



Not by demography alone: Neanderthal extinction and null hypotheses in paleoanthropological explanation

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Abstract

Neanderthal extinction is a matter of intense debate. It has been suggested that demography (as opposed to environment or competition) could alone provide a sufficient explanation for the phenomenon. We argue that demography cannot be a ‘stand-alone’ or ‘alternative’ explanation of token extinctions as demographic features are entangled with competitive and environmental factors, and further because demography should not be conflated with neutrality.

Keywords Extinction · Explanation · Neanderthal · Demography · Neutrality

Introduction

This is a paper about the Neanderthals’ evolutionary fate, and about demographic explanations of extinction generally. Hypotheses of Neanderthal extinction have tracked general currents in paleontology and archaeology. Earlier models relied on competitive exclusion (Flores 1998; Banks et al. 2008), shifting to accounts emphasizing the role of environmental change (Staubwasser et al. 2018), catastrophic climatic events (Fitzsimmons et al. 2013; Cooper et al. 2021) or pathogen transmission (Houldcroft and Underdown 2016; Greenbaum et al. 2019). Recently, aligned with the ‘demographic turn’ in archaeology (Collard et al. 2016) and explanations emphasizing the relationship between demographic fluctuations and decreases in cultural complexity (Shennan 2001; Henrich 2004; Powell et al. 2009),

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paleoanthropologists argue that Neanderthal demography played a crucial role in their extinction (Kolodny and Feldman 2017; Vaesen et al. 2019, 2021; Degioanni et al. 2019).

We're going to argue that although demography is very likely to be critical for explaining Neanderthal extinction, it should not be presented (even if only implicitly) as a competing, separate explanatory factor from environmental and competitive hypotheses.

There's a long tradition of attempting to identify *the* major driver or sufficient causal contribution among the abovementioned factors: was demography, environment, or competition responsible for Neanderthal extinction? Although many practitioners are ready to concede that one factor does not exclude the other, the explanatory relationship between demography and extinction has received less explicit attention. In particular, defenders of demographic explanation often argue (or at least imply) that (i) in principle, demography can *alone* explain Neanderthal extinction and (ii) demographic explanations are a priori preferable. We will deny both of these claims.

We'll argue that, for token extinctions, demography is inseparable from either competition or environmental factors. We are not arguing that demography plays no explanatory role *vis-à-vis* extinction, nor that demographic phenomena shouldn't be modelled or investigated abstractly in their own right. Our central focus is the relationship between demographic *phenomena* or *patterns*, and demographic *explanations* or *processes*. As extinction manifests itself demographically, in providing demographic explanations of it, care is required in distinguishing *explananda* and *explanans*. While recognizing the crucial importance of data on population history and diversity, we will make a case against demographic factors as 'stand-alone' or 'alternative explanations', as demographic features cannot be easily disentangled from (and might even reflect) factors affecting species' fitness and the environment.

The demographic turn has been partly enabled by a revolution in our access to human pasts: that of molecular and ancient DNA extraction and analysis methods, which provide new windows into population size, structure and dynamics. As such, we'll begin in Sect. 2 with a discussion of demographic information on Neanderthals, particularly demographic inferences from ancient DNA. As we'll see, despite important new data, it remains somewhat unclear whether Neanderthal demographic phenomena have been conclusively characterized (Degioanni et al. 2019).

We'll then turn to the nature of demographic explanations of extinction in Sect. 3. We frame the explanatory role of demography through difference-making. We'll then consider demographic explanations of Neanderthals in particular, sketching three recently proposed demographic hypotheses, analysing the explanatory role of the proposed demographic factors. That is, we'll provide an interpretation of how practitioners leverage demographic factors in Neanderthal extinction explanations and in what relation they stand to environmental or competition-based explanations. In short, they appear to think of demography as 'separable' from competition or environment.

In Sect. 4 we'll argue against separability: in token instances of extinction, demography factors act through and with competitive and environmental factors. In Sect. 5 we'll consider an increasingly common modelling strategy: representing

and exploring demographic explanations using ‘neutral’ or (so-called) ‘null’ models which show how Neanderthal extinction was possible without positing intrinsic differences between Neanderthals and *H. sapiens*. Often, in addition to mistakenly treating demographic features as separate from environment or competitive advantages, we’ll argue that interpretations of such models often conflate demography with neutrality.

Although our focus is on Neanderthals, we suspect that our complaint holds to differing degrees for many demographic approaches to *extinction*. The crucial complaint is against the thought that demographic factors should be considered as a separate explanatory factor and, in other arenas where demography is appealed to (the emergence and evolution of behavioural modernity, for instance, see d’Errico and Banks 2013; Meneganzin and Currie 2022; Sterelny 2021) such assumptions are not at play.

So, in this paper we will draw critical philosophical attention to the increasingly central role of demographic explanations in archaeology, palaeontology and paleo-anthropology. We’ll distinguish between demographic phenomena and explanations, suggesting that token demographic phenomena—such as extinction—may be partly explained by demographic factors, but in such cases demography does not work alone.

Demographic inference from ancient DNA data

Neanderthals and our lineage led separate evolutionary histories for at least five hundred-thousand years. Our ancestors evolved in Africa (Stringer 2016), dispersing from the continent around 70–65 kya¹ (Pagani et al 2016), at a time when Neanderthals already spanned across Eurasia and the near-East. The timing of Neanderthal demise is a crucial constraint on hypotheses of their extinction. The idea that Neanderthals succumbed rapidly after the expansion of *Homo sapiens* into Eurasia (e.g. Mellars 2004) has been overturned, radically reshaping the epistemic and explanatory landscape concerning Neanderthals, their extinction, and their relationship to our lineage.

First, work revising the radiocarbon dating record and stratigraphic sequences at many key archaeological sites across Europe showed that the disappearance of Neanderthals occurred at different times in different regions (Higham et al. 2014). This provides a more complex picture of the spatiotemporal relationship between Neanderthals and incoming *Homo sapiens*, indicating a much more significant temporal overlap between the two, and suggesting a mosaic pattern of population turnover during the Middle to Upper Paleolithic transition.

Second, a richer archaeological record also complexified the picture. The rapid replacement scenario was associated with the proliferation of sophisticated and symbolic expressions appearing relatively suddenly in the European Early Upper

¹ This refers to the major Out-of-Africa expansion wave (OOA). However earlier, minor waves have been proposed (cfr. Posth et al. 2017; HersHKovitz et al. 2018, Petr et al. 2020).

