

Climate, vocal folds, and tonal languages: Connecting the physiological and geographic dots

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We summarize a number of findings in laryngology demonstrating that perturbations of phonation, including increased jitter and shimmer, are associated with desiccated ambient air. We predict that, given the relative imprecision of vocal fold vibration in desiccated versus humid contexts, arid and cold ecologies should be less amenable, when contrasted to warm and humid ecologies, to the development of languages with phonemic tone, especially complex tone. This prediction is supported by data from two large independently coded databases representing 3,700+ languages. Languages with complex tonality have generally not developed in very cold or otherwise desiccated climates, in accordance with the physiologically based predictions. The predicted global geographic–linguistic association is shown to operate within continents, within major language families, and across language isolates. Our results offer evidence that human sound systems are influenced by environmental factors.

climate | language | adaptation | tone

A standard assumption in linguistics is that sound systems are immune to ecological effects (1). This presumption has been called into question by several recent studies providing evidence for a correlation between aspects of phonology (such as sonority) and climatic and geographic factors (such as temperature, plant cover, or terrain), as well as behaviors associated with such factors (2–9). Most recently, a correlation was uncovered between ejective sounds and regions of high elevation in a sample of nearly 600 languages (10). Although two plausible physiological motivations are offered in ref. 10 for the correlation between ejective use and reduced ambient air pressure, those explanations have yet to be supported by experimental evidence. The uncovered patterns could be epiphenomenal, and in general, the cross-linguistic statistical studies in question have not been buttressed by experimental support (11).

In this study, we offer evidence for a negative correlation between linguistic tone and characteristic rates of desiccation in ambient air. In contradistinction to the aforementioned studies offering geographic/phonetic correlations, however, we suggest this correlation is predicted by extensive experimental research on the properties of the human larynx. This research, which has been conducted by numerous laryngologists over the last decade and a half, has not been previously tied to the distribution of the world's tonal languages. We submit that the research predicts that the relatively precise manipulation of the vocal folds associated with tone, especially complex tone, should be more difficult to achieve in arid climates—particularly very cold ones—when contrasted to warmer and more humid climates. We offer global, continental, and intralinguistic-family data consistent with the expected geographic/tonemic association. Our results cannot facilely be ascribed to well-known phylogenetic and areal relatedness. We conclude by suggesting that the most reasonable interpretation of the data is that the articulation of linguistic sounds is ecologically adaptive, just like other forms of human behavior.

Effects of Ambient Air Conditions on Vocal Fold Physiology

The biomechanical properties of the vocal folds are influenced directly by hydration levels (12). For instance, dehydration of the vocal folds results in decreased amplitude of vocal fold vibration (13). Fundamental frequency is impacted by hydration or dehydration according to a variety of metrics obtained from in vivo and ex vivo laboratory studies. Increased hydration is associated with heightened vocal fold viscosity and facility of phonation (14). In contrast, dehydration of the vocal folds is associated with increased phonation threshold pressure (PTP) and increased perceived phonation effort (PPE) (14), although the extent of PTP increase remains a matter of inquiry (15). Laryngeal dehydration is also associated with alterations to the ionic composition of the vocal fold surface liquid, more specifically an increase in Na⁺ concentration and associated modulation to vocal fold elasticity (16, 17).

Most relevant for our purposes, a number of studies have demonstrated that the mere inhalation of dry air (rather than the artificial or ex vivo dehydration of the larynx) impacts vocal fold physiology and results in clear effects on phonation. Crucially, in the context of the present discussion, these in vivo studies demonstrate that even brief exposure to desiccated air can negatively impact precise phonation via increased rates of jitter (imprecise pitch) and of shimmer (varying amplitude) (18). The former finding is particularly pertinent in the context of a discussion of complex tone, which necessitates relatively precise phonation, and therefore reduced rates of jitter, given that three or more pitch variances are used in a phonemically contrastive manner in languages with complex tone (19).

As noted in ref. 18, “even after a short provocation with dry air, a significant increase in perturbation measures” is evident in

Significance

The sound systems of human languages are not generally thought to be ecologically adaptive. We offer the most extensive evidence to date that such systems are in fact adaptive and can be influenced, at least in some respects, by climatic factors. Based on a survey of laryngology data demonstrating the deleterious effects of aridity on vocal cord movement, we predict that complex tone patterns should be relatively unlikely to evolve in arid climates. This prediction is supported by careful statistical sampling of climatic and phonological data pertaining to over half of the world's languages. We conclude that human sound systems, like those of some other species, are influenced by environmental variables.

