies, it is common for the lyrics from the same text family to be sung to various different melodies, some of which may be closely related and others of which may be unrelated. Conversely, similar melodies from the same "tune family"⁵¹ can be used to sing unrelated texts from different text families. Future studies might explore coevolutionary relationships between lyrics and melodies using tools from evolutionary biology such as those designed for examining host-parasite relationships.^{94,95}

Bronson identified 4,125 melodies for 204 Child ballads (101 Child ballads became extinct without their melodies being preserved, leaving only lyrics). The number of melodies recorded for each Child ballad varied widely, up to 204 for the most popular ballad (No. 84, "Barbara Ellen"), with a median of 7 melodies per ballad (mean: 20.2).

Audio recordings for many of these English folk song melodies do not exist because most were documented before the widespread availability of audio recording technology. For example, the top melody in Figure S1A was transcribed by ear by Cecil Sharp in 1917 from a live performance before it was feasible to bring portable recording equipment, while the bottom melody was published by Jean Ritchie based on her recollections of her family's singing. However, a very similar version recorded by Jean Ritchie can be listened to at <https://open.spotify.com/track/2yzG6XTLWywGmFSol5mc87?si=yZTmGjXAQVOgk9N5ewDVfg>.

2) *日本民謡大観 [Japanese folk song anthology]*¹⁷ contained 5,937 melodies of traditional Japanese folk songs transcribed from field recordings made throughout Japan during the middle of the 20th century. The project involved dispatching various teams of researchers to all 47 Japanese prefectures to make comprehensive recordings of their traditional folk song repertoires. This project was led by Kasho MACHIDA and sponsored by the Japanese national broadcasting service NHK. This project included recording of the traditional music of Japan's primary ethnic minorities, the Ainu in Hokkaido⁹⁶ and the Ryukyu in Okinawa, but we chose to restrict this analysis only to Japanese-language songs for consistency. Machida had a particular interest in the evolution of tune families,⁹⁷ the study of which was one of the purposes of the survey. In contrast to the English sample, most Japanese melodies were transcribed from audio recordings – many of these recordings were published on CDs when this series was reissued.

Sequencing. PES (first author) manually converted all 10,062 melodies into sequences of letters directly from the staff notations, along with selected metadata (e.g., location, year of recording; this took a long time, but he reports that he "was singing along the whole time, so it was actually kind of fun"). Only the first appearance of the melody

was coded, ignoring repeated verses. Variant notes from subsequent verses (marked with parentheses, or with downward stems in the case of multiple notes at the same rhythmic position) were thus ignored. Future studies may wish to explore variation within vs. between songs (cf. ⁹⁸).

Melodies usually consisted of between four and eight phrases, each consisting of approximately 10 notes (median melodic sequence lengths: English = 40 notes [min: 23 notes; max: 124 notes]; Japanese = 50 notes [min: 17 notes; max: 213 notes]). The assignment of tonic (reference pitch coded as "C") followed the original editors' choices, which often but not always corresponded to the final note. A small number of obvious inconsistencies in Bronson's tonic assignment were corrected. Some melodies were reprinted in multiple volumes by Machida to highlight similarities among melodies: these reprinted melodies were excluded.

The question of appropriate choice of "tonic" or "tonal center" in Japanese folk song is more controversial than for English folk song.^{57,99} Machida stated that he transposed all melodies to show "G" as the tonal center in his transcriptions. We disagree with his choice in some cases, but we preserved his assignments for consistency. Disagreement about the correct choice of tonic assignment has no effect on any of our main analyses reported in Fig. 2, as functional position and substitution distance are independent of the label given to a note. However, such disagreement might theoretically cause the similarity algorithm to miss highly related melodies, or could affect the calculation of the note substitution matrix shown in Fig. 3C, points that should be kept in mind for future analyses using this method.

Note that we follow the convention from ref.¹⁶ of transposing melodies so that "C" represents the tonal center, compressing sequences into a single octave, and representing accidentals using lower case notes for flats rather than the more common "b"/"#" (e.g., the scale-degree 6 semitones above or below the tonal center is represented as simply "g" rather than "Gb₃", "F#₄", etc.). These conventions allow each note to be represented using a single symbol, simplifying the sequence alignment and comparison procedure and increasing comparability and consistency. The main text and figures use the more familiar accidentals (e.g., "E^b" rather than "e"), but the raw data uses the single-symbol version for analyses. See refs.^{16,100,101} for discussion of this method compared to alternative methods based on interval, contour, and/or rhythm.

Metadata coding:

In addition to melodic sequences, metadata on the date of recording, location (state/prefecture/county), song title, and singer name were coded for all highly related melodies when known. On rare occasions when the year was given as a range (e.g., "1820-1825"), we coded the mean year (rounded to the nearest whole number, so "1820-1825" would be coded as 1823). When the singer is unknown, this was coded as "unknown". For sensitivity analyses, pairs of melodies were coded as having the same singer when the singer name was the same, different singer when the names were known to be different or if it was obvious from contextual information that the singers were different (e.g., if one melody was sung by an 80-year-old and the other was sung by an unknown singer 50 years later), or NA if it was impossible to determine.