Paleolithic record. This inflection, which was taken to trace the arrival and dispersal of cognitively and technologically superior *Homo sapiens*, has been reevaluated in the last two decades (McBrearty and Brooks 2000). Further, the underappreciation of complex behavioural traits in the Neanderthal archaeological record has been increasingly recognized. In particular, there is evidence of personal adornments and symbolic behaviour at Neanderthal sites that predate the arrival of *Homo sapiens* in the continent (Colagé and D’Errico 2020), invalidating the hypothesis that *only* the cultural influence of *H. sapiens* could explain the more refined cultural expressions in Neanderthals. Although these expressions were not in the same number as those in later Aurignacian *Homo sapiens*, Neanderthals were capable of them.

Third and significantly for our argument, paleogenomic data in the last decade provided informative clues about population sizes and history: that is, demography. Besides a number of Neanderthal genomes of moderate quality (one-to three-fold coverage²), to date we’ve three high-quality (27–30 fold coverage) Neanderthal genomes available that can yield more accurate information about their past population history and genetic diversity: two from Siberia (one from Chagyrskaya Cave and the other from Denisova Cave,³ in the Altai Mountains) and one from Croatia (Mafessoni et al. 2020). Nuclear genomes have shown that Neanderthals lived in relatively low numbers, in isolated populations, showing signs of long-term inbreeding. In particular, the high-quality genome of a Neanderthal woman from Denisova Cave (Altai Neanderthal) has revealed very long runs of homozygosity, indicating her parents had a level of inbreeding comparable to that of half-siblings (Prüfer et al. 2014).

Moreover, the Altai Neanderthal genome has allowed inferences of population size change over time. The demographic history of the population was reconstructed (through pairwise sequentially Markovian coalescent model, PSMC) from the distribution of the times since the most recent common ancestor of the two copies of the genome, that each person carries (one from their mother and one from their father). Coalescent probability at a given time-depth is inversely proportional to the effective population size (N_e) at that time (*i.e.* the number of individuals who contribute offspring to the next generation).⁴ The demographic history of the Altai population was then compared to inferences from both the Denisovans (a sister population of Neanderthals) and present-day humans. While most hominin groups seemed to have experienced a drop in effective population size over time, this was especially marked in Neanderthal and Denisovans, who never recovered (while *Homo sapiens* did). The decrease was a long-term decline, rather than the effect of a recent

² Coverage in sequencing refers to the number of unique reads that align to, or “cover,” known reference bases in a reference genome.

³ The Denisova cave, in the Bashelaksky range of the Altai mountains (Siberia), is known to have been inhabited by multiple human forms (although, perhaps, not at the same time): the Neanderthals, the Denisovans – first identified from mtDNA extracted from bone fragments found in the cave (hence, “Denisova cave”) – and related hybrids (such as Denisova 11).

⁴ This means that the probability that two randomly chosen alleles share a common ancestor at a certain time frame t is inversely proportional to the effective population size at that time. The smaller the population size, the higher the probability of coalescence.

bottleneck or population crisis. The other two high-quality genomes seem to confirm these telling properties of Neanderthal populations. In the case of Chagyrskaya, 13% of the genome is homozygous, suggesting that the person lived in groups of no more than 60 individuals (Mafessoni et al. 2020). In the case of the Vindija Neanderthal (Prüfer et al. 2014) low levels of heterozygosity are confirmed, although without the high level of inbreeding observed in the Altai Neanderthal.

As we'll see, these demographic factors suggest a comparatively vulnerable Neanderthal metapopulation: a heightened (but not immediate) risk of extinction has been suggested for the Neanderthals based on population dynamics and genetic diversity alone.

Despite researchers agreeing on the “small size” of Neanderthal populations, precise and accurate estimations remain difficult (Degioanni et al. 2019). Bocquet-Appel and Degioanni (2013) have proposed for the entire Neanderthal population (the European and Asian census metapopulation) a maximum of 70,000 individuals. Prüfer et al. (2014) have suggested that the Neanderthal N_e ranged from 1000 to 5000 individuals. Higher estimates, like those of Rogers et al. (2017) suggesting an N_e of 15,000 individuals, have been criticized (Mafessoni and Prüfer 2017) and a relatively smaller N_e remains better supported, although more high-coverage genetic data might shift these estimates somewhat.

Crucially, genomic data reveals intricate patterns of admixture and interaction between Neanderthal and ourselves. Out of six sequenced Eurasian early *Homo sapiens* overlapping with Neanderthals, four show Neanderthal ancestors in their recent genealogy (Hajdinjak et al. 2021). Some of these, like the recently analysed genome of a 45 kyr old female individual from Zlatý kůň, Czechia, seem not have contributed to later populations (Prüfer et al. 2021). Others, like the 46–43 kyr old remains from Bacho Kiro Cave, Bulgaria, paint a different picture of early *Homo sapiens* in eastern Europe, with genomic data indicating a closer relationship with East Asians. This means that neither the Bacho Kiro population contributed to subsequent populations in Europe, since these appear to be the result of another expansion wave (cfr. Vallini et al. 2022). This seems to suggest multiple and differently-fated pulses of *H. sapiens* dispersing across the continent, throughout a temporal window of coexistence of at least 6,000 years in Europe.

Differently put: for 6,000 years (up to 20,000 if coexistence in the Levant is included after *Homo sapiens*' OOA) our evolutionary cousins kept our ancestors at the doorstep, enduring their incursions, admixing, interbreeding⁵ and perhaps intermingling culturally, as the controversial taxonomic affiliation of some transitional industries has long suggested (Roussel et al. 2016).

So, ancient DNA has revolutionized our picture of Neanderthal lifeways and their interactions with our species. It also highlights demographic features—their small, disconnected populations, high levels of inbreeding, and admixture with waves of *H.*

⁵ For the purposes of our argument, it is sufficient for us to say that evidence of interbreeding, as it commonly happens for other taxa for which molecular data are available, does not automatically invalidate a species-level taxonomic categorization (and, therefore, that of Neanderthals being a genuine extinction event). But we leave the details of this discussion for another paper.

sapiens immigrants over thousands of years—which could prove crucial for explaining their extinction. In the next section, we’ll analyse demographic explanations of extinction in the abstract before considering these in the Neanderthal context.

