

Testing Selection and Drift in Neandertal Populations

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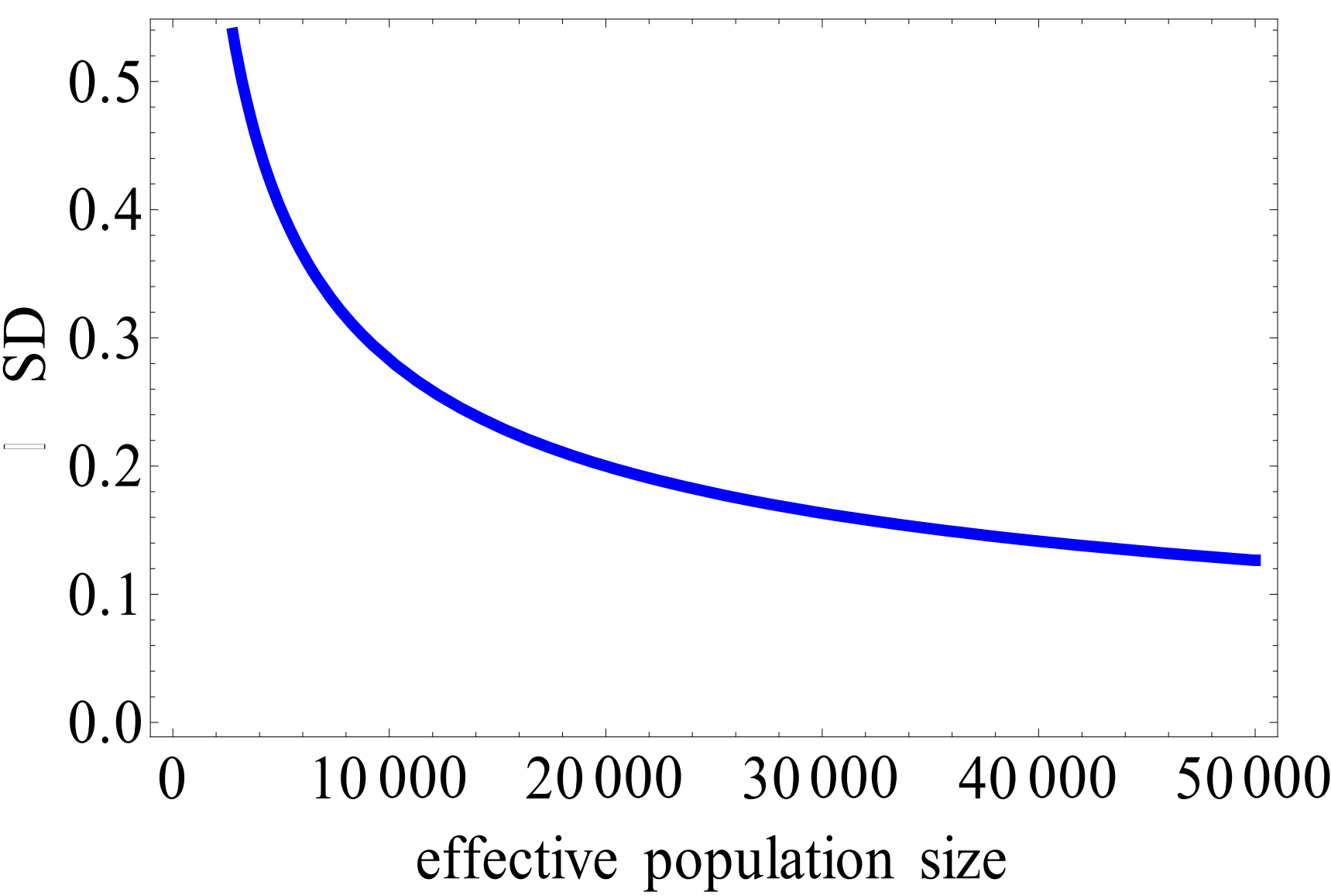
Introduction

Recent work has suggested that genetic drift has played a critical role in the evolution of modern humans. Scholars working under the neutral model of evolution have suggested that there is little evidence for natural selection between modern human populations (Coop et al. 2009; Pickrell et al. 2009), and Weaver and colleagues (Weaver et al. 2007; Weaver et al 2008) have argued that the cranial differences between modern humans and Neandertals are the product of genetic drift. Here, we test the role of drift in the Neandertal lineage, using a method which allows us to utilize a different sample set than previously examined and increase the probability of distinguishing between random drift and selection.