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phonation. This increase is due at least in part to the decreased viscosity of the laryngeal mucus and associated alterations to the cohesive forces at work during the contact portion of vocal fold oscillations. Inhalation of desiccated air resulted in subjective impressions of impaired voicing abilities among healthy subjects, impressions that were consistent with objective findings on jitter, shimmer, and noise-to-harmonic ratios (18). In the case of some subjects, jitter measurements increased over 50% after merely 10 min of inhalation of very dry air. Similar studies have replicated these findings with different methodologies, demonstrating that oral breathing (which, when contrasted to baseline nasal breathing, results in less treated/humidified air reaching the larynx) is directly associated with increases in PTP and PPE (20). Hydration and increased ambient humidity are positively associated with reduced PTP and PPE and, crucially, with decreases in jitter and shimmer (21–24). The effects of aridity on the vocal tract have long-term effects, as evidenced by the fact that otorhinological practice patients often exhibit throat ailments associated with dry working conditions. Low humidity is reported to be the cause of sore throat in 30% of cases (25). Also, it is well known that singers maintain tones less effectively in dry conditions (18). Clearly, the human larynx is susceptible to environmental aridity. Although nasal breathing mitigates such aridity, it does not do so completely, and furthermore, oral breathing is required at higher rates of respiration.

Frigid air is always dry, regardless of saturation level (i.e., relative humidity), due to its reduced water vapor capacity (26). Air at -10°C reaches water saturation at 2.3 g/m^3 , whereas air at 30°C does so at 30.4 g/m^3 . In other words, a difference of 40 degrees translates into a 13-fold difference in water vapor capacity. Independent of its desiccation, cold air inhaled via the nasal cavity yields greater bronchoconstriction and increased nasal fluid (27), two factors that promote oral breathing. Oral breathing, even of nondry air, promotes the desiccation of the vocal tract and the evaporation of the airway surface liquid of the vocal cords, and the latter has been shown to yield a variety of difficulties vis-à-vis precise phonation (14). The effects of breathing cold air on the vocal tract and the larynx have been supported by numerous studies of those active outdoors in frigid contexts (28, 29). These effects are not easily compensated for, and factors such as laryngitis and xerostomia (dry mouth) are recurrent among human populations in very cold regions (28). In short, under both laboratory and naturalistic conditions, the inhalation of very cold and arid air yields short-term and long-term desiccating effects on the vocal tract and the vocal cords. And desiccation of the vocal cords has been clearly tied to imprecision of phonation (14).

In addition to these findings, a recent study has found that muscle tension dysphonia (MTD), a laryngeal ailment that can be provoked or exacerbated by dry ambient air, has demonstrable negative effects on the production of phonemic tone. Various metrics offered in ref. 30 demonstrated that MTD-diagnosed Vietnamese speakers were more likely than speakers of nontonal languages to have anomalous patterns of laryngealization during the production of tones. MTD-characteristic influences on phonation included incomplete glottal closure and impacted pitch quality (two factors that influence pitch discrimination), and the authors concluded that the tonal status of Vietnamese had an effect on the heightened expression of some MTD symptoms during speech. So there is already work demonstrating that a pathology that is more prevalent in dry ambient conditions is associated with the impairment of the production of lexical tone among native speakers of a tonal language.

These deleterious effects of desiccated air on precise phonation have also been confirmed in a series of *ex vivo* studies with excised canine and ovine larynges (31–33). This confirmation suggests plainly that the sensitivity of speakers' vocal cords to desiccated air is genotypically and phenotypically normal and operative across all human populations. In short, it is well established that desiccated ambient air results in compromised voice quality, as

evidenced by increases to jitter, shimmer, PPE, and PPT. In contrast, conditions of humidity and hydration are positively associated with facilitated phonation and more specifically facilitated precise phonation, given the associated comparatively reduced rates of jitter and shimmer.

Languages with phonemic tone necessitate voicing at relatively precise pitches throughout an individual's normal range. As noted in cross-linguistic surveys of fundamental frequency, the typical pitch range for most human males is about 100 Hz (34–36). The just-noticeable difference between lexical tones is about 10 Hz (37), and a cross-tone pitch difference of at least 20–30 Hz is considered marginally sufficient to achieve phonemic contrast (38). These figures suggest that languages with more than three level phonemic tones present articulatory and perceptual challenges, a suggestion that is supported by work on the acquisition of tonality (39, 40). Some research suggests that the upper limit on level phonemic tones in a language is five (41), and languages with this many contrasts tend to resort to minor differences in laryngeal setting (creaky, breathy) to express tonal contrasts (34, 42). In short, producing complex tonality requires precise vocal control. The imprecision of phonation characteristic of desiccated contexts makes the task more challenging.

The Prediction. Given this series of facts, we hypothesized that languages should not be maladaptive vis-à-vis ambient air conditions. That is, like other forms of human behavior (see, e.g., refs. 43–45), the articulation of phones should evolve in accordance with ecological factors that directly impinge on their production. More specifically, complex tone (and to a lesser extent all phonemic tone) requiring comparably precise manipulation of fundamental frequency should be disfavored in extremely arid contexts. We predict as well that this tendency should be particularly apparent in frigid climates, given the extremely reduced water vapor capacity of cold air.