Demography and extinction

As we’ve seen, new archaeological, paleontological but—in particular—ancient DNA evidence has opened inroads to demographic patterns in Neanderthal and *H. sapiens* populations. This, in addition to the more general demographic turn in archaeology and paleoanthropology, has driven the development of demographic explanations of the extinction. In this section, we’ll first abstractly characterize demographic explanations, cash this out in the Neanderthal case, and show how some recent hypotheses present demography as separable from other putative factors.

Demographic factors as difference-makers

What makes an explanatory factor *demographic*? Demography investigates population-level characteristics and dynamics: changes in size (both the effective and the census size, *i.e.* the actual number of individuals), structure, movement, and so forth. A demographic *phenomenon*, then, concerns such changes. An archaeological example, say, is the arrival of human populations in Polynesia. Over several thousand years, and potentially in differing waves, Austronesian settlers moved eastward across the Polynesian islands (Kennett et al. 2006).

So, a phenomenon is demographic if it is characterized in terms of population-level properties like changes (or stability!) in population number, or in structure. What then is a demographic *explanation*? Demographic explanations cite features of populations to explain phenomena. For instance, one might cite population growth from settled areas as a driver of Polynesia’s settlement.

Although our account of demographic explanation needn’t commit us to any particular view of explanation, it is useful to draw on *difference-making* for precision’s sake. ‘Difference-making’ accounts of causation have been extremely popular in philosophy (e.g., Ney 2009; Woodward 2005). At base, such accounts say that some factor is a cause of some outcome just in case, were an ideal intervention to be made on that factor, the outcome would turn out differently. So, a ‘difference-maker’ is a feature that, if it were different, would have made a difference to the target phenomenon. That is, there is a true counterfactual that if the difference-maker hadn’t occurred (or occurred differently), then the target phenomenon wouldn’t have occurred (or occurred differently). A difference-making account of *explanation* claims that a feature is explanatory just when it is a difference-maker for the phenomenon of interest (Beatty 2017). As we’ll discuss below, we don’t take ourselves here to be committed to any particular story about the causality or otherwise

of demographic factors: difference-making is a convenient way of talking about explanation.

Let's go back to our toy example. Under a difference-making account of explanation, if the population-growth hypothesis of Polynesian settlement is correct, then if Polynesian originator populations had not been increasing, then Polynesia's settlement would have been different. Such claims might be false: if Sear et al (2020) are right, then it wasn't increases in population—demographic factors—that made the difference in settlement, but patterns in drought in western source regions, which instigated initial eastward explorations.

Taken as a complete account of explanation, difference-making is far too permissive: so long as some factor makes a difference, it is part of the explanation of the target. As such (and this is important for our argument below) we'll take it as a *necessary* feature of explanation, saying nothing generally about when an explanation is *sufficient* or *adequate*. We're not committed to whether, for instance, an explanation must cite as many difference-makers as possible, or any other general constraint on adequacy.⁶

Our arguments concerning demographic explanations of extinction agree that demography can be a difference-maker. Demographic patterns can (and should!) play a role in explanation, but not in a way that treats them as contrasting with competitive or environmental factors. It is plausible that if Neanderthal populations weren't so reduced, disconnected and highly inbred, potentially their extinction would have occurred with different timing, patterning and dynamics (or, some may speculate, wouldn't have occurred at all). However, we'll deny that demography is an independent factor, that it alone can be a sufficient explanation of token extinctions.

Demographic hypotheses for Neanderthal extinction

It is commonly suggested that accounts of Neanderthal extinction can be organized into three categories: environmental explanations (including extreme climatic events and pathogen transmission), competition with modern humans, and demography (Vaesen et al. 2021). Crucially, these categories are not taken to be mutually exclusive, but they are taken to be potentially independent and disentangleable, what we'll call 'separable'. That is, in principle environmental features, or competition, or demography could *alone* account for the extinction, or at least take the major share of blame for the extinction. In terms of difference-making, we could understand these factors as being *independently manipulable*: an ideal intervention could affect one factor, but not the other. Crucially: this is our interpretation of how practitioners frame the debate. In principle, there could be other ways to construe it,⁷

⁶ One might further deny that difference-making is a suitable necessary feature—and we think this plausible, however, our purpose for adopting difference-making conceptual machinery is largely pragmatic, and we'll leave the minutiae of the philosophy of explanation for a later day...

⁷ For instance, as suggested by a reviewer, one may simply want to name and tag different factors, thus isolating them in a 'weaker' sense. Again, it is far from obvious what a weaker sense would be, if the relative contribution of each factor is to be assessed (Vaesen et al. 2021) and the demographic explanation is an "alternative that should a priori be preferred" (Kolodny and Feldman 2017).

and indeed below we'll sketch some positive suggestions regarding the point of such work that *doesn't* require the notion of independent manipulation. Regardless, we think, it would be hard to get to grips with the proposed precedence of the demographic explanation if the separability of those factors were not implied.

Let's compare competition and demographic explanations.

According to competitive exclusion hypotheses, two species competing for the same resources cannot coexist at constant population values: the fitter species will replace others in that niche. By competitive hypotheses, Neanderthal demise was causally linked to modern humans arriving in their territories and exhibiting a direct or indirect competitive advantage (morphological, cognitive, technological or economic). However, in light of new archaeological revelations, the ongoing correction of Neanderthal stereotypes,⁸ disagreement over the extent of *Homo sapiens'* advantages, as well as a more fine-grained spatiotemporal characterization of Neanderthals' disappearance and archaeogenetic data, some researchers now hold that the demographic dynamics of Neanderthal populations might be sufficient to explain their extinction, even in the absence of direct competition with modern humans.⁹ It is plausible that non-competitive and non-selective explanations has been strongly impacted by the "Neanderthal renaissance" (Sykes 2020). While this reorientation of archaeological studies is of crucial importance and welcomed, caution is merited in the way demographic factors are leveraged, for hypotheses to be truly explanatory and reflective of the complexity of extinction as a phenomenon.

Let's consider some recent demographic explanations of Neanderthal extinction. Kolodny & Feldman (2017) suggest that recurrent waves of *H. sapiens* expansion into Europe, even at a low rate, would eventually lead to Neanderthal extinction without a *sapiens* selective advantage.