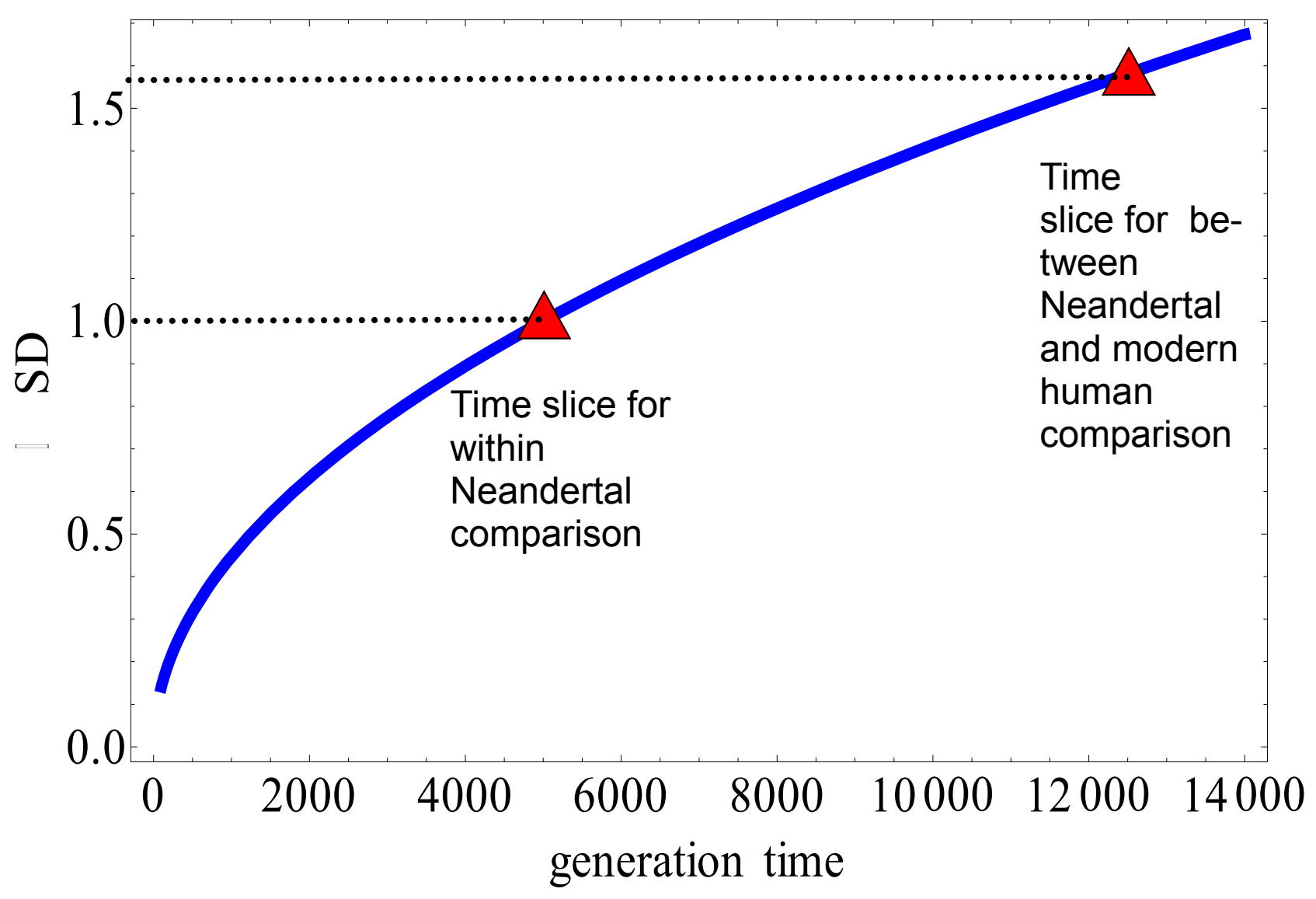
How to test for drift in the fossil record