Although languages with complex tone can be spoken in any geographic context—for instance, Cantonese speakers are more than capable of communicating in the Siberian tundra—it seems less likely that such languages would develop their complex tonality in areas with typically frigid and/or desiccated ambient air, given the factors propounded above. Ease of articulation, perception, and transmission is already known to be a strong motivator in the prevalence of some sounds in the world's languages—for instance, labial and velar plosives (46). The hypothesis does not predict that languages should necessarily trend diachronically toward (complex) tone in warm/humid regions but merely predicts that languages should be more likely to lose/never acquire that phonological feature if spoken in very cold or otherwise arid regions over a significant although undetermined time period.

We stress that this prediction follows naturally from our survey of the relevant experimental work on the influence of ambient air characteristics on phonation. Some attention has been paid to the global distribution of tonal languages in the literature, where it has been noted, for instance, that they correlate with the distribution of particular genes associated with brain development, namely ASPM (abnormal spindle-like, microcephaly-associated) and microcephalin, in human populations in the Old World (47, 48). There are no controls in these studies for the role of climate such as the one we are proposing. Although the explanations may not be mutually exclusive, we submit that our hypothesis has a clearer and experimentally buttressed motivation.

Distribution of the World's Tonal Languages

Many languages of the world use phonemic tone, in which pitch is used to contrast lexical meaning. Some estimates (49) suggest that over half the world's languages are tonal at least to a moderate extent, and of course, all spoken languages require the modulation of fundamental frequency for some purpose, be it word-level stress, phrasal stress, or general pragmatic functions.

Only a smaller portion of the world's languages use a system of complex tone, typically defined as a system containing three or more pitch-based phonemic contrasts (50). In contrast to other linguistic uses of pitch modulation, systems of complex tone generally require greater precision of pitch modulation at the level of individual segments of sound, as phonemic categorization and associated semantic judgments can be directly impaired by imprecision of pitch in such cases.

We examined the geographic distribution of languages with phonemic tone, paying particular attention to those with complex tone in two large independently coded phonological databases, the World Atlas of Linguistic Structures online (WALS) of the Max Planck Institute and the Phonotactics Database of the Australian National University (ANU). These databases have been constructed by prominent linguistic institutions and are based on careful sampling of source materials collected by field linguists throughout the world (see refs. 51 and 52 for details on the creation of these databases). The 527 languages in the WALS database were chosen so as to somewhat equitably represent world regions and linguistic families, although rigorous phylogenetic controls were not applied (51). In contrast, the creators of the ANU database simply strived to represent as many languages as possible (52). For that reason, we relied on the ANU database in our Monte Carlo analysis below, which allows for stricter controls of genealogical relationships.

The language locales in these databases represent the best estimates of the places to which the respective languages are indigenous. Fig. 1 is a map representing the distribution of languages with and without systems of complex tone, for the larger ANU database (3,756 languages). As we see in the figure, languages with complex tone ($n = 629$) are located primarily in tropical regions and are generally absent in extremely desiccated environments, whether high latitudes or regions such as the Atacama, Sahara, Gobi, Arabian, and Australian deserts. Two alternate maps, including a heat map of tone "hot spots," are presented in Figs. S1 and S2.

Phoneticians have also noted that tone tends to be more heavily associated with particular linguistic areas than with linguistic families (50). Such areas are, in line with our prediction, largely restricted to major warm regions of high humidity, most notably Southeast Asia, sub-Saharan Africa, and New Guinea. In the Americas, languages with complex tone are found primarily in the southern regions of North America and, in the few cases they exist in South America, in Amazonia.

The prediction is further supported by the distribution of languages according to the mean specific humidity (MH) and mean annual temperature (MAT) values of their locales. (Specific humidity refers to the ratio of water vapor to total air content.) We extracted MH data for each locale from the climate database in ref. 53, which includes monthly averages for regular geographic points across the earth from 1949 to 2013. For each point and each month, the average MH was calculated over all years. Then, the mean of each monthly mean was used as the MH for that geographic point. We used specific humidity for our global analysis, rather than relative humidity, as our predictions are strongest for very frigid regions and the absolute water content of subfreezing air approaches zero, or is otherwise negligible, regardless of saturation rate (26). MAT data for each pair of coordinates were gathered via the bio-clime package accessible through ArcGIS, a geographic information system platform (www.arcgis.com). MH and MAT were collected for the language locales in both the WALS and ANU databases. For Fig. 2 and Fig. S3, we relied on the WALS data, as those data fairly equitably represent different regions and language families.