Although a stochastic process, this replacement was certain to occur... given the estimated migration pattern near the onset of the interaction between the two populations, namely repeated migration of small propagules of Moderns out of Africa into the Levant and Europe. (p. 7)

On their model, because Africa has a larger variety of demes than Europe, even if particular waves of *H. sapiens* migration fail, they would be replaced by a constant influx of replacements. The explanation, in effect, is that migrating *H. sapiens* have a larger base of original populations to draw from. So, despite the randomization of

⁸ For a historical examination of the origins of the "brutish Neanderthal" narrative, (see Madison 2021).

⁹ It is worth noting that the very same data could be used to infer a small but significant competitive advantage: after thousands of years of coexistence, something gave *H. sapiens* the decisive edge. A variant of the demographic explanation, the assimilation scenario, posits much more frequent episodes of admixture between dispersing *H. sapiens* and Neanderthal populations over wide areas and has been recently suggested to explain the Neanderthal ancestry found among the earliest *Homo sapiens* in Europe. Proponents of this view argue that Neanderthals were absorbed into larger and expanding *Homo sapiens* populations and that the Neanderthal signal would have been later diluted by differential demography and successive population replacements (Smith et al. 2005; Lalueza-Fox 2021). Under this view, it would be inaccurate to refer to Neanderthals as being truly extinct. It remains unclear, however, to what extent this hypothesis is constrained by available evidence and whether this scenario better applies to localized contexts than to the broad macroevolutionary pattern.

whether a particular European deme is occupied by *H. sapiens* or Neanderthals, over time *H. sapiens* will replace Neanderthals. Unlike our evolutionary cousins, modern humans groups were supplemented by recurring African reinforcements, enough to tip the balance in our favour.

A different set of explanations appeal to the comparatively small size of Neanderthal groups: “Even in the absence of competition with modern humans, Neanderthal populations might, generally, have been too small to persist in the long run” (Vaesen et al. 2021). Small populations, with limited interconnectedness, would lead to a reduction in fitness due to inbreeding, slower population growth due to difficulty in finding mates and stochastic fluctuations in births, deaths and sex ratios (see Vaesen et al 2019). What these explanations suggest is that Neanderthal populations, already small before the arrival of modern humans, were doomed to decline below the minimum viable population threshold regardless of incursion from *H. sapiens*. If modern humans were to play a role, this would have had nothing to do with resource competition, but rather with restructuring the distribution of resident Neanderthal populations and reinforcing the effects of inbreeding and stochasticity.

A final example, presented by Degioanni et al. (2019), interrogates the demographic changes needed over a period of 10,000 years to lead to the Neanderthals’ demise. Their demographic models suggest that a decrease in the fertility of young Neanderthal women (primiparous) could lead to plunging Neanderthal population sizes. They emphasize the apparently small but continuous decrease required (less than 4%) for this effect and argue that their modeling suggests that catastrophic scenarios (epidemics, extreme climatic events) or the direct or indirect intervention of *H. sapiens* are not necessary to produce the observed decrease in population size.

In each of these examples a *demographic property*—*H. sapiens* migration, small, disconnected groups, a decrease in fertility—is claimed to be a difference-maker for Neanderthal extinction. That is, if young female fertility didn’t decrease, or if Neanderthal had larger, or more connected groups, or if *H. sapiens* migrations didn’t occur as it did, then the Neanderthal extinction would not have occurred, or occurred differently.

Demography as separable

We have no in-principle objections to the potential importance of demographic factors in the Neanderthal extinction. Further, authors are careful to not present such hypotheses as *mutually exclusive* with competitive or environmental factors: in actual fact competition with *H. sapiens*, or environmental factors, could have also been difference-makers vis-à-vis the extinction. However, they *do* present these causal factors as in-principally *independent* of environmental or selectively advantageous factors: they are *separable* in the sense of being independently manipulable. In this section we’ll provide textual evidence in support of this interpretation.

Consider Kolodny & Feldman:

Here we show that a scenario of migration and selectively neutral species drift predicts the Neanderthals’ replacement. Our model offers a parsimonious

alternative to those that invoke external factors or selective advantage, and represents a null hypothesis for assessing such alternatives (abstract)

Migration is presented as a separate explanatory factor, an alternative to selection or other external factors (environmental pressures). Although they might together make a difference to the occurrence of the phenomenon, an ideal intervention could target one and not the other and, in principle, one could account for the phenomenon without the others. This point is reiterated in the discussion:

We have shown that a simple selectively neutral model of population dynamics, random drift in finite populations with migration, can account for the replacement of the Neanderthals by Moderns...(7)

We'll discuss neutral models and null hypotheses downstream. The important implication here is that the population dynamic model can alone explain the replacement, in contrast with factors like environmental shifts or competition. This implies that demographic factors can make a difference without any changes in environment or competition.

The same assumption of separability is seen in Vaesen et al.:

An explanation solely in terms of the internal dynamics of the Neanderthal population, as the one presented here, serves as a null hypothesis against which competing, and less parsimonious, hypotheses are to be assessed. (Vaesen et al 2019).

The less parsimonious hypotheses they refer to are, again, selective competition and environmental disruption. As we'll discuss below, the idea that demographic explanations should act as a 'null hypothesis' implies that to show the extinction was due to competition for the same resources or environmental pressure, we must first show that demographic factors cannot account for these alone. These factors are then treated as independent or separable.

Separability is strikingly presented in Vaesen et al. (2021). They argue there is a consensus amongst paleoanthropologists that demography wasn't simply a possible explanatory feature, but the principal cause of the extinction, while there would be no consensus regarding other factors. As they say:

It appears that received wisdom is that demography was the principal cause of the demise of Neanderthals. In contrast, there is no received wisdom about the role that environmental factors and competition with modern humans played in the extinction process; the research community is deeply divided about these issues. (abstract)

The conclusion is supported by a survey of practicing paleoanthropologists. Their data is, we think, telling. In Table 1 we see how Vaesen, Dusseldorp & Brandt divide up the causal factors. Respondents weren't asked about competitive, environmental or demographic features per se, but about more fine-grained features, randomly presented, such as Allee effects (reduction in population growth rates due to problems in mate-finding) or stochasticity (for demography),

Table 1 (from Vaesen et al. 2021). Mean, minimum and maximum scores, and standard deviations (SD) for the items in the questionnaire, as well the percentage of respondents who indicated “Don’t know”

	Mean	SD	Minimum	Maximum	Don't know (%)
Causal factors					
<i>Demographic composite (DEM)</i>	3.41	1.13	0	6	
Allee effects	2.74	1.60	0	6	17.45
Inbreeding	3.12	1.59	0	6	4.67
Population size	4.44	1.36	0	6	2.78
Stochasticity	3.03	1.54	0	6	7.51
<i>Competitive composite (COMP)</i>	2.40	1.41	0	6	
Cognitive advantage(s)	2.19	1.81	0	6	4.19
Economic advantage(s)	2.63	1.80	0	6	13.15
Morphological advantage(s)	1.51	1.56	0	6	4.67
Social advantage(s)	3.19	1.83	0	6	7.48
Technological advantage(s)	2.60	1.88	0	6	1.40
<i>Environmental composite (ENV)</i>	3.08	1.54	0	6	
Climatic factors	3.20	1.72	0	6	2.34
Epidemics	2.76	1.72	0	6	30.19

or cognitive and economic advantages (for competition), and the three factors are presented as average composites.

