

Research



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Evolutionary biology

Evolutionary shifts in extant mustelid (Mustelidae: Carnivora) cranial shape, body size and body shape coincide with the Mid-Miocene Climate Transition

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Environmental changes can lead to evolutionary shifts in phenotypic traits, which in turn facilitate the exploitation of novel adaptive landscapes and lineage diversification. The global cooling, increased aridity and expansion of open grasslands during the past 50 Myr are prime examples of new adaptive landscapes that spurred lineage and ecomorphological diversity of several mammalian lineages such as rodents and large herbivorous megafauna. However, whether these environmental changes facilitated evolutionary shifts in small- to mid-sized predator morphology is unknown. Here, I used a complete cranial and body morphological dataset to examine the timing of evolutionary shifts in cranial shape, body size and body shape within extant mustelids (martens, otters, polecats and weasels) during the climatic and environmental changes of the Cenozoic. I found that evolutionary shifts in all three traits occurred within extant mustelid subclades just after the onset of the Mid-Miocene Climate Transition. These mustelid subclades first shifted towards more elongate body plans followed by concurrent shifts towards smaller body sizes and more robust crania. I hypothesize that these cranial and body morphological shifts enabled mustelids to exploit novel adaptive zones associated with the climatic and environmental changes of the Mid to Late Miocene, which facilitated significant increases in clade carrying capacity.

1. Introduction

The exceptional lineage and phenotypic diversity found across the tree of life is often associated with increases in ecological opportunities through the evolution of innovations, extinction of competitors or environmental changes [1–3]. Simpson [1] was one of the first to recognize that the adaptive landscapes of phenotypic traits can shift (jump) in response to environmental changes. The global cooling, increased aridity and habitat shift from forest to grasslands during the past 50 Myr [4–7] is a prime example of environmental changes that spurred evolutionary shifts in phenotypes. Several mammalian clades have adapted to these environmental transitions towards more open, grass-dominated habitats. Rodents and lagomorphs diversified and shifted towards increased tooth crown height (i.e. hypsodonty) to eat tougher grass material and evolved adaptations for more efficient burrowing, jumping and cursorial locomotion across the open habitats (reviewed in [8]). Herbivorous ungulates also shifted towards hypsodont dentition during the Oligocene to Miocene, along with the lengthening of limbs for more efficient cursoriality during the late Miocene [9–12]. Similarly, ecomorphological diversity of carnivores increased [13–15], with large carnivores shifting from ambush specialists to active pursuit specialists during the late Miocene to

Pleistocene [16,17]. Although numerous studies have examined evolutionary shifts in small and large terrestrial mammals, how the phenotypes of mid-sized predators responded to environmental transitions has rarely been tested (but see [17]).

In this study, I use a comprehensive morphological dataset derived from the cranial and axial skeletons to examine if extant mustelid subclades within Musteloidea (Mephitidae, Ailuridae, Procyonidae and Mustelidae) exhibited evolutionary shifts in morphology coinciding with the Mid-Miocene Climate Transition (MMCT), 15.97–11.61 Myr ago. Researchers have long hypothesized that the expansion of grasslands [7,18] and diversification of rodents and lagomorphs [8,19,20] during the Middle to Late Miocene led to increased clade carrying capacity within extant mustelids, particularly mustelines, lutrines and ictonychines (e.g. weasels, polecats, otters) [21–23]. Recent work corroborated these hypotheses, revealing evolutionary shifts towards small, elongate body plans during the Middle to Late Miocene that may have facilitated diversification by allowing mustelids to chase prey in burrows and small crevices [24]. Although these studies revealed associated transitions between body size and shape and the behaviour of entering subterranean habitats, it remains to be explored whether traits tied directly to prey capture and consumption also exhibited evolutionary shifts near the MMCT. The cranium is the primary apparatus used by most mustelids to capture, kill and consume prey. Despite recent comparative studies elucidating the ecomorphological and functional diversity of mustelid cranial morphology [25–28], the timing of evolutionary shifts in the adaptive landscape of mustelid crania is still unexplored.