Fig. 2 shows the cumulative proportion of languages observed as the specific humidity increases. This distribution increases more slowly for complex tone languages than languages without tones. Languages with complex tone are clearly unlikely to occur in regions with extremely low MH. MH data are the most crucial for our case, as they factor in all arid locales—whether hot deserts or frigid regions. The languages with complex tone clearly distribute primarily in regions with higher humidity values and are absent in the most desiccated regions. Furthermore, there is a clear step-wise gradation whereby languages with simple tone occur in desiccated regions at a higher rate than languages with complex tone, but at a lesser rate than languages without any tone. The findings vis-à-vis MAT also reflect this pattern, as evident in Fig. S3. Languages in very cold regions uniformly avoid complex tone and, to a lesser extent, simple tone. This is particularly true in subfreezing contexts. Consider that, of the 629 languages with complex tone in the larger ANU database, there are only two clear instances of languages spoken in subfreezing (MATs of less than 0 °C), very desiccated regions, or 0.32%. In contrast, 101 of the 3,127 (3.2%) remaining languages are found in such regions; they occur at exactly 10 times the rate in such contexts.

However, analyses of aggregated data, even those that strive to represent diverse regions and families (like the WALS data), might be misleading. No rigorous genealogical control was performed on the typological data thus far examined, so larger

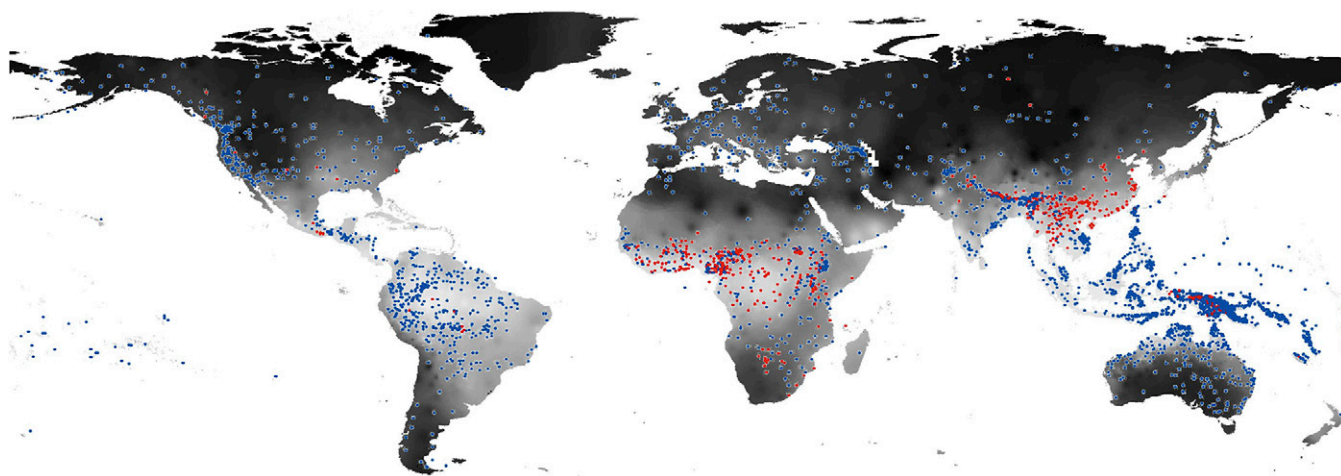


Fig. 1. Distribution of languages with complex tone (red dots) and without complex tone (blue dots) in the ANU database. Darker shading on map corresponds to lower MH.

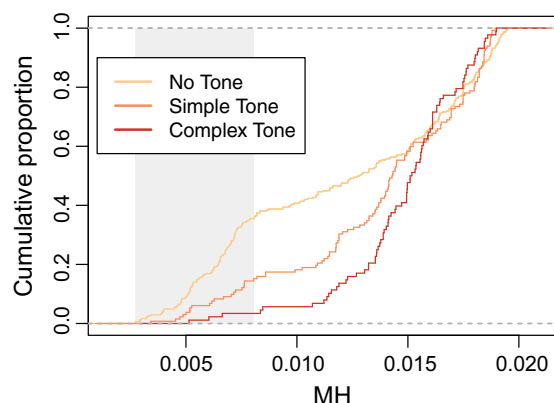


Fig. 2. Empirical cumulative distribution function for languages according to the MH of their locations, WALS sample. The bottom quartile of language locales (by MH) is shaded.

families could be better represented than smaller ones or language isolates. Also, the number of languages with complex tone is smaller than that with simple or no tone, so one could argue their narrower distribution around warmer regions (where most of the languages of the world exist) is accidental.

To assess the significance of our results while more carefully controlling for these factors, we conducted an analysis of range in a Monte Carlo framework. This type of analysis allows us to test for differences in the shape of the distributions of language types while also controlling carefully for genealogical influences. In every run of the simulation, a balanced sample of languages with complex tone was chosen at random from the ANU database by taking only one representative of each linguistic family among those in which complex tone was attested; the same was done for languages with simple or no tone. The goal was to compare whether the distributions of these samples differed for the two groups of languages. We ran 5,000 simulations at the 15th, 25th, 50th (median), and 75th percentiles of MH and MAT values, for each of the two language types; this yielded a total of 40,000 simulations. The lower percentiles are particularly crucial, as our predictions are strongest for low MH and MAT values.