Scale classifications:

We classified scales based only on the observed notes and their relationship to the specified tonal center (set to “C”). The relative frequency of scale degrees was not included. Therefore, if a melody used a note even once in passing, this was counted as a scale degree. For example, if a melody only used the 5 notes “C”, “D”, “F”, “G”, and “A”, it would be classified as the 5-note scale “CDFGA”, but if it used the note “E” one time, this would be classified as the 6-note scale “CDEFGA”. We did not attempt more nuanced classifications such as distinguishing between scales and modes or between degrees of relatedness between scales/modes (cf. ^{50,102–104}).

Similarity/alignment. Pairwise similarities among the melodies were automatically calculated using the method identified as performing best for the purposes of aligning related melodies within British-American and Japanese tune families.¹⁶ This method used the Needleman-Wunsch global pairwise alignment algorithm³⁹ with a gap opening penalty (GOP) of .8 and a gap extension penalty (GEP) of .2, including differences in mode (i.e., not re-coding lower-case letters as capitals). Percent identity was then calculated for each pairwise alignment using the equation:

$$PID = 100 \left(\frac{ID}{\frac{L_1 + L_2}{2}} \right)$$

where “PID” represent percent identity, “ID” represents the number of aligned notes that are identical, and L_1 and L_2 represent the lengths of the two sequences.^{16,105} For comparison, the two melody excerpts in Fig. S1A have a PID of 88.9% (ID=16 identical aligned notes, $L_1 = L_2 = 18$ notes total in both melodies).

Note that another set of parameters (GOP=12, GEP=6, ignoring mode) performed slightly better for *identifying* related melodies, but that method performed slightly worse for actually aligning related melodies once identified, making it less appropriate for our current purpose of aligning and calculating similarity among highly related melodies. The choice of algorithm makes no difference to the final alignments used in the analyses, because all alignments were manually corrected. Instead, the effect of using different algorithms is that the parameters used (GOP=.8, GEP=.2) result in identifying a larger number of highly related melodies.

Because it was computationally infeasible to calculate PID for all 50,616,891 pairs among the 10,062 melodies, and because any similarities that might be identified between traditional English and Japanese folk songs would likely not be due to recent shared descent, we calculated similarities among the 4,125 English melodies and the 5,937 Japanese melodies separately. This produced PID values for 8,505,750 and 17,621,016 pairs, respectively (Fig. S2; these calculations took approximately one month total to run on a standard 2.7GHz 13-inch 2015 Macbook Pro).

Percent identity calculations revealed 917 pairs (774 English, 143 Japanese) of melodies that were highly related to at least one other melody by $\geq 85\%$. We chose this threshold because it was used in similar analyses of protein evolution to minimize chances of miscounting successive mutations⁵³ and to avoid alignment error, which is particularly important in melodic evolution given the high rate of insertion/deletion.

These 917 pairs contained a total of 871 individual melodies (i.e., 8.7% of all 10,064 melodies; 651 English [15.8%] and 220 Japanese [3.7%]; the number of individual melodies is less than double the number of pairs because some melodies are highly related to more than one other melody). The higher rate of highly related melodies in English compared to Japanese is likely due to the sampling methodologies: the English melodies were compiled in order to collect large numbers of related melodies of a specific subset of 305 traditional ballads, whereas the Japanese sample was intended to be a comprehensive sample of all traditional folk songs throughout the nation. There is no reason to suspect that such sampling differences would have any effects on the evolutionary dynamics we are investigating, but if they did they would presumably only serve to weaken the cross-cultural similarities we identified.

We filtered these 917 pairs to remove identical pairs (i.e., 26 pairs with 100% similarity: 14 English, 12 Japanese) and pairs sharing melodies with other pairs (i.e., “tune families” where certain melodies were highly related to more than one other melody). In such cases only the most similar non-identical pair was retained to avoid quasi-duplication with the same melody contributing to evolutionary rate calculations for multiple pairs. Note that differences in numbers of related melodies or numbers of tune families in the English vs. Japanese samples should not affect our analyses because rates were calculated independently for these two samples.

This resulted in a total of 328 highly related pairs used to calculate evolutionary rates (242 English, 86 Japanese). Automated alignments of these 328 highly related pairs were manually checked by PES and GC against the original score notation and corrected where necessary based on rhythmic information (which is not incorporated in the automated sequence alignment).

While pairwise alignment using high similarity thresholds of 85% loses some information in contrast to approaches such as multiple alignment and phylogenetic analysis that preserves more distantly related melodies within a clade/family, it also avoids making additional assumptions about evolutionary processes that would be involved in such analyses. For example, detailed multiple alignments and analyses of large linguistic or genetic phylogenies incorporate assumptions based on data such as date calibration (e.g., of biological fossils or ancient texts) and rates of transitions between units (e.g., between different phonemes or different DNA nucleotides)^{106–108} But there is currently little corresponding musical data,¹⁰⁹ and in fact some of these assumptions are precisely what the current study is trying to estimate (e.g., rates of change between different notes), so such assumptions could risk making our conclusions circular.

