Response to Comments on "Phonemic Diversity Supports a Serial Founder Effect Model of Expansion from Africa"

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Concerns have been raised about my proposal that global phonemic diversity was shaped by a serial founder effect during the human expansion from Africa. I welcome this discussion of new data and alternative interpretations. Although this work highlights interesting questions for future research, it does not undermine support for a serial founder effect model of expansion of language from Africa.

I hypothesized that phoneme inventory size is subject to a serial founder effect like that observed in population genetics (1). The plausibility of such a process is grounded in theoretical models of cultural and linguistic transmission, which predict that small populations should carry fewer phonemes (2–4), and an observed positive correlation between phonemic diversity and speaker population size (1, 5). If phonemes are more likely to be lost in small founder populations, a succession of founder events during range expansion should progressively reduce phonemic diversity with increasing distance from the point of origin. I show that global variation in phonemic diversity is clinal and, like our genetic diversity, fits a serial founder effect model of expansion from Africa. As for any correlational finding, it is important to consider alternative causal explanations, and so much of the paper (1) and subsequent discussion (6–10) is devoted to examining potential alternatives. Here, I continue this process, addressing a number of concerns that relate to the data and assumptions on which the result is based (11–13). Although these warrant consideration and raise interesting questions for future research, I argue that they do not undermine the hypothesis presented in the paper.

Cysouw et al. criticize my use of the term "phonemic diversity" to describe the number of phonemes in a language, arguing that although phenotypic or genetic diversity measure within-population variation, phonemic diversity measures between-population variation. Phonemic diversity is a convenient shorthand, but I am agnostic about the use of the term, particularly if it engenders confusion. To be clear, phonemic diversity is not a measure of variation between populations; it is simply a property of populations—the measured number of phonemes carried by speakers. Although phonemic diver-

sity is measured in a different way from genetic diversity, the analogy holds in the sense that the link with population size that predicts a serial founder effect in genetic diversity can also be applied to phonemic diversity.

The results I reported are based on phoneme counts derived from the *World Atlas of Language Structures* (WALS) (14), combining binned estimates of relative vowel, consonant, and tone inventory size and assigning equal weights to each. This equal weighting was criticized as being inappropriate (11–13) because, for example, there are many more consonants in languages than vowels or tones, and the binning procedure used in WALS may lose information in a way that biases results.

Cysouw et al.'s serial founder analysis of reweighted WALS data, controlling for population size and language affiliation, also supports an African origin. Residuals from a regression of population size and language affiliation against their UCLA Phonological Segment Inventory Database (UPSID) (15) data are highest in North America, but this does not speak to the independent effects of population size and distance from Africa on phonemic diversity. When the UPSID data are used in a serial founder analysis controlling for population size and language affiliation, Cysouw et al. also find support for an African origin, even when the two most highly diverse Khoisan languages are excluded, although the inferred origin is expanded to include the Caucasus.

Wang et al. analyze a selection of languages from their own source of phonemic diversity data and show that although the relationship between total phonemic diversity and distance from Africa remains significant, there is a stronger relationship with distance from Europe and central Asia. However, this result is dependent on four closely related outliers in Wang et al.'s data from southeast Asia (two Tai-Kadai languages and two Wu dialects). Removing these nonindependent outlier languages again favors an origin in Africa ($r = -0.471$, $P < 0.001$) over central Asia ($r = -0.455$, $P < 0.001$) or Europe ($r = -0.461$, $P < 0.001$).

Including all languages in the same hierarchical linear modeling approach used in the original paper to control for population size and account for relatedness between languages within the same family, Wang et al.'s data also favors an African origin [Bayesian information criterion (BIC) = 776.9], over central Asia (BIC = 787.4), or Europe (BIC = 777.7)], although the improvement over a European origin is not decisive.

Van Tuyl and Pereltsvaig use Wikipedia to identify some cases of possible disagreement in levels of phonemic diversity. There is clearly some ambiguity or discrepancy in phoneme assignments and what exactly is counted between sources. As I have advocated elsewhere (6), the way to resolve this is to continue work to standardize phoneme inventory data and evaluate the serial founder effect model and its alternatives against multiple sources. This work has already begun (6), and Cysouw et al. and Wang et al. continue this process.

In line with previous genetic and phenotypic studies (16), I used a BIC threshold of four units to identify the credible origin area. This value is more conservative (allowing greater uncertainty in any inferred origin area) than the value of two suggested by Cysouw et al. The fact that the method I used identifies spatially contiguous areas of origin is not a disadvantage. This emerges naturally from the fact that model fit for different putative origins is spatially autocorrelated, but the method need not identify a single origin area or any clearly defined area. As Cysouw et al.'s own simulations show, when the method is applied to random data, the area supported using a BIC threshold of four includes the whole world, correctly indicating that the random data do not point to any particular origin location.