Table 1 (from Vaesen et al. 2021). Mean, minimum and maximum scores, and standard deviations (SD) for the items in the questionnaire, as well the percentage of respondents who indicated “Don’t know”.

The ‘consensus’ claim comes from the comparative average score that demographic factors achieved over competition and the environment: 3.41 versus 2.4 and 3.08 effectively (where the rating is between 0 and 6). Putting aside whether these are significant differences, we’ll make some points about these results which lead to our arguments concerning the nature of demographic explanations of extinction.

Note that the demographic composite outperforms the others squarely due to one factor: population size.¹⁰ If population size is removed from the demographic composite, it in fact underperforms environment (2.96 versus 3.08). If anything, there is a consensus that population size specifically, not demography generally, was the primary factor. This is significant because, on the face of it, population size is surely

¹⁰ It remains underspecified, also in the supplementary materials of the paper, what respondents *precisely* had in mind when selecting “population size” (the population approaching the minimum viable threshold; population structure having narrowed down mating and fitness opportunities, etc.). Again, we are not implying that citing population size as a factor in extinction can only be done in a tautological or descriptive sense, but care is required in disambiguating meanings and therefore distinguishing *explanantia* from *explananda*.

crucial for any explanation of extinction. After all, what is extinction but ultimately a change in population size¹¹?

Citing population size as a factor in extinctions should clearly distinguish extinction as a phenomenon with an explanation of an extinction. When we explain an extinction, at base our *explananda* is a decrease in population size: a decrease to zero. It doesn't follow from this that population size cannot also be an *explanans*. For instance, Neanderthals starting at a smaller population, or organizing themselves into smaller groups, can be a difference-maker in the eventual extinction. Generally, however, this means that we should carefully distinguish between *describing* demographic phenomena and *explaining* them (note that we're not claiming that Vaesen et al., nor their respondents, made such a conflation: simply that as read their results are ambiguous).

More importantly for our argument, note that although these factors are not presented as mutually-exclusive factors, insofar as they can all co-occur—can all be difference-makers for the extinction—they *are* presented as independent insofar as they can vary independently and could (in principle) account for the extinction alone. We think that although demographic factors can be difference-makers, we *do not* think they are independent in this sense. The risk is framing the debate in a way that implies biologically unrealistic standards of explanation. This is because any demographic feature can either be explained as an instantiation of a difference in Neanderthal-*H. sapiens* competitiveness, or as due to differences in environment. Let's turn to that argument now.

Demography is not separable

We've interpreted some recent work on demography in Neanderthal extinction as assuming *separability*, that is, the assumption that we can consider an extinction being (in principle) caused by demography and not environment or competition. In this section, we'll argue against separability.

Demography alone?

Earlier, we characterized demographic factors as occurring at a population-level, involving changes to (or stability in) population size or structure. This is an ambiguous characterization, and indeed in itself doesn't seem to distinguish demography from, for instance, competition. After all, competitive exclusion hypotheses are all about changes in population size and structure due to selective effects, and evolution by natural selection can itself be characterized as a population-level process. Moreover, environmental effects are not easily distinguishable from selection, given that traditionally selection is in the business of filtering for those traits best suited

¹¹ We are concerned here with demographic or phyletic extinction. There can be other modalities of extinction: extinction by hybridization (the production of a hybridogenous species from two mother species), extinction by anagenesis and extinction by cladogenesis (cfr. Delord 2007).

to the environment. As such, there is a case to be made that *conceptually-speaking*, demography, competition and the environment cannot be disentangled, or at least that what counts as a demographic explanation (as opposed to a selective one, say) is confused because what counts as a demographic factor is underexplained. We think there's something to this conceptual confusion, but we'll side-step it for what we take to be a stronger argument. Even if a clear, precise (and exclusive!) definition of demographic factors could be provided, such factors cannot act alone at a token-level. To see the shape of the argument, we'll briefly turn to an illustrative case.

In the mid-14th Century the 'black death', a form of bubonic plague, spread throughout North Africa and Eurasia, with populations in Europe dropping precipitously as a result. The plague was spread by fleas infected with the yeast *Yersinia pestis* carried by rats (Prentice et al. 2004). An oft-cited reason for the plague's transmissibility is demographic: European urban populations were highly condensed.¹² Condensed populations are a plausible difference-maker: if populations were more spread out, disease vectors would have less opportunity to spread (Reyes et al 2013). Compare that factor—*condensed populations*—with another: *European Urbanization*. This is also a difference-maker: had Europe been less urbanized, then the plague would not have spread as virulently as it did. These two factors are clearly not independent: European populations were condensed *because* of European urbanization. To treat urbanization and condensed populations as independent causes of the plague's transmissibility is confused. Similar, we'll argue, can be said of treating demography as independent of competition or environment.

Let us first consider Kolodny and Feldman's migration explanation. Here, as they said, random drift plus migration can account for the extinction. This obscures a critical explanatory factor in how the result is generated: the environmental differences between Europe and Africa. In their models, Africa has a larger number of demes than Europe, which affords the continual migrations from one location into another. This is not merely a demographic factor; it is also an *environmental* factor. As such, although the migrations are a difference-maker they are not one that is independent from environments. That is, they cannot be independently varied even by an ideal intervention.