Lande (1976) provides equations to test for the strength of selection vs. drift. We take Lande’s original equations and convert the equation into units of standard deviation to calculate how far from the parent population the daughter population must be in order for drift to be too weak to have caused the recorded change:

$$N = 2t/Z^2$$



Results of simulation showing how different values for effective population size and generation time affect the chance of disproving drift



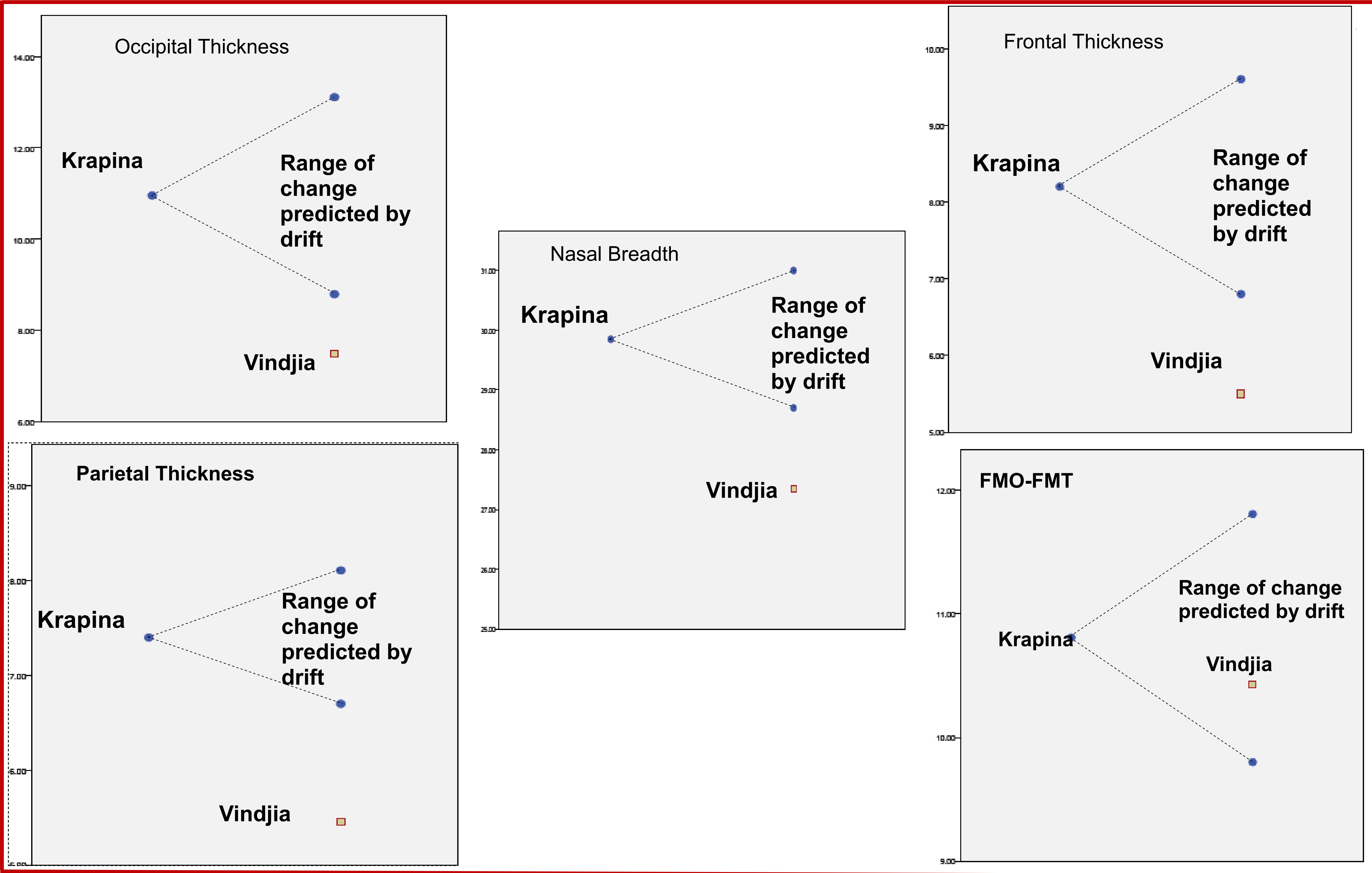
Can we disprove drift in a skeletal population?