Thus, pairwise alignment of highly related melodies is an appropriate method for attempting an initial estimation of rates of melodic evolution that could be built on in future phylogenetic reconstruction/analysis using multiple alignment of more distantly related melodies. Importantly, while pairwise alignment of highly related melodies might be expected to capture only surface-level, drift-like mechanisms, this should only allow us to identify random drift, not directional evolution. The fact that we identify directional, cross-culturally consistent evolutionary trends suggests that our choice of alignment methodology is appropriate, and opens up the possibility of more complex and deeper multiple alignment-based methods in future studies.

Note regarding temporal ancestry: We chose to avoid making assumptions about temporal ancestry (e.g., by attempting to calculate absolute rates of change per year or to assign one of the melodic variants as ancestral). In a preliminary analysis,¹¹⁰ we attempted to calculate absolute rates by treating the older melody as the ancestral version and calculating rates of melodic evolution over time, based on the assumption that the more recent melody may directly descend from the older melody (e.g., melodies known to be transmitted from parents to children or teachers to students, or known to be reprinted from older editions). However, in many cases it is unclear whether more recent melodies are directly descended from older melodies or whether both melodies share a more ancient common ancestor (or ancestors) that may not have been recorded.¹¹¹ This is particularly likely when melodies were recorded within a short time span during the course of a single recording trip (e.g., during the same year or even the same day). In such cases, even if melodies are recorded from a parent and their child on the same day, the extent to which the parent's version has changed since the time they originally taught it to their child is unknown. Furthermore, assuming that the time between recordings represents the true time of evolutionary change is likely to substantially inflate perceived rates of change. For example, in the case where a parent and child are recorded on the same day, changes between the versions will be calculated as having arisen in less than a day, when in fact they have probably been evolving for many years in between the first time the parent first taught the child and the time both were recorded.

QUANTIFICATION AND STATISTICAL ANALYSIS

Hypothesis testing:

All hypotheses were tested once for the samples of English melodies (n=242 highly related pairs) and once for the sample of Japanese melodies (n=86 highly related pairs) identified above.

Confirmatory analyses.

1) Rhythmic function: Because lyrics in our sample were often not directly matched with their notes, coding of functional position followed the standard approach of being based on metrical accent¹¹² rather than syllable accent.¹⁴ Notes falling on the downbeat of all bars were coded as rhythmically stressed (in bold). Appoggiatura and acciatura (short ornamental notes indicated using small notation) were coded as ornamental (in italics). The last note of a melody was coded as final (underlined). All other notes were treated as unstressed (regular text). A given note could only be coded for one function (i.e., multicoding was not used). Specifically, this meant that final notes that fell on the downbeat were coded as final, but not stressed.

Note that we focused on function as defined by rhythmic accent, rather than tonal functions of the kind often explored in music cognition research. Our reasons for this were: 1) classic measures of tonal function (e.g., tonal hierarchy probe-tone ratings^{101,113}) are derived from Western tonal music and may not apply to the different Japanese tonal system shown in Fig. 3; and 2) previous research has identified rhythmic accent as likely to play a major role in folk song melodic evolution.¹⁴ However, tonal hierarchies (defined as the perception of "ordering of structural significance or stability" among pitches)¹⁰¹ have been shown to be strongly related to note frequency

distributions (e.g., the most common pitch classes in Western classical music are the tonic [C] and dominant [G], and these are also perceived as the most stable).⁴⁵ This relationship may be because our perceptions of stability are statistically learned from experience, or alternatively certain combinations of pitches may be more common precisely because they are intrinsically more stable (e.g., due to overlap in their harmonic series).¹¹⁴ Interestingly, C and G are also the most common in our Japanese folk song sample, but other pitch classes that are very common in the English folk song sample are absent or nearly absent in the Japanese sample (e.g., E, B) and vice versa (e.g., Db). Because our regression model finds a consistent effect for note frequency while controlling for pitch class as a random effect (Table S3), this allows us to control for possible effects of tonal function on melodic evolution.

For analysis, we treated final and stressed notes as “stronger function” and unstressed and ornamental notes as “weaker” function. This was partly in order to avoid problems of statistical power related to the fact that only a subset of melodies contained notated ornamental notes, and partly to avoid parameter inflation when conducting the generalized linear model analysis (see below). See Fig. S3A for alternative analyses differentiating between all four functional types. Specifically, Fig. S3A shows that final notes and stressed notes are both more stable than either unstressed notes or ornamental notes, ensuring that our results are not driven simply by one type of functional note (e.g., only due to a tendency for final notes to end on the tonic).

We used directional, paired t-tests to compare stability of strong functional types (final and stressed notes) vs. weak functional types (unstressed and ornamental). Strong functional types were predicted to be more stable than weak functional types. Stability was estimated by calculating percent similarity for all stronger function sites role for a given highly related pair of melodies, and then the same for all weaker function sites, so each pair of melodies functioned as its own control. Stability (measured as percent similarity) was predicted to be higher for stronger functioning notes.