If the tendencies apparent in the density distributions were mere artifacts of genealogy or areal effects, then every pair of Monte Carlo samples should exhibit similar climatic properties. In other words, sampled languages with complex tone would have higher MHs and MATs than languages without complex tone in about 50% of the cases, at each percentile. The distributions of the languages with and without complex tone clearly differ. The 15th, 25th, 50th, and 75th MH percentiles of balanced samples of languages with complex tone have higher MHs in 89%, 88%, 43%, and 49% of the sample cases, respectively, when contrasted to the simulations' balanced samples of the same percentiles of remaining languages. This is exactly in line with our predictions, as languages with complex tone overwhelmingly have higher MHs in the lower percentile ranges, suggesting clearly that such languages are extremely infrequent in very arid contexts, regardless of temperature. The 15th, 25th, 50th, and 75th MAT percentiles of balanced samples of languages with complex tone have higher MATs in 93%, 77%, 17%, and 19% of the sample cases, respectively, when contrasted to the equivalent simulations' balanced samples of remaining languages. These results also pattern neatly in the direction of our prediction, as languages with complex tone are clearly particularly avoided in very cold regions but also in very hot, arid regions. In Fig. 3, the Monte Carlo simulations based on the lower percentiles of MH and MAT, for which our account makes the strongest predictions, are summarized graphically. For our Monte Carlo results, the difference distributions have location

parameters outside the 95% confidence interval for the null hypothesis. This is unsurprising given the large effect sizes depicted in Fig. 3. Figs. S4 and S5 present all of the Monte Carlo simulations. (Fig. S5 also includes some additional comments regarding the avoidance of complex tone in the hottest regions, also consistent with our account.)

The distribution of the seven language isolates with complex tone is also restricted to warm, comparatively humid regions: Amazonia (Ticuna, Pirahã), sub-Saharan Africa (Laal, Bangime) and New Guinea (Damal, Lepki, Morori). In contrast, the 108 isolates without tone are spoken throughout the Americas, Eurasia, Africa, and Australia. A number are spoken in high latitudes in North America, South America, and Eurasia, as well as in numerous other arid regions. For both MH and MAT, there are clear disparities across isolates with and without complex tone, respectively. The average MH for isolates with complex tone is 0.017, whereas the average for other isolates is 0.013. This cross-group disparity is significant ($P = 0.02$, Mann–Whitney). Similarly, the average MAT for isolates with complex tone, 23.7°C , is greater than the average for the remainder of isolates, 19.1°C ($P = 0.07$, Mann–Whitney). These disparities correspond neatly with the predictions of our account, despite the small number of isolates with much tonality. Given the geographic breadth of the isolates, the disparity cannot be ascribed to areal effects either.

We also considered the language families with complex tone that straddle extremely diverse ecological zones: Afro-Asiatic, Sino-Tibetan, Nilo-Saharan, and Niger-Congo. Languages without tone in these language families are much more likely to be found in comparatively arid regions, when contrasted to those with tone and especially complex tone, and this disparity is statistically significant in each case (*SI Text, Intrafamily Analysis*).

Much as it is not simply due to phylogenetic confounds, the global pattern in question is not driven by one or a few linguistic

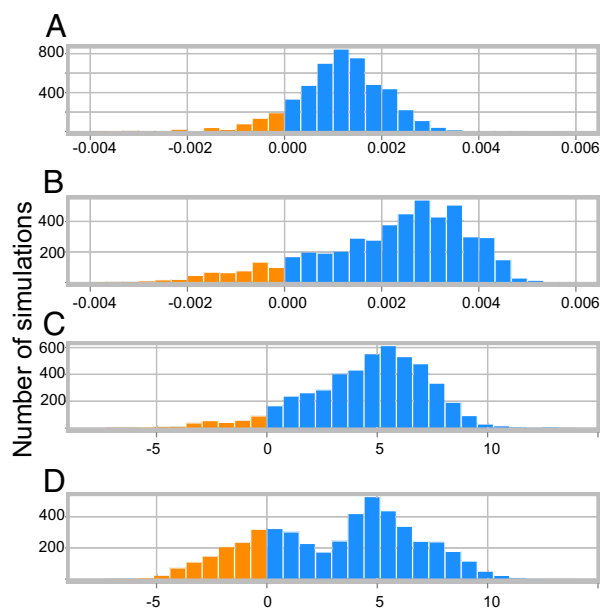


Fig. 3. Monte Carlo results. Distribution of the differences in the (A) 15th and (B) 25th percentiles of MH as well as the (C) 15th and (D) 25th percentiles of MAT. Each chart represents 5,000 samples. For each sample, one language per family among all languages with complex tone is considered, and the same number of languages without complex tone is sampled, again with only one representative per family. The values at each percentile are then contrasted, for sampled languages with and without complex tone. Blue results represent cases in which the MH and MAT for languages with complex tone were higher than that of the remaining languages. The x axis describes the disparity in MH for A and B and in degrees Celsius for C and D. The y axis represents number of samples.

areas. It surfaces clearly within Africa and Eurasia. Also, because some languages with complex tone do exist in southern North America (particularly Central America) and Amazonia but are generally absent elsewhere in the Americas, the pattern surfaces in the New World despite the generally reduced reliance on tonality in that part of the world. In addition, one of the other major noncontiguous regions with relatively robust levels of complex tonality is New Guinea. The statistically significant within-continent correlations are described in *SI Text, Intracontinental Analysis*.