The objectives of this study are two-fold. First, I determined whether extant mustelid subclades exhibited evolutionary shifts in cranial shape near the MMCT. I predicted that extant mustelids would exhibit shifts in cranial shapes that favour the ability to generate relatively larger bite forces to capture and consume prey that can be up to 10 times larger than their own body mass [29]. Second, I examined the timing of evolutionary shifts in body size and body shape. Previous work used a model selection approach with *a priori* hypotheses to determine where evolutionary shifts in body size and shape occurred between designated clades [24]. However, these *a priori* hypotheses represented only a fraction of all possible shifts and may unintentionally hide additional shifts that are important in driving trait evolution [30]. Therefore, I reexamined extant mustelid body sizes and shapes using data-driven approaches.

2. Material and methods

I tested for evolutionary shifts in mustelid cranial shape, body size and body shape using phylogenetic comparative methods with the most recent molecular phylogeny of extant mustelids [23]. I also included the other three musteloid families to provide a phylogenetic background and increase statistical robustness for model fitting [31]. Cranial shape, body size and body shape measurements of 60 extant musteloids were obtained from [27,23], and [24], respectively (see full methods in electronic supplementary material).

I used an *a priori* hypothesis-driven approach to examine evolutionary shifts in cranial shape. I used a principal component (PC) analysis and Bookstein's [32] method implemented in Morpho v. 2.6 [33] to reduce the dimensionality of the cranial shape dataset and to retain the first two PC axes of cranial morphospace. I then fitted four evolutionary models using maximum likelihood with mvMORPH v. 1.0.8 [34]: single-rate Brownian motion (BM1),

single peak Ornstein–Uhlenbeck (OU1), a two-peak OU model in which a clade of Helictidinae, Guloninae, Ictonychinae, Mustelinae and Lutrinae (hereafter HGIML-clade) exhibited a separate cranial shape optimum from the remaining phylogeny (OUM_HGIML), and a two-peak OU model in which a clade of Ictonychinae, Mustelinae and Lutrinae (hereafter IML-clade) exhibited a separate optimum from the remaining phylogeny (OUM_IML). Previous analyses found decoupled diversification dynamics towards the HGIML-clade and differential rates of body length and mass evolution towards the IML-clade [23]. I assessed model support with small sample corrected Akaike weights (AICcW).

I then identified evolutionary shifts in the three traits without *a priori* hypotheses of adaptive optima using bayou v. 2.1.1 [35] and PhylogeneticEM v. 1.2.1 [36]. These data-driven approaches detect evolutionary shifts towards different optima without influences of *a priori* groupings on the tree. Bayou uses a reversible-jump Bayesian approach to estimate the placement and magnitude of evolutionary shifts [35], appropriate for the body mass and head–body elongation ratio (ER) datasets, which are univariate. Shifts with a posterior probability (pp) > 0.5 were determined as significant. Because cranial shape is multivariate, I identified shifts in cranial shape (PC1 and PC2) with PhylogeneticEM, which uses a scalar OU model that infers the full evolutionary rate matrix and accounts for correlations within multivariate datasets (i.e. PC1 and PC2) [36].

3. Results

Extant musteloids exhibited great variation in cranial shape, body size and body shape (figure 1). Within cranial morphospace, musteloids with low PC1 and PC2 scores exhibited relatively elongate rostrum and relatively smaller faces and braincases driven by the narrowing of the nuchal crests and zygomatic arch breadth. By contrast, musteloids with high PC1 and PC2 scores exhibit relatively stout rostrums and relatively broader braincases, mastoid breadth and zygomatic arch breadth (figure 1a).

The OUM_IML model was best supported (AICcW = 0.47; table 1), suggesting an evolutionary shift in cranial shape towards the IML-clade. PhylogeneticEM also detected an evolutionary shift towards the IML-clade (figure 2a), thus corroborating the model selection approach. However, the OU (AICcW = 0.30) and OUM_HGIML (AICcW = 0.22) models were also relatively well supported (table 1), suggesting that additional shifts may be hidden from the *a priori* hypothesis-driven approach. PhylogeneticEM detected five additional shifts towards other musteloid clades.