2) Substitution distance: Distances in semitones for all substitutions were counted after manually checking the original staff notation to determine whether a substitution was rising or falling (e.g., a substitution between C and D could represent rising by 2 semitones or falling by 10 semitones). One case of a substitution of greater than an octave (12 semitones) was excluded to allow all analyses to be applied through a within-octave analysis framework.

We used directional (1-tailed) correlation tests with Spearman's rank correlation coefficient to test our prediction of a negative correlation between substitution distance and substitution frequency. Note that Spearman's coefficient is a non-parametric, rank-based method, which takes account only relative order, not absolute values. We also report correlations using Pearson's coefficient for comparison.

Bootstrapped intervals: In Figure 4B and S3B, bootstrapped 95% CI estimate the population error rate in distance substitutions. Bootstrapped estimates are calculated by counting the number of substitutions at each interval for 1000 sets of 328 song pairs, sampled with replacement. We then calculate 95% CI intervals using the variation in counts for each of those subsets. The total counts of substitutions at each interval provide us with information on the sample of songs we analyse, bootstrapped intervals

provide us with an indication of how confident we should be that our sample is representative of the population.

Sensitivity analyses. To examine the sensitivity of our primary analyses to various assumptions, we conducted the following sensitivity analyses by re-running the primary analyses for the following subsets (Tables S1-2):

Quantification method: We examined the effects of quantifying substitution distance grouping into intervals of 2nds-7ths rather than raw semitones (1-11), and of analyzing the four functional note types (final, stressed, unstressed, ornamental) separately rather than grouping them into only strong vs. weak (cf. Fig S2).

Time: To examine whether the dynamics change over time, we split both English and Japanese samples in half based on the median recording date (1914 and 1960, respectively) and reran the analyses separately for the older and younger samples (older sample, English: n=119 pairs; Japanese: 24 pairs; younger sample, English: n=122 pairs; Japanese: n=34 pairs). 1 English pair and 27 Japanese pairs were excluded from these sensitivity analyses because they lacked recording year metadata.

Singer: Some pairs are made up of melodies sung by the same singer (at different times or for different texts), while others were sung by different singers. To examine whether this affects our analyses, we reran the analyses twice for both English and Japanese sub-samples: once using only pairs containing melodies sung by the same singer (n=21 English pairs, 37 Japanese pairs), and once using only pairs containing melodies sung by different singers (160 English, 35 Japanese). These sensitivity analyses excluded pairs where it cannot be determined whether the singers are the same or different (61 English, 14 Japanese).

Coder blinding: All songs were converted from music notation into sequences of letters by lead author PES, who was not blind to the hypotheses. PES manually corrected automatic alignments/note sequences and coded functional position and substitution distance for 168 pairs, while GC corrected alignments/sequences for the remaining 160 pairs while blind to the study hypotheses. All songs were previously transcribed into music notation by various researchers and curated/edited by Bronson and Machida. Some of these previous researchers may have had their own ideas about musical evolution but none were specifically trying to test the hypotheses presented here. To examine whether having a different coder blind to the hypotheses align and code the data affects results, we examined subsets of the data that were coded by PES (168 pairs; unblinded) and by GC (160 pairs; blinded).

Paired vs. unpaired t-tests: In a previous preliminary analysis, we used unpaired t-tests to compare rates for different note function types.¹¹⁰ However, we were unsure whether our previous use of unpaired t-tests was most appropriate for our data since it contained multiple measurements of different evolutionary rates for the same melodies. To determine whether our results were affected by our choice of statistical test, we also repeated the analysis using paired t-tests. In other words, we ran the analyses once treating the rates for stronger function and weaker function as paired, and once treating them as unpaired.

Sensitivity analysis conclusions: Across the different sensitivity analyses we examined the effects on the magnitude and direction of the t- and r-coefficients (we concentrate on these parameter estimates rather than p-values due the reduction in sample sizes). All effects were in the same direction and generally had similar magnitudes (substitution distance (Table S2): mean $r_s = -.93$, SE = .02; rhythmic function (Table S1): mean $t = 7.5$, SE = .9). This suggests that our results are robust to the specific assumptions of our analyses.

Missing data

The only quantitative variable with missing data was ornamental evolutionary rates, which can only be calculated for the 104 pairs containing melodies with ornamental notes. Missing data ("NA") were excluded for this variable. Note that because ornamental and unstressed notes are combined for our confirmatory hypothesis testing of functional type, our primary analyses contain no missing data. Missing metadata for dates, locations, or singer names was ignored (see above).

Explanation of existing data/deviations from previous analysis methods

Our analyses were not formally pre-registered. However, our predictions and results based on analysis of the sample of 4,125 English folk song melodies was previously published in 2017 as Chapter 3 from PES's PhD dissertation¹¹⁰ prior to beginning any coding or analysis of the Japanese sample. We had originally planned to publish the English analysis by itself, but decided our claims that these mechanisms were cross-culturally general would be more compelling if we could replicate our findings on a similar sample of unrelated non-Western songs. During the process of analyzing the Japanese sample and comparing it with the English sample, we realized that we needed to modify several methodological parameters for consistency. Further changes were then incorporated during the peer review process. Specifically, we decided to:

1) consistently define "stressed" notes as the first note of each bar for English and Japanese samples (rather than also including other metric beats following recommendations based on patterns of syllable accent in English folk song).