Our intrafamily, cross-isolate, and Monte Carlo analyses suggest that the distribution in question is not due to phylogenetic factors. Our finding that the pattern surfaces within continents, in addition to our balanced Monte Carlo and cross-isolate results, suggests strongly that influences associated with specific regional patterns of linguistic contact also do not account completely for the patterns. From our perspective, we must ask why linguistic tone is so pervasively transferred across languages in some regions and why those regions tend to have arid borders. We believe that our account offers a natural explanation for this tendency and directly explains why the regions in which interlinguistic contact has led to pervasive use of tone—for example, sub-Saharan Africa and Southeast Asia—are warm humid regions. Put differently, it seems likely that tone spreads across languages more effectively via interlinguistic contact in regions with favorable ambient conditions, and very cold/dry regions apparently serve as barriers to the spread of (complex) tone. Both external and internal diachronic processes may be impacted to some degree by such ambient conditions, in ways that, at the least, merit serious consideration.

Discussion and Conclusion

This paper used findings from vocal fold physiology to predict that climatic factors constrain the use of phonemic tone. Our investigation showed that the distribution of tonal languages is in line with this prediction.

Phonetic accounts of tonogenesis, focusing on the role of laryngeal consonants in conditioning the fundamental frequency of adjacent vowels (54, 55), are crucial to the understanding of the development of tone but fail to explain the climatic patterns we find. After all, prevocalic voicing contrasts are extremely common in the world's languages, but tone and more particularly complex tone only develop in some cases. Whatever the etiology of contrastive pitch in a given language, maintaining and augmenting the phonemic burden of pitch requires the relatively precise manipulation of the vocal folds, which is not easily learned even during normal acquisition (35, 36). Given the requisite absolute precision of vocal fold manipulation in languages with phonemic tone (especially complex tone), it seems natural that intricate tonal contrasts would be avoided when environmental pressures also work against such manipulation. This avoidance could be facilitated diachronically through, for example, reduced accuracy/increased jitter in the production of borrowed words with complex tones.

Previous work has suggested that aspects of language appear to be adapted to ecological or social niches (56). For example, linguistic diversity is correlated with biodiversity (57) and pathogen prevalence (58), and morphological complexity is related to

population size (59). Our results are further suggestive of external influences on language. In contrast to previous work on putative geographic/climatic influences (2–10), however, the causal relationship we are suggesting is supported by many experimental results. It is also supported by patterns in a much larger sample of the world's languages, including patterns within language families and among language isolates. Like the communication systems of avian species (60, 61), it appears that human languages are environmentally adaptive. This is not necessarily surprising given the general adaptability of human behavior (62, 63) and human biology (64, 65) to cold climes and given the existence of other ecological effects on nonconscious patterns in human behavior (66).

We have not made specific claims vis-à-vis the time scale involved in this ecological adaptation. Numerous complex factors contribute to diachronic sound shifts (67, 68), and it is possible that in the short term some sound changes may be inconsistent with this adaptation. Nevertheless, the synchronic distribution of the world's languages suggests that the adaptation is at work over the long term.

The physical components of speech articulation all represent exapted portions of the upper respiratory and digestive tracts that have more primal functions. In other words, speech articulation is ultimately a biological phenomenon. We think that, absent any of the distributional data we have considered, it is actually natural to expect that phonetic patterns are susceptible to environmental pressures. The fraction of research in laryngology we have surveyed suggests in and of itself that the expectation of such pressures is more than reasonable. Particularly in light of the ubiquity of speech in the human experience, we suspect that human sound systems are susceptible to ecological pressures. In cultures in which speech volume has been assessed quantitatively, it has been found that humans produce on average 15,000+ words per day (69). So, if speakers rely on a sound pattern that is maladaptive (even in minor ways) in particular ambient conditions, they do so ubiquitously. In the case at hand, languages with complex tone require the pervasive implementation of a particular behavior, very precise phonation, which is according to all extant pertinent experimental work simply ill-suited to desiccated contexts.

We submit that our central claim is the most plausible available conclusion in light of the relevant linguistic, physiological, and quantitative evidence, and furthermore that the latter two sorts of data are crucial for shedding light on the distribution of language types. Although we believe our account is extremely plausible, we recognize that more research is required to fully explore these issues. We hope that experimental phoneticians and others examine the effects of ambient air conditions on the production of tones and other sound patterns, so that we can better understand this pivotal way in which human sound systems appear to be ecologically adaptive.