For body size, I found an initial increase in body mass optimum at the root of Mustelidae (pp = 0.56; θ = 7.74 kg; $\theta_{\text{ancestral}}$ = 2.56 kg) before the MMCT. I found a decrease in body mass optimum towards the IML-clade (pp = 0.58; θ = 0.59 kg) during the MMCT. Mustelines exhibited a further shift towards smaller body masses (pp = 0.57; θ = 0.35 kg), whereas lutrines exhibited a shift towards larger body masses (pp = 0.61; θ = 11.71 kg; figure 2b).

For body shape, I found evolutionary shifts towards more elongate bodies within the HGIML-clade (pp = 0.61; θ = 6.17; $\theta_{\text{ancestral}}$ = 5.08; figure 2c), followed by further shifts towards more elongate bodies in musteline weasels (Mustelinae; pp = 0.63; θ = 7.19) and the African striped weasel (*Poecilogale albinucha*, Ictonychinae; pp = 0.88; θ = 8.01). By contrast, there was an evolutionary shift towards a reduction in body elongation in otters excluding the giant otter (*Pteronura brasiliensis*) (Lutrinae; pp = 0.53; θ = 5.58), followed by a further

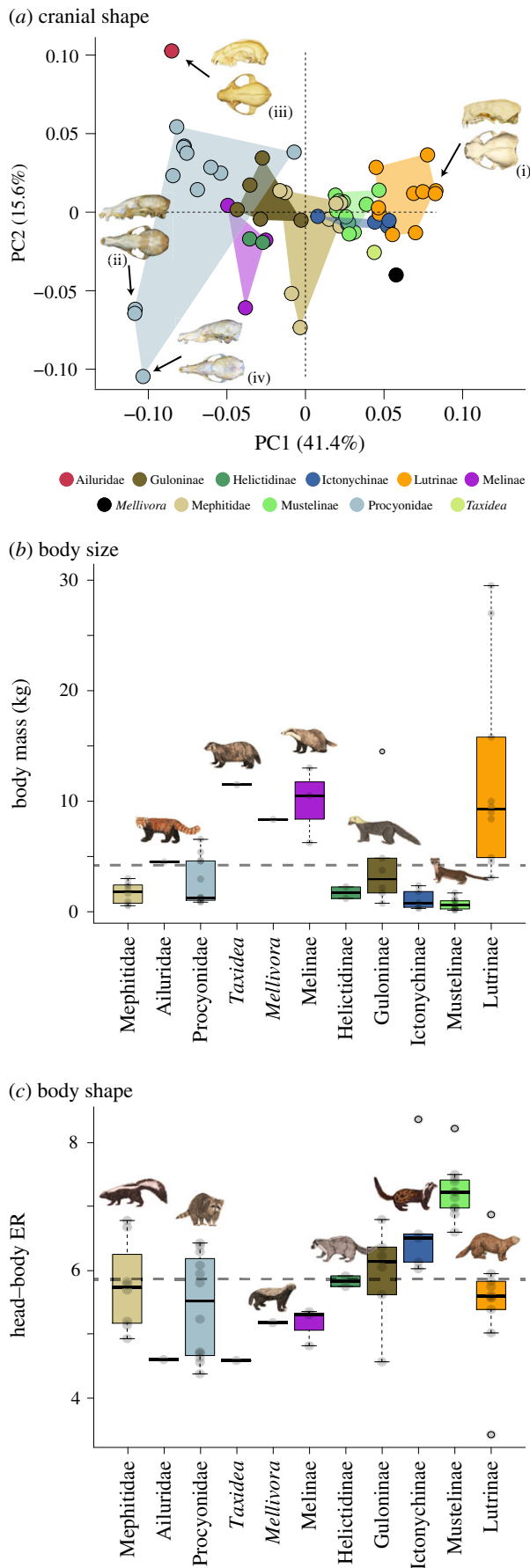


Figure 1. Morphospace of (a) cranial shape defined by principal component (PC) axes 1 and 2, and box plots of (b) body mass and (c) body shape. Cranial photos in (a) are of a (i) sea otter (*Enhydra lutris*), (ii) ring-tailed coati (*Nasua nasua*), (iii) red panda (*Ailurus fulgens*) and (iv) western mountain coati (*Nasua olivacea*). Grey dashed lines in (b,c) represent the mean body mass and head–body ER of all musteloids, respectively.