2) consistently use the gap opening penalty (GOP) of 0.8 and gap extension penalty (GEP) of 0.2 found to be best for aligning sequences WITHIN tune families, rather than GOP=12 and GEP=6 used previously (which was better at distinguishing BETWEEN tune families).¹⁶

3) automate the selection of highly related pairs. Changing the alignment parameters above and automating the selection process had the effect of increasing the total number of highly related English pairs found from 172 to 242 (which included many but not all of the original 172 pairs).

4) remove predictions and analyses that included estimates of evolutionary rates over time, as we realized that it was not possible to accurately measure these parameters because so many of both English and Japanese samples were collected during the same collection trips and we are not yet confident in our ability to reconstruct ancestral relationships between melodies.

5) remove the prediction and analysis comparing songs recorded directly from known singers (oral tradition) vs. those from printed editions without attribution (written tradition), because almost all Japanese songs were recorded from oral tradition and so this comparison could not be performed for both Japanese and English samples.

6) combine final and stressed notes into a "strong function" category and combine unstressed and ornamental notes into a "weak function" category in order to avoid problems of missing data when calculating ornamental note evolutionary rates and accordingly increase our statistical power (the original comparison of ornamental vs. unstressed notes was non-significant and involved a small sample size of pairs containing ornamental notes [originally $n = 34$ pairs]).

7) change our t-test from unpaired to paired, as this seemed more appropriate given that our data consist of multiple measurements of evolutionary rates from different parts of the same pairs of melodies.

8) modify our sensitivity analyses to make them more rigorous and more appropriate for our revised methods, by:

a) adding an analysis examining effects of songs sung by same vs. different singers to address potential differences in the sampling methods

b) having GC code a subset while blind to our hypotheses and using this for sensitivity analyses to investigate the possibility of confirmation bias due to PES not being blind to the hypotheses (GC completed training and coding of his subset of melodies before he was informed of the hypotheses or goals of the study).

c) adding a comparison of the effects of using paired vs. unpaired t-tests

d) removing analyses involving assumptions about temporal ancestry (which were no longer relevant)

e) removing analyses involving regional differences (as these were now superseded by the cross-cultural comparison)

9) A new regression model was added (see below) to directly compare effects of substitution distance vs. rhythmic function using the same framework

10) Fig. 4A (quantifying substitution distance on a scale of 1-11 semitones) and Fig. S3B (grouping semitones into intervals of 2nds-7ths) were swapped in order to better visualize the variability and interactions between substitution distance and tonality.

11) Predictions and analyses about frequency-dependent selection were added in previous versions (<https://psyarxiv.com/5rj6y>), then deleted because these could not be analyzed in the new regression model in a way that would allow direct comparison with substitution distance and rhythmic function.

12) A new analysis of rhythmic function vs. overall melodic similarity (Fig. S4A) was added to address possible effects of our choice to select only highly related melodies (see below)

13) During data/code review we found and corrected a small number of miscodings of substitution counts in the raw data file. These changes are all documented at <http://github.com/pesavage/melodic-evolution>. When we re-ran all analyses, this

resulted in a number of minor changes to precise numbers, but no substantive differences to our results.

Addressing the effect of selecting only highly related melodies

It is conceivable that our rhythmic function results could be due to our decision to sample only highly related melodies, if more similar pairs of melodies tended to have larger differences in stronger vs. weaker functioning notes. If sampling highly related melodies biased our analyses toward finding an effect of rhythmic function, then we would expect that the magnitude of that effect to be strongest at the very highest levels of overall similarity. However, comparing differences between stronger and weaker function notes against melodic similarity of the full pair of melodies shows a trend in the opposite direction – the relationship between similarity and strength of functional changes is if anything *negative* (English: $r = -.30$, $df = 240$, $P < .001$; Japanese: $r = -.18$, $df = 84$, $P = .09$); Fig. S4A). A negative correlation is consistent with the idea that highly related melodies have less opportunity to display large differences in rhythmic function (because there are few differences of any kind), but as melodies become more different the effect of rhythmic function can be seen more often and more clearly.

Note that the trend for stronger functional notes to be more stable than weaker functional notes is observable even for highly similar melodies (i.e., even points near the right hand of Fig. S4A tend to fall above 0 on the y-axis), but tends to be stronger as the difference between melodies becomes greater. Thus, choosing to focus on more highly related melodies does not appear to have the effect of enhancing or reversing the trend - if anything, they make this trend appear weaker. This suggests that our finding that stronger rhythmically functional notes are most stable is not an artifact of our choice to limit our sample to pairs of highly related melodies.