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Supporting Information

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SI Text

Intrafamily Analysis. The geographic distribution of complex tonality within the relevant language families straddling very diverse ecologies is consistent with the hypothesis being proffered. For example, complex tone is thought to have been a feature of Proto-Afro-Asiatic, according to some analyses (1). This feature has been lost in the northern branches of that family, which have gradually moved northward over the last few millennia according to one widely accepted theory on this family's development (2). The most recent estimate of the Proto-Afro-Asiatic homeland places it in West Africa, although there appears to be little consensus on this issue (3). In contrast, the Proto-Nilo-Saharan homeland is conjectured to have been in eastern Africa, with some researchers placing it north of Lake Victoria (2). Although the status of tone in the language is unclear, the distribution of the feature in its daughter languages is entirely consonant with our account. Rather than simply noting that languages of the Sahara are not characterized by complex tone as their sub-Saharan counterparts are, we suggest that the Sahara has served as a geographic barrier to the northward spread of complex tone within major language families encompassing Saharan and sub-Saharan ecologies.

Niger-Congo languages with complex tone are relatively less prevalent in the arid regions of southern Africa, when contrasted to the more tropical regions of the continent. The homeland of Proto-Niger-Congo (which is assumed to have had complex tone) was quite probably in West Africa, and so complex tone has apparently been lost in a number of the more southern members of the family, spoken in more arid regions. The precise homeland of Proto-Sino-Tibetan remains a source of debate, as does the presence of complex tone in the language. One suggested urheimat is in Sichuan, whereas the most recently posited is in Nagaland, India (2). Neither region has an arid climate presently. There is consensus among many specialists, although by no means all, that tone systems in Sino-Tibetan languages are not directly cognate and have arisen independently. According to alternate accounts, Proto-Sino-Tibetan had a two-tone system that was lost in the Himalaya branch of Tibeto-Burman (see discussion of these issues in ref. 4). Under either interpretation, our account offers a potential explanation as to why such tone systems became less prevalent in branches spoken in more arid, cooler regions on the Tibetan plateau and as to why complex tone in Sino-Tibetan was somewhat favored in comparably warmer, humid regions.

To further test the role of climate on the distribution of tonality within language families, we conducted regressions based on tonality and the MH and MAT of language locations, for each major language family in question. Such tests also allow us to test our hypothesis without binning data into "complex" and "non-complex" tone categories. Languages in the ANU database are categorized as having 0 or 2–12 phonemic tonal contrasts. In the case of the 290 Sino-Tibetan languages, with a maximum of eight phonemic tones, tonality correlated significantly with MH (Pearson's $r = 0.150$, $P = 0.005$) and MAT (Pearson's $r = 0.138$, $P = 0.009$). This MAT and MH variation is likely due in part to the generally higher mean elevation of Sino-Tibetan languages without complex (3+) tone (2,049 m vs. 1,503 m, $P < 0.01$, Mann-Whitney). In the case of Afro-Asiatic, there are a total of 117 languages in the ANU database, with the maximum number of phonemic tones being 5. A striking intrafamily correlation was observed between MH and number of tones (Pearson's $r = 0.442$, $P < 0.001$), as well as between MAT and number of tones (Pearson's $r = 0.471$, $P < 0.001$). In the case of the 304 Niger-Congo

languages in the ANU database (with a max of 12 tones in a language), MH once again correlated with tone (Pearson's $r = 0.276$, $P < 0.001$). MAT was not associated with number of tones in a significant manner. In the case of the 83 Nilo-Saharan languages in the database (with a maximum of six tones), MH was associated with number of tones (Pearson's $r = 0.172$, $P = 0.06$), whereas MAT was not. (Given the locations of the Nilo-Saharan and Niger-Congo languages, the absence of MAT associations is not surprising. As stated in the text, the MH data are most crucial for testing our account.)

In short, the significant within-family discrepancies are plainly in line with the predictions and offer strong additional support for our hypothesis. Phylogenetic influences are clearly not responsible for the global pattern in question, as it surfaces clearly within the only major families for which our hypothesis can be tested.

Intracontinental Analysis. We analyzed the climatological and tone data separately for languages in North America, South America, Africa, and Eurasia, respectively. The four major landmasses include numerous frigid and dry regions, as well as many tonal and nontonal languages, enabling us to test our hypothesis in ways that some linguistically dense regions (Polynesia, Indonesia, Papua New Guinea, and Australia) do not. Once again, we tested for correlations between MH and number of tones in a language, as well as MAT and number of tones, in the languages of the ANU database. In the case of the 554 African languages, a positive tone association was found for MH (Pearson's $r = 0.306$, $P < 0.001$) and a weaker yet significant tone association was also observed for MAT (Pearson's $r = 0.150$, $P < 0.001$). For the 862 Eurasian languages, a positive correlation was again observed for both MH (Pearson's $r = 0.314$, $P < 0.001$) and MAT (Pearson's $r = 0.182$, $P < 0.001$). In the case of the 336 North American languages, weak associations between tonality and MH (Pearson's $r = 0.073$, $P = 0.090$) and between tonality and MAT (Pearson's $r = 0.065$, $P = 0.117$) approached significance. The comparative weakness of the association in North America is unsurprising given how relatively few tonal languages there are in that region. In the case of the 391 South American languages in the database, the predicted association between MH and tonality again surfaced in a significant manner (Pearson's $r = 0.127$, $P = 0.006$), whereas the relationship between MAT and tonality was weaker but also significant (Pearson's $r = 0.087$, $P = 0.042$). These associations are largely due to the fact that in Amazonia there are seven languages with complex tone, representing five distinct linguistic stocks. None of the languages in South America outside Amazonia are characterized by complex tone. In short, the prediction that languages with tone, particularly complex tone, should not typically surface in very desiccated regions is also supported by the intracontinental data.