Table 1. Comparisons of evolutionary model fit for evolutionary shifts in cranial shape (PC1 and PC2).

model	AICc	$\Delta AICc$	AICcW
BM	−387.26	33.66	0.00
OU	−420.05	0.87	0.30
OUM_HGIML	−419.43	1.49	0.22
OUM_IML	−420.92	0.00	0.47

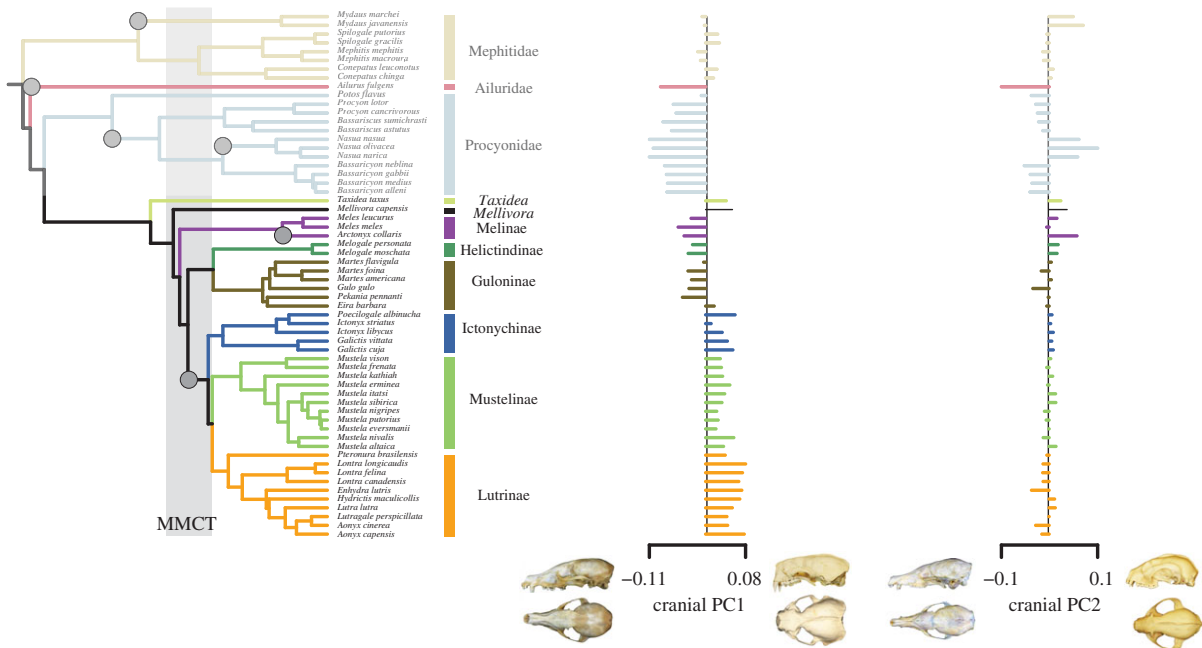
reduction in the sea otter (*Enhydra lutris*; $pp = 0.95$; $\Theta = 3.64$). The wolverine (*Gulo gulo*, Guloninae) also exhibited a reduction in body elongation ($pp = 0.87$; $\Theta = 4.70$). I also found independent evolutionary shifts towards more elongate body plans in other musteloid genera well after the MMCT.