Regression model to explore interaction between substitution distance and rhythmic function

During the review process it was suggested to examine potential interaction between our two hypotheses (i.e., whether substitution distance effects are related to the position in the melody where the substitution occurs). While the distance effect does appear to be slightly stronger at functional sites than non-functional, this interaction was non-significant (Fig. S4B; Table S3). These regression analyses also controlled for differences in individual notes frequencies. Controlling for note frequencies allows us to build a baseline model of random change, while also serving as a proxy estimate for tonal hierarchies that can be compared between Western and non-Western repertoires. This allows us to confirm that our results were not simply an artefact of baseline differences in note frequencies, and to quantify the interaction between substitution distance and tonal relationships. We found that note frequency did have a strong effect on substitution rates; for example, a note that does not appear in a given culture's scale (e.g., B in the Japanese sample) will obviously never be substituted. But since the English and Japanese samples showed different note frequency distributions, these note frequency effects were not consistent for a given pitch class (see Fig. 3c and Table S3).

We performed this exploratory analysis by constructing a generalized linear model to quantify and compare the effects of, and possible interactions between substitution

distance, rhythmic function, and note frequency on rates of melodic evolution (Fig. S4B and Table S3).

The outcome variable in this model is the number of substitutions for each note pair, conditioning on function and semitonal distance. There are 66 possible substitutions within a 12 note octave. Allowing for substitutions at “near” or “far” semitonal distances means there are 126 possible note pair substitutions accounting for distance ($66 \times 2 - 6 = 126$ because 6 note pairs are 6 semitones above and below each other). When accounting for strong to strong or weak to weak substitutions we end up with 252 substitutions categories (126×2). Substitutions with differing functions were excluded from analyses, since these were very rare (only 3% of all 769 substitutions). Using C-A as an example for how substitutions are calculated for a single note-pair: the substitution C-A occurs 35 times in English songs. 33 times this is between two notes with weaker rhythmic functions, and two times it is between notes with stronger rhythmic functions. All but one of these substitutions represent the smaller substitution distance of 3 semitones (only one C-A substitution of 9 semitones was observed, between two notes with weaker rhythmic functions). For a C-A note-pair there are then four entries in the outcome variable: 3 Semitones and weak = 32 substitutions; 3 Semitones and strong = 2; 9 Semitones and weak = 1; 9 semitones and strong = 0.

Model of substitutions:

We analyse this outcome variable in six different models. Four models are nested, with increasing complexity, and two subset the data to sets of strong and weak substitutions, to assess the strength of semitonal distance within each category. Models are Poisson Bayesian linear regression models implemented in brms¹¹⁵ and are applied separately to subsets of English and Japanese data.

Nested models

The null hypothesis for the nested models is that, if note substitutions occur at random (i.e. with equal probability) then note pair substitutions should occur in proportion to the product of the frequencies of each note in the pair, and the base rate of stronger or weaker notes. Residual variance from this model is proportional to the rate of change in any functional-distance-note-pair, and is what more complex models hope to explain. We refer to this model as the baseline model. Note frequency and note function frequency variables are divided by their maximum value to aid in model convergence.

We extend the baseline model to test two hypotheses: a) smaller substitution distances should result in more frequency changes; and b) substitutions between two functional notes should occur less often than between two non-functional notes. This is done iteratively by first adding a binary variable for function type, then by adding a continuous variable indicated semitonal distance, and finally by adding an interaction variable between these two. All models include a random effect accounting for note-pairs, in order to account for the possibility that some note-pairs may be more likely than others to be substituted (e.g., due to tonal function).

Using LOO model comparison, we find that a model including both semitonal distance and function is more than 2SE away from the function-only model, suggesting both predictors are important. However, there is little statistical difference between a model with an additive and interaction relationship between function and semitonal distance,

suggesting that these dimensions are independent of each other. We conclude that the best model to represent these relationships is a model without an interaction between semitonal distance and function, which comes in the following form:

$$y_i \sim \text{Poisson}(\lambda_i)$$

$$\log(\lambda_i) = \alpha + \beta_1(\text{Note 1 count} \times \text{Note 2 count} \times \text{Functional note count})$$

$$+ \beta_2 \text{Semitonal Distance} + \beta_3 \text{Note Function} + (1 \mid \text{Note Pair})$$

$$\beta \sim \text{Normal}(0, 5)$$

This model is visualised in Figure S4B for the English and Japanese sample. The English sample has a Bayesian R^2 of 0.95, and the Japanese sample has a Bayesian R^2 of 0.89.

Under this model, we expect that an increase of one semitone for a weak note reduces the probability of a substitution by 41% in the English sample, and 43% in the Japanese sample. In the English sample we find that weak function substitutions are 3.5 times more likely to change than strong function substitutions, however, we do not find a significant effect of function in the Japanese sample. This result supports hypothesis (a) in both samples: smaller semitonal distances result in more frequent substitutions. We only find significant support for hypothesis (b) that weak function substitutions are proportionally more likely to occur than strong function substitutions in the English sample.