Second, we have Degioanni et al. 2019's explanation. Here, a decrease in female fertility would lead to plunging populations. This explanation is not independent of selection: fertility is directly related to expected progeny, and thus to fitness. Given the 400 k years or so Neanderthal persisted in Europe, we are led to ask after the causes of the putative decrease in fertility during the last 10,000 years before their extinction. Interestingly, Degioanni and colleagues' focus on the fertility reduction among primiparous women is justified as being known in large mammals as one of the first demographic rates affected by environmental variation¹³ (p.2). So, the authors themselves seem to suggest that fertility rates might track the effects of environmental factors: changing climates and environments and likely food stress, which

¹² Naturally, this is only a small part of the explanation: a lack of natural immune resistance to the new strain in Europeans, unfortunate weather, malnutrition and other aspects have been discussed.

¹³ There is in principle no reason why *Homo sapiens* should have been immune to this problem in Europe, although, as seen above, this might have been tempered by continuous migration waves from Africa.

affects the amount of stored body fat that is known to influence fertility in women. But perhaps we might link food stress to indirect or direct competition: migrating *H. sapiens* could have further increased resource scarcity in an already depleted environment and fragmented already distanced Neanderthal populations, affecting foraging success and exacerbating between-group competition. On either story, we see the demographic difference-maker being realized by either environmental or competitive factors, so we are left wondering why these would qualify as “demographic weakness” understood as competing with the other factors.

Third, we have Vaesen et al (2019)’s appeal to the small sizes of Neanderthal populations. Neanderthals living in small bands with limited connections put pressure on their collective fitness due to inbreeding depression, Allee effects impacting reproduction and population growth, and stochastic fluctuations in births, deaths and sex ratios. Again, there is a direct connection between demography and fitness. Further, why Neanderthal groups were small in the first place, even if it’s a feature that has accompanied them throughout their entire evolutionary history, is a crucial part of the explanation here.

Paleoclimatic data suggest that Neanderthal populations lived under highly fluctuating climatic conditions (Sanchez- Goñi et al. 2008), so they have likely been subject to repeated shrinking, each time probably drawing from a smaller base of genetic diversity and producing the downward trend observed in their N_e . In this case, Neanderthal demography would track the effects of environmental conditions and the failure of the population to recover from them. Or, from a different angle, the fact that Neanderthal populations persisted at low levels for hundreds of thousands of years and collapsed only a few thousand years after contact with modern humans, could indicate that the adopted lifestyles were sufficient for keeping them above the minimum viable threshold in the absence of competition, thus revealing relevant biologically or culturally-mediated differences in group organization between them and *Homo sapiens*. Again, the demography is due to either the vagaries of environmental effects or differences in fitness.

So, we’ve looked at three instances of putatively demographic explanations of Neanderthal extinction and shown that demographic factors are in no obvious way *independent* of other factors such as competitive exclusion or environmental effects, but are linked to them through a covariance relationship—*i.e.* changes in the relevant environment or competitive factors will be paired to changes in the demographic parameters: the former will co-vary with the latter. As such, citing demography *as opposed to* environment or competition is a mistake in these instances. What are we to conclude from this? Is it that *in principle* demography alone is never a sufficient explanation of extinction, or is it simply so in these instances? We think the former, stronger, claim can be made.

One way of construing the argument returns to our account of explanation. Recall that we understand difference-making as a necessary but insufficient factor for successful explanations. Extinction phenomena involve decreases in population—a demographic factor—so presumably plunging populations are difference-makers in extinction events (if the population did not decrease, or did not decrease as it did, the extinction would not happen or would not happen as it did). However, this is not sufficient for population decrease to be explanatory because it fails to distinguish

between *explanans* and *explanandum*. Our claim is that any attempt to make this distinction when explaining extinction with demography will either render the explanation insufficient (“the extinction occurred because the population decreased”) or will appeal to environmental or competitive factors, as we saw in the three cases above.

There are two responses to this idea. First, claim that in some instances demography takes explanatory precedence over other factors due to its robustness. Second, align demography with neutral explanations of extinction. In this section we’ll consider the former, in Sect. 5 we’ll turn to the latter.

Consider the potential *robustness* of demographic features in extinction: regardless of environmental or selective context, the Neanderthal’s fate could be sealed demographically insofar as what made the extinction occur in a non-accidental, modally robust sense, were demographic features. As a matter of fact, the demographic features may have been instantiated by environmental or competitive factors, but across those possibilities, demography is the stable factor. This response requires demography to be in some sense independent of selection or the environment and if, as we’ve argued, this is not so, then even if the demographic level captures something explanatorily important about the nature of Neanderthal extinction, it only does so in virtue of selective and environmental instantiations of those patterns. In short, even if demography is critical in explaining extinctions at the type-level, it doesn’t follow from this that it is sufficient or independent at the token-level.

Although we might explore demographic factors abstractly, across multiple instantiations, for actual, token extinctions, demographic factors are inseparable from the environment or competition.

Statisticalism?

At this juncture, it might be tempting to think that our claims about demography track a long-toothed debate in the philosophy of biology: statisticalism about natural selection (for a critical review, see Otsuka 2016). We don’t take ourselves to be committed to statisticalism about demography, and hopefully clarifying this will zero-in further on our position.

In brief, statisticalism is a claim about the nature of evolution by natural selection, namely, that it can be construed as a purely statistical phenomenon, with models of evolutionary change citing statistical properties of trait distribution and remaining silent about the causes of population change (Walsh, Ariew and Matthen 2017). Under this view, natural selection emerges as a higher-order effect, or as a statistical aggregate of individual-level dynamics, as opposed to something causal in and of itself. Contrast facts about natural selection—say, the distribution of a given phenotype within a population over time and the phenotype’s fitness—with particular, let’s call them, ‘fitness promoting’ properties and events within that population. Within an actual population, critters breed, die, escape predators, find food, and so on, and the chances of these events occurring turn in part on the particular phenotypes of those critters. The statisticalist will claim that it is in those individual-level properties that we’ll find causation. ‘Natural selection’ is not a force, but rather

a summary of those events: as such, there would be no need to posit higher-order causes to explain a higher-order effect. Others—causalists—instead argue that natural selection is causal, that over and above the individual-level events there is a higher ‘level’ of causation that the theory of natural selection describes. Like any debate this long-in-the-tooth, various subtleties and difficulties have arisen, but for our purposes we’ll stick to this fairly simple characterization.