4. Discussion

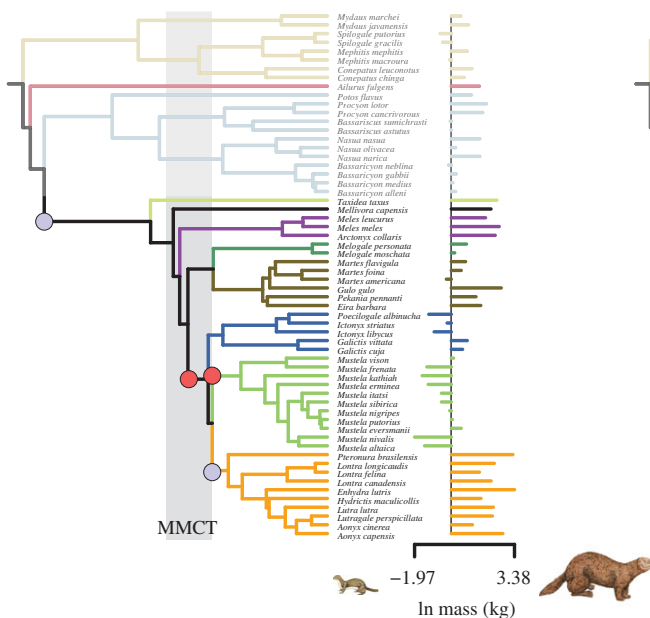
Evolutionary shifts in phenotypes can serve as innovations to exploit new adaptive zones and facilitate lineage diversification [1]. Here, I take advantage of a comprehensive morphological dataset that incorporates cranial shape, body size and body shape to understand phenotypic evolution in a clade of extant small- to mid-sized predators. I found that within extant mustelid subclades (particularly Ictonychinae, Mustelinae and Lutrinae), evolutionary shifts towards more robust crania, small body sizes and elongate bodies all occurred during the MMCT, a period of time characterized by arid climates [5], open habitat expansions [7,18] and rodent and lagomorph diversification [8,19,20]. Shortening the rostrum and broadening mastoid and zygomatic arch breadth are often associated with increases in relative bite forces [37–39]. Therefore, an evolutionary shift towards these broader cranial shapes favouring larger jaw muscle attachment areas may counteract the weaker bite forces associated with smaller body sizes [27,40]. Concurrent shifts towards smaller, more elongate body plans would enable these mustelids to actively chase prey down into burrows or crevices, and their relatively large bite forces for their smaller sizes would facilitate the successful dispatch of prey that can be up to 10 times larger than many mustelids [29]. These results corroborate the hypothesis that evolutionary shifts in cranial and axial adaptations parallel the exploitation of novel grassland habitats and rodent prey associated with the MMCT [24], which led to significantly greater clade carrying capacity within Mustelidae [23].

The incorporation of unaccounted shifts with data-driven approaches provided a more comprehensive understanding of the evolution and timing of cranial and body morphology across extant mustelids. These data-driven approaches revealed that shifts towards more elongate bodies appeared to have evolved first within the HGIML-clade followed by subsequent shifts towards more robust crania and smaller bodies within the IML-clade. Extant mustelines further shifted towards even smaller, more elongate bodies, whereas extant lutrines further shifted towards bigger, more robust bodies. In all three traits, the data-driven approaches not only corroborated the best selected model (table 1; [24]) but also detected additional shifts that were previously unidentified when using model selection approaches with designated *a priori* hypotheses. For example, the *a priori* model selection approach identified a single shift