Subset models

We additionally test the effect of distance within a subset of strong and weak substitutions. The outcome variable now only holds categories for note pairs and near or far substitution distance. This reduces the size of the outcome variable from 252, by half to 126. Within the English sample, we find similar results to in the combined model: for weak to weak substitutions, an increase in semitonal distance decreases the probability of a substitutions by 40%, and for strong to strong substitutions 46%. Within the Japanese sample, we find that between weak function substitutions, an increase of one semitone decreases the probability of substitution by 44%, but in strong-strong substitutions an increase of one semitone decreases the probability of substitution by 57%.

Overall, the regression models suggests that our primary findings of effects of rhythmic function and substitution distance are independent of one another and not an artefact of the fact that different notes and different functional positions have different base frequencies. The regression model confirms the robustness of our substitution results using a different analysis framework, and partially confirm the effects of rhythmic function, with the exception that the analysis does not show a significant effect of rhythmic function on substitutions within the Japanese sample (95% CI of the regression coefficient overlaps with 0). We suspect that this ambiguous result partially reflects the fact that the Japanese sample is based on a smaller number of highly related pairs of melodies (n=86 pairs, rather than n=242 pairs from the English sample). More importantly, our main analysis of rhythmic function included the relative rates of insertion/deletion of stronger vs. weaker functional notes, while this regression framework can only incorporate substitutions, which are substantially less frequent than insertions/deletions (cf. discussion of indels in main text). For example, the Japanese

sample of highly related melodies contains 154 non-matching strong functional notes, but these only include 32 strong-function substitutions.

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Figure S1. Examples of coding, aligning, and analysing musical evolution for highly related pairs included in the analysis. Related to Figure 1.

These are identical to Fig. 1 but use the following examples from the analysis (the “Scarborough Fair” versions shown in Fig. 1 were not included in *The Traditional Tunes of the Child Ballads*):

(A) An excerpt from “Lord Thomas and Fair Eleanor” (Child ballad #73) shown as sung in Kentucky by girls at Hindman school (1917, top melody) and by Jean Ritchie’s family (1955, bottom melody). Possibly offensive lyrics are redacted and replaced with “etc.” (many Child ballad lyrics discuss topics such as murder, rape, domestic violence, etc. and many are sexist, racist, or otherwise offensive by contemporary standards). Audio recordings for these variants do not exist, but a similar version sung by Jean Ritchie can be heard at <https://open.spotify.com/track/1B3NfizHr6b461yGSJaUXS?si=KI2SZeNRQSKeQ91Of2rHYw>

(B) An excerpt from the Japanese folk song “Itsuki no Komori Uta (Lullaby of Itsuki)”, shown as notated by Tansui Kikuchi (1951; top melody) and Yuji Koseki (1952; bottom melody). Audio recordings for these variants do not exist, but a similar version sung by Shigeri Kitsu can be heard at https://open.spotify.com/track/20foSAVGzh3KrfAsIIS9hb?si=g7_4_yw3R-ecoeXT8eZgnnw. Note that this transcription ends on an “F” rather than a “C” because we follow the editor (Kasho MACHIDA)’s tonic assignment (see STAR Methods for explanation of tonic assignment),

Figure S2. Distributions of percent melodic identity of all pairwise alignments within the English and Japanese samples. Related to Figure 2.

(A) Histograms of pairwise similarities (dashed line represents the threshold of 85% used to define “highly related” melodies for evolutionary analysis). Y-axis is plotted on a log scale for better visibility.

(B) Heat map of pairwise similarities among melodies. Heat maps have been reordered using seriation to group more similar melodies together.

Figure S3. Alternative analyses of substitution distance and rhythmic function. Related to Figure 4.

This figure is identical to Fig. 4 except that:

(A) functional type is split into four types (ornamental, unstressed, stressed, final) instead of grouped into two (strong vs.weak), and

(B) substitution distance is grouped into six intervals (2nds-7ths) rather than number of semitones (1-11).

Note that for A, only a subset of each sample contained ornamental notes (English: $n = 49$ pairs; Japanese: $n = 55$ pairs).

Figure S4. Additional exploratory analyses. Related to Figure 4.

(A) Analysis of difference in functional vs. non-functional stability against overall similarity. X-axis shows the overall % identity of all notes within a given highly related pair, and the y-axis shows the difference when this % is calculated using only the subset of stronger functional notes minus when it is calculated using only the subset of weaker functional notes. English $n=242$ highly related pairs, Japanese $n=86$ pairs.

(B) Regression model exploring interactions between substitution distance and rhythmic function. Data points represent the number of substitutions between all possible pairs of 12 scale degrees, counted separately whether both notes are coded as stronger function (red) or weaker function (blue; $n = 252$ possible note pairs total). Left-hand side represents counts among our sample of 242 highly related pairs of English folk song melodies, right-hand side represents 86 highly related pairs of Japanese folk song melodies (total counts are correspondingly lower for the smaller Japanese sample). The y-axis shows substitutions (number of times a given substitution between two notes appeared). The x-axis shows the substitution distance between a given pair of notes. Solid lines represent model estimates for given rhythmic functions, lighter shading represents 95% confidence intervals.