Van Tuyl and Pereltsvaig make much of the fact that the global cline in phonemic diversity does not hold within all continents. However, looking for individual within-continent trends greatly reduces statistical power and is more affected by recent population movements and nonindependence due to relatedness between languages in a region. Such a pattern does not undermine the global trend. When effects of continent and by-continent variation in the relationship with distance from Africa are added to a hierarchical linear model that incorporates language affiliation information, model fit is decisively worse than when region is ignored (BIC is 807.1 with region effects and 773.2 without). Even in the regional model, the global effect of distance from Africa remains significant [$\beta = -7.34$ to -2.05×10^{-5} (95% highest posterior density); $P < 0.001$]. Further, Van Tuyl and Pereltsvaig's own analysis shows a significant stepwise decline in phonemic diversity between continents with increasing distance from Africa.

Van Tuyl and Pereltsvaig also focus on the precise location of the best-fit origin in Africa, questioning the level of support for a western African origin. Although this is an interesting

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line of inquiry, particularly given the view that eastern Africa represents the cradle of humanity, none of the interpretation in my paper relates to the specific origin location within Africa; as I make clear, the family-level analysis identified an origin area spanning all of Africa.

Cysouw *et al.* report the fit of a model of phonemic diversity as a quadratic function of distance. Rather than the gradual global cline predicted under a serial founder effect, fitting a quadratic model will tend to identify steeper localized gradients in phonemic diversity. This model finds an African best-fit origin for the WALS data, but the best-fit model for the UPSID data is a positive quadratic function with distance from New Guinea (i.e., phonemic diversity is lowest in New Guinea and increases with distance). Although these more complex models may identify previously unrecognized patterns, unlike arguments for a simple serial founder effect model of phonemic diversity, we have no a priori reason to think a positive quadratic function of distance is a good model of how phonemes change. Likewise, there is no reason to expect that aspects of language "complexity," like the assortment analyzed by Cysouw *et al.*, should all show a founder effect. Such features can be expected to behave quite differently. Indeed, as Cysouw *et al.* mention, loss of complexity in one domain is thought to be compensated with elaboration in other domains. There are clearly interesting large-scale geographic patterns in some of these features that warrant further research. Although I am in favor of the rigorous examination of these patterns, the blanket application of a founder analysis to such features tells us little about the processes that generated them and does not refute the findings with regard to phonemic diversity.

Cysouw *et al.* also suggest that levels of between-language variation in phonemic diversity (which they measure as the standard deviation in phonemic diversity across a language and its five nearest neighbors) contradict the predictions of a founder effect model. The founder effect model is a prediction about mean levels of diversity that we expect to see across an expansion—the result of a balance between merging, splitting, and borrowing processes (*1*). Variance in phonemic diversity between neighbors will depend largely on their statistical independence (due to relatedness, recency of expansion, borrowing, and the density of sampling), whether there are upper or lower limits on diversity, and variation in other factors such as population size and the nature of local language formation mechanisms.

Hence, although a low standard deviation in New Guinea/Australia and western Africa is interesting, it is does not contradict a serial founder effect from Africa.

The relationship I report between population size and phonemic diversity also holds for Cysouw *et al.*'s reweighted WALS and UPSID data. When restricted to small speaker population sizes, this relationship is in the correct direction, but Cysouw *et al.* point out that the trend is not statistically significant for their measures. Likely distortions of smaller population sizes since European colonial expansion combined with fewer data points may undermine the ability to detect a significant relationship among small populations. For the full data set, phonemic diversity appears to relate reliably to demography in the manner predicted by simulations of cultural evolution (*2–4*) and consistent with a serial founder effect. More detailed analysis of a larger sample of smaller populations may be needed to determine whether the nature of the relationship is fundamentally different among small groups.

Wang *et al.* and Cysouw *et al.* question whether phonemic diversity is stable enough to reflect migration events on the scale of the human expansion from Africa. Cysouw *et al.* point out that tone may be influenced by genetic variants that postdate the African expansion, but together these genes explain only 7% of the variance (*17*). Studies examining typological stability on phylogenies indicate that rates of phoneme replacement vary across families but are generally comparable to other structural features (*18*). Cysouw *et al.* cite evidence that consonant inventories may be less stable than other features, including vowel and tone inventory (*19*). However, these inferred rates are contingent on the binning procedure used to code the data and so do not provide an absolute estimate of long-term stability. Moreover, horizontal transmission due to borrowing can inflate rates of evolution on a phylogeny without disrupting geographic patterning. As I highlighted in my paper, phonemic diversity appears highly stable at the language-family level, with family affiliation explaining about 50% of the variance around the globe (*1*).

Admixture or horizontal transfer of phonemes between languages due to borrowing is not, as Cysouw *et al.* and Van Tuyl and Pereltsvaig claim, problematic for the serial founder effect model. In fact, as is the case in population genetics (*20*), horizontal transfer can help to maintain a cline, because neighboring populations at similar points in the expansion (e.g., in Africa versus in Aus-

tralia) are more likely to encounter similar phonemes and levels of diversity. Nonetheless, I agree with Cysouw *et al.* that there is more to language change than phoneme inventories and serial founder effects; I do not expect this result to be the last word on language origins. Some of the most promising avenues of future research address questions touched on in these and other commentaries (*6–10*), including explicitly modeling rates of evolution of individual sound changes (*21*), rates of borrowing on a phylogeny (*22*), and determining population structure without assuming a tree-like model of evolution (*23*). I look forward to more research applying these and other quantitative methods to identify the key drivers of global variation in human language.

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