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Commentary

On fossil recovery potential in the *Australopithecus anamensis–Australopithecus afarensis* lineage: A reply to Žliobaitė (2020)

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1. Introduction

We thank Žliobaitė (2020) for the interest in our article (Du et al., 2020) and the resulting dialogue. In this response, we briefly summarize Du and colleagues' analysis and Žliobaitė's commentary, respond to the points raised by Žliobaitė, and conclude with some thoughts on why the distribution of *Australopithecus anamensis–Australopithecus afarensis* fossil horizons does not conform to a wax–wane pattern (see Table 1 glossary).

1.1. Brief summaries of Du et al. (2020) and Žliobaitė (2020)

A fossil taxon's observed temporal range almost always underestimates its true range due to incomplete fossil preservation and recovery (Marshall, 2010; Wang and Marshall, 2016; Wood and Boyle, 2016). That is, a taxon's first appearance in the fossil record is almost always younger than its true origination date, and its last appearance is almost always older than its true extinction date. Du et al. (2020) used a model developed by Strauss and Sadler (1989) to estimate the true origination and extinction dates for the *A. anamensis–afarensis* lineage. One key assumption of this model is that over the duration of a taxon's true temporal range, the probability of recovering a fossil horizon is constant through time. This probability is called the fossil recovery potential (FRP; Table 1). A constant FRP results in observed fossil horizons that are uniformly distributed through time. Du et al. (2020) assessed the uniformity of *A. anamensis–afarensis* fossil horizons with a uniform probability plot (their Fig. 5) and concluded that the observed temporal distribution of horizons is consistent with a uniform distribution. Because the Strauss and Sadler model assumptions appear to be satisfied, Du and colleagues concluded that their estimated origination and extinction dates for *A. anamensis–afarensis* are unbiased.

Žliobaitė (2020) does not challenge Du et al.'s (2020) finding that the temporal distribution of *A. anamensis–afarensis* horizons is uniform: “[Strauss and Sadler's (1989) model] assumes uniformity of fossil horizons, and Du et al. (2020) go out of their way to convince the reader that the assumption is satisfied. I am convinced, at least there does not seem to be any more plausible choice” (Žliobaitė, 2020:1). However, Žliobaitė argues that the Strauss and Sadler (1989) model has a hidden assumption, namely that a taxon's abundance is assumed to be constant through time. Žliobaitė finds this assumption to be “too counterintuitive” (Žliobaitė, 2020:1), given the generality that other fossil taxa wax and wane through time in their abundance, as inferred from their waxing and waning occupancy (Table 1) and geographic range size (Jernvall and Fortelius, 2004; Foote, 2007; Foote et al., 2007; Liow and Stenseth, 2007; Liow et al., 2010; Quental and Marshall, 2013; Bibi and Kiessling, 2015; Raia et al., 2016). Therefore, why is waxing and waning not observed in the temporal distribution of *A. anamensis–afarensis* fossil horizons? Žliobaitė (2020) conducted simulations to show how the temporal distribution of a taxon's

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Table 1
Glossary of terms in the general order that they appear in the current article.

Fossil recovery potential (FRP)	The probability of recovering a taxon's fossil horizon at any given time period.
Fossil horizon	A time period yielding at least one specimen from the taxon in question.
Wax—wane	The pattern of increasing then decreasing occupancy, geographic range size, and thus inferred abundance within a taxon's temporal range. That is, a taxon originates with low abundance and is geographically restricted, reaches peak abundance and geographic spread in the middle of its temporal range, and then decreases in abundance and geographic range size, culminating in its extinction.
Occupancy	The proportion of sites across space occupied by a taxon in a given time period.
Wax—wane FRP	FRP is hump-shaped over a taxon's true temporal range. That is, it is lowest near the taxon's origination and extinction and is highest in the middle of the taxon's range.
Constant FRP	FRP is constant throughout a taxon's true temporal range. This is an assumption made by the Strauss and Sadler (1989) model.
Age gap	The amount of time separating two consecutive fossil horizons.

fossil horizons would appear under a constant abundance versus a wax—wane model. Žliobaitė interprets the simulation results as suggesting that either model is consistent with the observed distribution of *A. anamensis—afarensis* fossil horizons: "… one could argue that either of the two scenarios agrees with the data better" (Žliobaitė, 2020:2), and "… it is up to individual interpretations whether the middle plot shows an 'S-curve,' which would be characteristic of waxing and waning, or it is a flat line, which would be consistent with constant abundances" (Žliobaitė, 2020:2).