Table S1 | Sensitivity analyses modifying assumptions of the analyses for our predictions regarding rhythmic function. Related to Figure 4. See STAR Methods for details.

	English		Japanese	
	t	df	t	df
(B) Sensitivity analyses for rhythmic function				
0. Primary analysis (Fig. 4A)	15.2	241	6.8	85
1a. Function: final vs. stressed (cf. Fig. S3A)	4.6	241	1.2	85
1b. Function: stressed vs. unstressed (cf. Fig. S3A)	12.8	241	4.9	85
1c. Function: unstressed vs. ornamental (cf. Fig. S3A)	6.2	48	5.2	54
2a. Time: older sample	9.3	139	4.7	29
2b. Time: younger sample	12.3	142	3.0	40
3a. Singer: same	4.3	20	2.3	36
3b. Singer: different	12.9	160	6.5	34
4a. Coder: PES	10.0	121	4.7	45
4b. Coder: GC	11.6	119	4.9	39
5. Unpaired t-tests	14.9	456	6.4	157

Table S2 | Sensitivity analyses modifying assumptions of the analyses for our predictions regarding substitution distance. Related to Figure 4.
See STAR Methods for details.

	English		Japanese	
	r_s	n	r_s	n
0. Primary analysis (Fig. S3B)	-1.00	6	-.90	6
1. Substitution distance measured in semitones (cf. Fig. 4B)	-.81	11	-.82	11
2a. Time: older sample	-1.00	6	-.94	6
2b. Time: younger sample	-1.00	6	-.88	6
3a. Singer: same	-.93	6	-.90	6
3b. Singer: different	-1.00	6	-.88	6
4a. Coder: PES	-1.00	6	-.90	6
4b. Coder: GC	-1.00	6	-.94	6

Table S3 | Regression results modeling interactions between substitution distance, rhythmic function, and note frequencies. Related to Figure S4 and Figure 4.

Bracketed values represent 95% confidence intervals. See STAR Methods for details.

Model	Sample	N	Intercept	Function	Subs.	Function x Substitution	Note frequency 1 x 2	Note frequency interaction x Proportion functional	ELPD
Null	English	252	-1 (-1.9, -0.31)	-	-	-	-	-	-972.96 (118.77)
Note frequency	English	252	-1.7 (-2.5, -1.1)	-	-	-	7.9 (5.8, 10)	-	-972.09 (118.26)
Baseline: Note Function & Frequency	English	252	-1.5 (-2.1, -0.99)	-	-	-	-	8 (7.1, 9.1)	-751.15 (86.67)
Distance model - strong function only	English	126	-0.4 (-1.5, 0.55)	-	-0.61 (-0.85, -0.41)	-	-	20 (13, 29)	-
Distance model - weak function only	English	126	1.1 (0.39, 1.8)	-	-0.52 (-0.6, -0.45)	-	-	8.1 (6.1, 10)	-
Function	English	252	-2 (-2.6, -1.4)	1.3 (0.91, 1.7)	-	-	-	3.7 (1.9, 5.4)	-722.62 (86.12)
Function + Distance	English	252	0.29 (-0.4, 0.89)	1.2 (0.86, 1.7)	-0.52 (-0.6, -0.45)	-	-	4.1 (2.4, 5.8)	-254.17 (23.27)

Function * Distance	English	252	0.33 (-0.46, 1)	1.2 (0.64, 1.8)	-0.54 (-0.7, -0.39)	0.019 (-0.13, 0.18)	-	4 (2.3, 5.8)	-253.69 (23.12)
Null	Japanese	252	-2.9 (-4.2, -2)	-	-	-	-	-	-296.52 (44.99)
Note frequency	Japanese	252	-3.4 (-4.6, -2.5)	-	-	-	6.3 (4.2, 8.8)	-	-288.25 (43.01)
Baseline: Note Function & Frequency	Japanese	252	-2.7 (-3.5, -2)	-	-	-	-	4 (3, 5)	-264.65 (38.69)
Distance model - strong function only	Japanese	126	-0.27 (-1.6, 0.78)	-	-0.85 (-1.2, -0.53)	-	-	14 (9.7, 21)	-
Distance model - weak function only	Japanese	126	0.076 (-0.95, 0.88)	-	-0.59 (-0.77, -0.44)	-	-	5.7 (4.4, 7.4)	-
Function	Japanese	252	-2.9 (-3.9, -2.1)	0.45 (-0.11, 1)	-	-	-	3.2 (1.6, 4.7)	-264.7 (38.43)
Function + Distance	Japanese	252	-0.27 (-1.2, 0.49)	0.28 (-0.25, 0.85)	-0.56 (-0.72, -0.43)	-	-	3.9 (2.3, 5.3)	-141 (19.45)
Function * Distance	Japanese	252	-0.07 (-1.1, 0.85)	0.075 (-0.72, 0.85)	-0.65 (-0.95, -0.41)	0.1 (-0.15, 0.39)	-	3.8 (2.2, 5.2)	-143.42 (19.95)