Note that, for our intracontinental and intrafamily results, MH and tonality generally correlate in a more powerful manner than MAT and tonality. Because aridity characterizes both very cold and otherwise dry regions, this is consistent with our account. In many hot, dry regions, tone is generally less prevalent (see also Monte Carlo results in Fig. S5). This tendency does not support a simple association between MAT and tonality, however. In contrast, this distributional fact is reflected in regressions based on MH and tonality.

Languages with complex tone are actually somewhat common in warm (but not extremely hot) humid regions, and this commonality cannot pithily be ascribed to the general linguistic density of such places. They are, however, a geographical oddity in frigid regions and other arid regions. Indubitably, the

Figure 1 consists of four histograms, labeled a, b, c, and d, showing the distribution of MH values. The x-axis for all plots is 'MH' ranging from -0.004 to 0.006. The y-axis for all plots is 'Number of simulations'.

- Plot a:** Shows the distribution of MH for $N=1000$ and $T=1000$. The distribution is centered around 0.001, with a peak frequency of approximately 800.
- Plot b:** Shows the distribution of MH for $N=1000$ and $T=1000$. The distribution is centered around 0.003, with a peak frequency of approximately 450.
- Plot c:** Shows the distribution of MH for $N=1000$ and $T=1000$. The distribution is centered around 0.000, with a peak frequency of approximately 600.
- Plot d:** Shows the distribution of MH for $N=1000$ and $T=1000$. The distribution is centered around 0.000, with a peak frequency of approximately 1500.

Fig. S4. Monte Carlo distribution of the difference in MH in the (A) 15th, (B) 25th, (C) 50th, and (D) 75th percentiles. Each chart represents 5,000 samples. Blue bars represent samples in which languages with complex tone had higher MH values than languages without. The lower percentiles of MH for languages with complex tone are clearly higher, across the vast majority of randomized simulations, than the lower ranges of MH for the remaining languages. The significant results in Fig. S4 suggest plainly this cross-language-type disparity is not due to phylogenetic confounds.

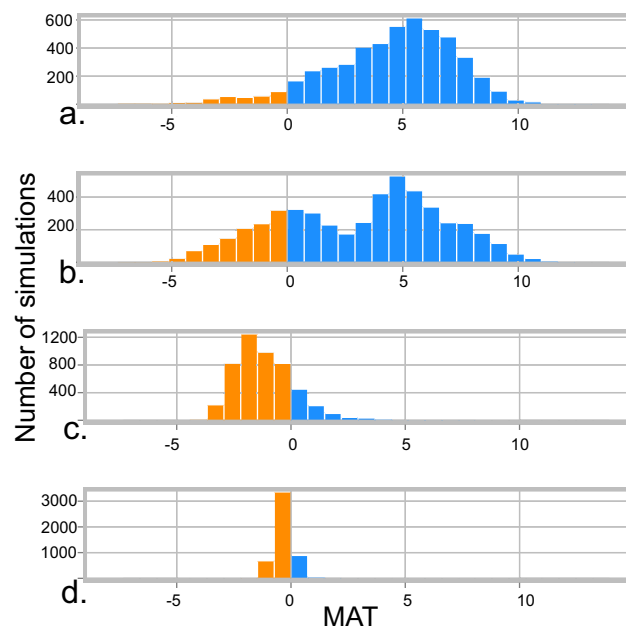


Fig. S5. Monte Carlo distribution of the difference in MAT in the (A) 15th, (B) 25th, (C) 50th, and (D) 75th percentiles. Each chart represents 5,000 samples. Blue bars represent samples in which languages with complex tone had higher MAT values than languages without. The lower percentiles of MAT for languages with complex tone are clearly higher, across the vast majority of randomized simulations, than the lower ranges of MAT for the remaining languages. At the higher percentiles, MAT values for languages with complex tone are generally lower. In other words, these data suggest that languages with complex tone are avoided in some of the hottest regions as well, in line with our hypothesis. As evident in Fig. 1, they are lacking in, for example, the Australian, Arabian, and Saharan deserts. (They are also absent on the hot Indian subcontinent.) This is also consistent with our hypothesis, as such regions are associated with desiccation and dehydration.