(a) cranial shape



(b) body size



(c) body shape

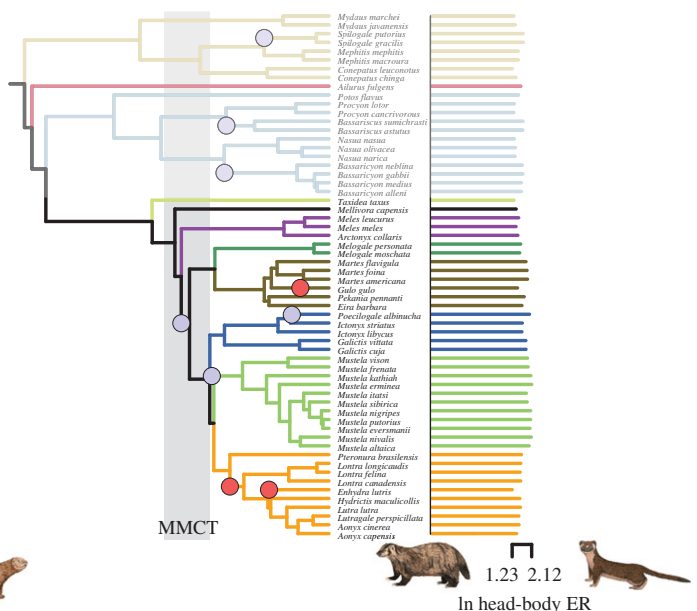


Figure 2. Regime shifts of (a) cranial shape, (b) body size and (c) body shape across mustelids with background musteloid clades. PhylogeneticEM shifts on cranial shape are shown as grey circles. Bayou shifts ($pp > 0.5$) on body mass and body shape are shown as blue and red circles, which represent increases and decreases in optimal values, respectively. Branches on the phylogenies are coloured according to musteloid clade. Grey boxes underlying phylogenies represent the Mid-Miocene Climate Transition (MMCT) from 15.97 to 11.61 Myr ago.

towards smaller, more elongate body plan along the branch leading to the HGIML-clade [24]. Bayou, however, identified additional shifts not detected by *a priori* groupings and therefore provided a more nuanced conclusion regarding the evolution of mustelid body size and shape. Specifically, bayou detected that mustelids exhibited multiple—rather than just one—evolutionary shifts within the HGIML-clade. The first shift occurred along the branch leading to the HGIML-clade and led to body optima that were 76.9% smaller and 21.5% more elongate compared to ancestral musteloids. The second shift occurred in mustelines, indicating that mustelines shifted towards even smaller (86.3%) and more elongate (41.5%) bodies compared to ancestral musteloids. Lastly, the third shift occurred within lutrines, which led to body optima that were 357.4% larger but

10% less elongate compared with other mustelids within the HGIML-clade. Therefore, these data-driven approaches revealed that body size and shape evolved through successive evolutionary shifts rather than as a single shift, providing further evidence that incorporating phylogenetic natural history [30] can elucidate further insights of trait evolution.

5. Conclusion and future directions

This study provided evidence that extant mustelid subclades evolved robust cranial shapes and small, elongate bodies to exploit new adaptive landscapes, which in turn facilitated significant increases in clade carrying capacity during the Late

Miocene to present [23]. However, a caveat to this study is the absence of paleontological data. Extinct mustelids were ecomorphologically diverse, with over 400 described species [41–44]. Unfortunately, the phylogenetic framework and morphological data needed to incorporate these extinct taxa are unavailable. Previous work has demonstrated that incorporating the fossil record in macroevolutionary analyses dramatically improves the model selection of trait evolution [45–47]. This present study only used extant taxa to infer cranial and body trait evolution and its association with the MMCT; consequently, I was unable to fully elucidate the evolutionary transitions of cranial and body traits across historical time that led to the traits observed in extant species. Only the incorporation of the fossil record will elucidate whether selection for smaller, more elongate bodies and stronger jaws occurred within extant species of the HGIML-clade, suggesting an evolutionary response to the MMCT, or if basal ancestors of the HGIML-clade already exhibited those characteristics, suggesting that these traits were not associated by the MMCT. The inclusion of the fossil record can also elucidate the timing of trait shifts. My neontological-based analyses suggested that shifts in cranial and body traits occurred within 2.5 Myr from 14 to 11.5 Myr ago, approximately 1–4 Myr after the onset of the MMCT. Compared to large mammals, it is tempting to suggest that smaller mammals may be more likely to respond faster to environmental changes owing to a variety of life-history factors such

as shorter generation times, smaller ranges and greater number of locally adapted populations [48–51]. Under this hypothesis, shifts in diversity and ecomorphology of small mammals correspond closely with the timing of environmental transitions, whereas diversification and ecomorphological shifts of large mammals may lag millions of years [8,9,11,52]. As mid-sized mammals, the timing of evolutionary responses of mustelids seemingly occurs intermediate to small and large mammals; nevertheless, the incorporation of the fossil record is needed to quantify differences in rates of phenotypic transitions between mammalian clades and their timing with respect to environmental changes. Future work combining neontological and paleontological datasets under a total evidence phylogeny will provide a more complete understanding of the patterns, timing and mechanisms of trait evolution.

Data accessibility. Dataset and R script are uploaded on Dryad Digital Repository: doi:10.5061/dryad.58p45tb.

Authors' contributions. C.J.L. conceived the study, performed analyses and wrote the manuscript.

Competing interests. I declare I have no competing interests.

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