‘Statisticalism’ about demography would claim that demographic factors (say, population migration) should be understood as a statistical summary of individual-level events (say, particular individuals shifting from one biome to another). Alternatively, we could take some demographic factors to be properly-speaking causal: migration literally causes, let’s say, increased population density (and thus perhaps an increased chance of epidemics). Our position regarding demographic explanations of Neanderthal extinction can be run on either view. Recall our complaint: defenders of demographic explanation often cast it as *alternative to* environmental or competitive factors. But demographic factors are realized by environmental or competitive factors – they are not independently manipulable. The analogy with selection would be to claim that some evolution event could be due to some combination of individual-level fitness properties and events (particular deaths, etc....) and due to population-level natural selection. But both the statisticalist and their opponent will see the mistake here: the statisticalist will say that as natural selection is nothing more than a summary of the individual-level events, we cannot treat these as separable in the relevant way; their opponent will say that although natural selection is itself a cause, as a ‘higher-level’ cause it shouldn’t be treated as independently manipulable from the lower-level realizers in token cases.

There is still a debate to be had, we think, about whether the explanatory burden should be demographic or environmental or competitive, but ours is a different debate concerning explanatory sufficiency (see our discussion of robustness above). At base, we needn’t take a position on statisticalism in order to run our argument.

Demography and extinction in a comparative context

We’ll close this section by pointing out that the connections between demographic factors and vulnerability to extinction are more complex than they might appear. Even if we agree that robust demographic causes should sometimes be granted explanatory precedence, more is required than sketching how some demographic properties make a population less evolutionarily resilient. Unfortunate demographics do not necessarily make a dead-clade-walking.

Studies of non-human primate species have shown that apparently unfavourable demographic histories, although presenting an increased risk of extinction, do not imply its inevitability. Mountain gorillas (*Gorilla beringei beringei*) are an endangered ape subspecies, currently at a high risk of extinction and a major focus of conservational efforts. Genomic studies (Xue et al. 2015) probing the genetic diversity of mountain gorilla populations have revealed that they have experienced a prolonged population decline over the past 100,000 years (along with the eastern lowland subspecies, *Gorilla beringei graueri*). This decline in

effective population size resulted in very low genetic diversity and increased burden from deleterious mutations. However, the same data shows that mountain gorillas have survived for thousands of generations at very low population levels; indeed, it has been hypothesized that they may even have developed behavioural strategies to mitigate the effects of inbreeding (such as migration and breeding away from the birth area, i.e. “natal dispersal” or gene flow between isolated populations) (cfr. Pusey et al. 1996). Unsurprisingly, what raises concerns about gorilla survival is a more recent, severe population decline that likely tracks human encroachment in their habitat and poaching activities (Xue et al. 2015), not their low populations over a 100 k period.

Small populations, inbreeding, and other demographic factors, then, should be understood in the context of the lineage in question’s adaptive regime: their niche, breeding strategy, etc.... Both mountain gorillas and Neanderthal survived with small, disconnected populations for thousands of years. Those factors should be taken as background to the explanation, rather than explanations in and of themselves.

Moreover, conservation geneticists have criticized the use of genetic diversity alone as a barometer for assessing population health and extinction risk. No simple general and linear relationship holds between genetic diversity and adaptive potential (Teixeria and Huber 2021). Species such as the wandering albatross, the cheetah or the channel island fox went through major bottlenecks throughout their evolutionary history, and these explain the very low levels of genetic heterozygosity observed in present-day populations, yet these species seem to have persisted in relatively stable populations for thousands of years (cfr. von Seth et al. 2018). These are clearly a few success stories, and we are by no means suggesting that such demographic risk factors should be overlooked, but these cases suggest they are insufficient to guarantee a species’ trajectory towards extinction. As neither low heterozygosity nor population size is a sufficient proxy for *immediate* extinction risk (see also Diez-del-Molino et al. 2018), additional information is needed to estimate adaptive potential in endangered species today, as well as the causes of extinction in past taxa.

Further, the demise of the Neanderthal is not the only episode of extinction registered in the fossil record after 40kya. The Denisovans, a hominin lineage mostly known from aDNA evidence, seem to have had lower heterozygosity levels with respect to their sister species (Prüfer et al. 2014). Although their demographic profile was less disadvantaged than that of Neanderthals, they nonetheless went extinct within the same temporal window (although leaving a much bigger genetic trace in the populations that encountered them). Further, recent studies of other extinctions during the Pleistocene (that of the woolly mammoth for instance), even when emphasizing different causes over others, present demography as complexly intertwined with environmental and competitive factors (see Fordham et al 2021 for instance). Interestingly, these studies have suggested approaching population decline from a process-based perspective, thus overcoming limitations of previous research focused on extinctions of populations already at critically small thresholds, rather than on the causes of smallness itself, in a broader temporal window (e.g. Fordham et al. 2021).

Indeed, Neanderthal demography could be informative of cultural fitness. Broadly defined here as the ability of a cultural variant or an innovation to be stored, transmitted, and influence individuals, cultural fitness might have well been affected by unfavourable demographic parameters. It has been shown that, assuming that innovations are rare, smaller and isolated societies have lower innovation rates and their transmissibility is less resistant to loss by chance (Richerson et al. 2009). We suspect, then, that demographic and competitive models focusing on differences in cultural factors and transmission are a potential source of powerful explanations of Neanderthal extinction.

There is an option over and above environmental or competitive factors that, you might object, we've been ignoring: stochasticity. As opposed to environmental or competitive factors, Neanderthal populations might have dipped, or been sent on an extinction-trajectory, due to bad luck. That is, the usual cycles of birth and death, fluctuations in population connectivity, and so on, may have happened to dip below some margin. Here, we agree, the explanation doesn't seem to appeal to environments nor to competition. However, discussions of demographic explanations in the literature are insufficiently careful in distinguishing between neutral explanations and demographic explanations. To see this, we'll turn to a discussion of the kinds of models currently being used to test and explore demographic explanations of Neanderthal extinction.

Demography and neutrality

In discussing separability in 3.3, we saw reference to demography playing the role of a 'neutral' or 'null' model. In this section we'll return to this notion, arguing that demography should not be considered as such.

Following traditions in paleontology (Raup et al 1987) and ecology (Rosindell et al 2012), paleoanthropologists have been developing simple models and simulations aimed at probing neutral explanations of Neanderthal extinction. These are often understood as fundamentally demographic explanations and further are often described in terms similar to what Bausman & Halina (2018) have called 'pseudo-null hypotheses'.