2. Fossil recovery potential is not equivalent to abundance

We respectfully suggest that Žliobaitė (2020) is incorrect in stating that Strauss and Sadler (1989) assume a taxon's abundance is constant through time; in fact, Strauss and Sadler never mention 'abundance'. Rather, Strauss and Sadler assume only that a taxon's FRP is constant through time. Žliobaitė (2020) implicitly equates abundance with FRP, implying that changes in the former must be reflected in the latter, but this need not be the case.

FRP is the proximate, or immediate, determinant of the temporal distribution of a taxon's fossil horizons. It is a complex function of a myriad of factors through time, including a taxon's abundance, the existence of depositional environments, fossil preservation, collection methodology, and publication, among others (Patzkowsky and Holland, 2012). As a result, none of these factors in isolation is necessarily strongly related to FRP, unless that factor exerts a dominant influence on FRP. Thus, the only way a wax—wane abundance pattern will result in a wax—wane FRP is if (1) other non-abundance factors also wax and wane, thereby reinforcing the wax—wane pattern, which is unlikely, or (2) the wax—wane abundance signal is strong enough to overcome the noise created by the complex interaction of the other factors (this latter point is similar to the idea of abundance being related to FRP 'on average' or 'with all else held equal'). This second scenario is made less likely by the fact that *A. anamensis—afarensis* is rare, typically on the order of 1% of all specimens or individuals in the large mammalian communities where it is found (White et al., 2006; Su and Harrison, 2008; Bobe et al., 2020; Villaseñor et al., 2020). As a result, the abundance trajectory of *A. anamensis—afarensis* is likely to be noisy to begin with and thus more easily obscured by other non-abundance FRP factors. In sum, because abundance is only one of many factors that interacts in complex ways to produce FRP, abundance and FRP may not have any apparent relationship, and this may be particularly true for rare taxa like *A. anamensis—afarensis*.

Therefore, the assumed 'abundance' trajectories within Žliobaitė's simulations (Žliobaitė, 2020's Fig. 1a, b), which directly determine the temporal distribution of fossil horizons, are more accurately characterized as FRP trajectories. Hence, we hereafter refer to the constant and wax—wane abundance models as constant and wax—wane FRP models. The complex relationship between abundance and FRP also complicates estimating abundance from the temporal distribution of fossil horizons as suggested by Žliobaitė (2020:2—3).

Because the temporal distribution of a taxon's fossil horizons is a direct function of FRP, one can use the distribution to infer FRP through time. Empirically, the temporal distribution of *A. anamensis—afarensis* fossil horizons is consistent with a uniform distribution (Du et al.'s [2020] Fig. 5; see Section 3), but Žliobaitė (2020) argues that it is also consistent with a wax—wane FRP (see Section 1.1). We discuss this possibility in the next section.

3. The constant fossil recovery potential model fits the data better than the wax–wane model

A premise of the constant FRP model is that FRP is uniform over the duration of a fossil taxon's true temporal range (Table 1). The wax—wane FRP model, on the other hand, postulates that FRP is low when a fossil taxon originates, increases to its maximum value in the middle of the taxon's range, and decreases to zero when the taxon goes extinct (i.e., FRP is hump-shaped over a taxon's true temporal range; Table 1). It is important to determine which FRP model better fits the *A. anamensis—afarensis* fossil horizon data. Du et al. (2020) estimated origination and extinction dates for this taxon, using a model that assumes FRP is constant through time (Strauss and Sadler, 1989). If *A. anamensis—afarensis* FRP instead follows a wax—wane pattern, then Du et al.'s estimated origination and extinction dates—along with their confidence intervals—are too young and old, respectively (Marshall, 1997; Žliobaitė, 2020). In this section, we show that when the results are quantified and not just visually evaluated, Žliobaitė's own analyses demonstrate that the observed distribution of *A. anamensis—afarensis* fossil horizons is better fit by the constant FRP model than by the wax—wane FRP model. All analyzed data and R code v. 4.0.2 (R Core Team, 2020) are provided as Supplementary Online Material (SOM).

Under the assumption of a constant FRP, the distribution of age gaps—the amount of time separating two consecutive fossil horizons (Table 1)—is expected to be independent of time. Under the assumption of a wax—wane FRP, age gaps are expected to follow a U-shaped pattern through time: age gaps will be larger toward the ends of a taxon's range when it is harder to sample a fossil horizon and smaller in the middle when horizons are more likely to be sampled. These patterns are seen in Žliobaitė's (2020) simulations (their Fig. 1c, d). Visually, the observed *A. anamensis—afarensis* age gaps appear to be constant through and independent of time (Fig. 1). This visual assessment is quantitatively supported by an estimated ordinary least squares slope that is effectively zero (−0.0046, 95% CI = [−0.0459, 0.0367]; Fig. 1). On the other hand, a U-shaped age gap pattern would be expected to have a significant, positive quadratic term when added to the linear model. The estimated quadratic term is statistically indistinguishable from zero (0.0313, 95% CI = [−0.1052, 0.1678]) and is of such low magnitude