Before testing for selection amongst the Neandertal lineage, we first need to check if our drift test is robust enough. We collected data on modern human fossils from the Early Upper Paleolithic, the Later Upper Paleolithic and the Mesolithic. Many scholars have suggested that significant changes occurred in the biology of these people in response to changes in mobility and subsistence, so it is the perfect dataset to test out method against.

Sample	Elements	# Traits examined	Percent drift is rejected	Source
Upper Paleolithic-Mesolithic	limb bones	12	100%	Frayner 1981
Early Upper Paleolithic– Late Upper Paleolithic	dental	16	81%	Frayner 1977
LUP-Mesolithic	dental	16	31%	Frayner 1977
EUP-Mesolithic	dental	16	81%	Frayner 1977
EUP-LUP	limb bones	52	63%	Holt 2003
LUP-Meso	Limb bones	52	62%	Holt 2003
EUP-Meso	Limb bones	52	52%	Holt 2003
EUP-LUP	limb bones	36	69%	Jacobs 1985b
LUP-Meso	Limb bones	37	60%	Jacobs 1985b
EUP-Meso	Limb bones	40	58%	Jacobs 1985b
Egyptian Mesolithic to transitional Hunter-gatherers	cranial	14	93%	Carlson and Van Gerven 1977
Trans. HG to Fully agriculture	Cranial	14	57%	Carlson and Van Gerven 1977
Egyptian Mesolithic to fully agriculturalists	Cranial	14	86%	Carlson and Van Gerven 1977

Neandertal sample

If natural selection has not lead to any significant differences between these two populations of early humans, we would expect that within the Neandertal sample itself there should be little evidence for selective pressures causing change throughout the lineage. To examine this idea we compare the Krapina sample (~130,000 ya) to the Vindjia sample (~30,000-40,000 ya).



Scatterplots of results from drift test, with mean values for each population and the amount of change expected by drift . If the Vindjia sample falls outside this range, it is more likely that another force, possibly selection, is the principal cause of change.

Conclusions

Of the 20 metrics analyzed, 55% have morphological changes that are too large to be explained by drift. These results are not in line with previous research. One reason may be the time span we analyzed. Previous work compared the whole population of Neandertals to modern humans, thus comparing a time span of 250,000-300,000 years. By taking a shorter time slice, roughly 100,000 years, it allows a better chance to see selection. As the number of generations between populations increases, the probability of accepting the null hypothesis of drift even though it is false increases as well. We are thus testing for selection in a time period where we have the power to detect the difference between the two forces. Secondly, concentrating on specific metrics allows us to utilize a larger sample size with more fragmentary fossils, an approach that is complicated when using 3D morphometrics. Finally, comparisons between a sample of early Europeans and the classic Neandertals show a similar pattern of selection, suggesting that adaptive pressures may have played a greater role in the diversification of the human lineage than previously supposed.

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