A 'neutral model', at base, aims to explore how population dynamics can change without intrinsic (as opposed to relational) differences between populations or individuals within them. In the context of ecology and paleontology, they are often cited to undermine views positing that selective factors—differences in fitness—are required to explain various phenomena (increases in complexity over macro-evolutionary time for instance). As is often the case in ecology, paleoanthropologists using such models often discuss these as if they were 'null' models, or that there is some preference we should have for these over non-selective explanations.

The approach seems to be (i) to identify one hypothesis as the 'null' in virtue of its 'simplicity', (ii) hold that before accepting any alternative explanation, the null must be rejected, finally, (iii) If the null cannot be rejected, then it should be considered the best explanation for the phenomenon at hand (see Bausman 2018 for

ecological examples). As we've seen, such a strategy is recognizable among demographic explanations for Neanderthals' extinction. Let's look at a final quote from Kolodny and Feldman:

Many studies that assign a major role to a selective advantage of Moderns in the Neanderthals' demise do so based on the premise that such an advantage had to exist in order to explain the Neanderthal's demise, and they focus on determining what the selective advantage could have been. In this study we show that this assumption is unnecessary: selection may have played a role in the Neanderthal's replacement, but the replacement could also have been the result of selectively neutral demographic processes, a parsimonious alternative that should a priori be preferred (Kolodny and Feldman 2017).

So, neutral models are taken to provide a (1) privileged/preferable explanation (inasmuch it represents a 'null' hypothesis) which is (2) both demographic *and* neutral. We'll discuss these claims in opposite order.

Point 2 is fairly straightforward. We've argued that demographic features are not independent of environmental or competitive features in token explanations of extinctions. As such, a model which represents demographic features *alone* does not thereby act as a neutral model as, depending on how the model is interpreted, it may smuggle in environmental and competitive features. Perhaps the easiest example of this is Kolodny and Feldman's model. In their simulations, whether a European location is occupied by *H. sapiens* or Neanderthal is chancy, but this is not sufficient for the model to be demographic as opposed to environmental. Because the environmental (/indirect competitive!) property of Africa having more demes is relevant for why *H. sapiens* replacement occurs. As such, the model does represent demographic features, but not independently of environmental ones, thus it fails to be neutral at least insofar as the most plausible interpretation points to a driven trend. Specifically, one driven by Africa's wider base for seeding migration.

Now, to point 1. Should such models be preferred a priori? No: either interpreted as demographic explanations or 'drifty', neutral explanation, such processes are no doubt important for understanding extinction, but there is no general reason we can see to privilege them. If the models capture demographic processes, which might be instantiated by selective and environmental features, then the point is moot. If we restrict interpretations to purely neutral interpretations, note that such models are not null hypotheses. They are treated as alternative or competing hypotheses to selective ones. A null hypothesis, within an experimental context, serves to demonstrate that the detected effect of intervention could be chalked up to unaccounted noise. As Bausman & Halina put it:

The fact that researchers require that one reject the null before accepting the alternative hypothesis makes sense within this [experimental] context. Accepting the null means the noise created by random extraneous variables was too large for the potential effects of the independent variable to be detected. In practice, accepting the null is a negative finding about the alternative, experimental hypothesis (Bausman & Halina 2018, 29-30).

So, such models do not function as null hypotheses: selective or environmental explanations of extinction needn't jump a bar set by neutrality in order to be on the table. The question, then, is whether there is any reason to think that a neutral explanation has some epistemic virtues over and above those positing selective or environmental effects. Perhaps appeals to simplicity might do this? We think not.

It is unclear what should be made of appeals to 'simplicity' and parsimony in these contexts. Regardless of whether in principle we should link epistemic virtues like simplicity to likelihood,¹⁴ at best what is meant by 'simple' here seems to mean *fewer causal factors*. But a purely selective, or a purely environmental, explanation is presumably just as simple as a purely neutral explanation. But more importantly: given that it is increasingly becoming clear that Neanderthal extinction is due to a mixture of factors—that it was a complex, multi-faceted processes—then it makes no sense to claim epistemic priority due to simplicity. Although the variables are (we think erroneously) treated as *independent*, they are not treated as *mutually exclusive*. As Vaesen et al. say of their survey: “endorsement of any single explanation may or may not be to the exclusion of other hypotheses” (2021, 2). Appeals to simplicity must be made against the backdrop of what we know, and we have very good reason to think environmental and selective effects were active amongst Neanderthal populations.

As we briefly argued above, demographic explanations should not be automatically equated with neutral explanations: just because, for instance, selection is not explicitly represented in the model—it is not a variable—doesn't mean that demographic patterns are not due to fitness differences themselves.

So, we don't think good reasons to privilege demographic explanations of Neanderthal extinctions, or extinctions generally, have been articulated here. And as we've seen, the models do not distinguish between neutral and selective trends. What work, then, do these models do?

Such models are in the business of explicitly representing and exploring the mechanics of demographic explanations. Clearly, they establish the *possibility* of demographic forces playing critical roles in extinctions. They represent potentially difference-making demographic properties such as population size, distribution, migration, and so forth. However, as demographic patterns may be instantiated and shaped by environmental or individual-level fitness variables not explicitly represented in the model, they do not represent an independent explanation.

Thus, the models allow us to examine the results of demographic factors at a high level of abstraction, potentially allowing for generalization across cases including those where, for instance, the underlying causes of the demographic patterns are heterogeneous. Potentially, identifying and exploring how demographic properties increase or decrease the probability of extinction generally is extremely useful, even if in every particular case some story about the environment or selection must also be told. Further, there may be good reason to think that an explanation which relies on, say, increased migration due to a larger number of demes, or decreasing fertility,

¹⁴ For what it is worth we don't: following others, we think such virtues are only justified given local conditions, not a-priori considerations (see, for instance, Sober 1991; Currie 2019).

has some epistemic priority over ones appealing to more dramatic competition or environmental calamities. But appeal to ‘simplicity’, a priori preference, or similar, is not sufficient. Such arguments would need to be made explicitly.

Conclusion

Not only is extinction a demographic phenomenon, demographic factors can be critical for explaining extinctions: demographic patterns can be partly due to demographic processes. However, extinctions do not occur by demography alone. Demographic factors emerge from, and are entangled with, environmental effects and fitness differences. Exploring how demography can influence and shape extinctions generally speaking doesn’t mean that demography alone or independently explains token extinctions.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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