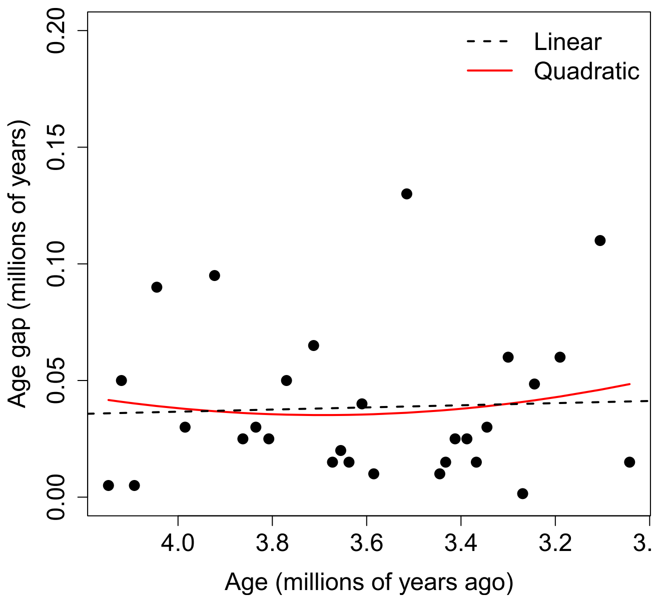

Figure 1. *A. anamensis–afarensis* age gaps through time. Dashed line is a fitted ordinary least squares model, and the red line is the same but with an added quadratic term. Age is plotted as proceeding from left to right, so the linear model slope appears to be positive even though it is estimated to be negative. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

that the fitted model is effectively linear over the range of the data (Fig. 1). Therefore, we can conclude that the observed *A. anamensis–afarensis* age gaps more closely follow the expectations from a constant FRP model than a wax–wane FRP model. This is also borne out by Žliobaitė's (2020) analyses, wherein the observed *A. anamensis–afarensis* age gaps do not exhibit any distinct U-shape through time and fall mostly within one standard deviation of the constant FRP model (Fig. 1c in Žliobaitė, 2020). In contrast, the wax–wane model systematically underestimates observed age gaps between 3.8 and 3.4 Ma, and many observed age gaps appear to fall outside two standard deviations (Fig. 1d in Žliobaitė, 2020).

We can also calculate goodness of fit (i.e., r^2) and model selection statistics (i.e., Akaike Information Criterion; AIC) to determine whether the *A. anamensis–afarensis* fossil horizon data are better fit by the constant rather than the wax–wane FRP model. We use code from Žliobaitė (2020; https://github.com/zliobaite/Australopithecus-hat/blob/master/run_uniformity.R) to estimate *A. anamensis–afarensis* fossil horizon ages expected from either model. Briefly summarizing the analysis, Žliobaitė kept the oldest and youngest *A. anamensis–afarensis* fossil horizons fixed, while randomly sampling the 28 horizons in between from predetermined FRP distributions (Fig. 2 insets). This was repeated 1000 times, and the 30 horizon ages averaged over all 1000 iterations are the expected ages (these ages are identical to the y-axis values from Fig. 1e and g in Žliobaitė, 2020). Our results show that the observed *A. anamensis–afarensis* fossil horizon ages are better fit by the constant FRP model ($r^2 = 0.987$; Fig. 2A). The wax–wane model produces a lower r^2 (0.934), and its predictions systematically depart from the data: predicted ages are too young from 4.1 to 3.6 Ma and too old from 3.6 to 3.4 Ma (Fig. 2B). We also calculate AIC scores—assuming normally distributed errors with constant variance (Burnham and Anderson, 2002, pg. 63)—to weigh our models' fits against each other. The calculated AIC for the constant and wax–wane FRP models are −197.67 and −149.38, respectively. Lower AIC values indicate a more strongly supported model, and the fact that the wax–wane AIC is larger by >10 points suggests that this model receives essentially zero support (Burnham and Anderson, 2002, pg. 70). This finding is supported by transforming AIC scores into weights, where weights sum to one across models and larger values indicate greater model support (Burnham and Anderson, 2002, pg. 75). The AIC weight for the constant FRP model is ~1.0, whereas it is 3.27×10^{-11} for the wax–wane model. Thus, the results of our fossil horizon analysis corroborate the results of the age gap analysis, in that the constant FRP model fits the observed *A. anamensis–afarensis* data better than the wax–wane FRP model.

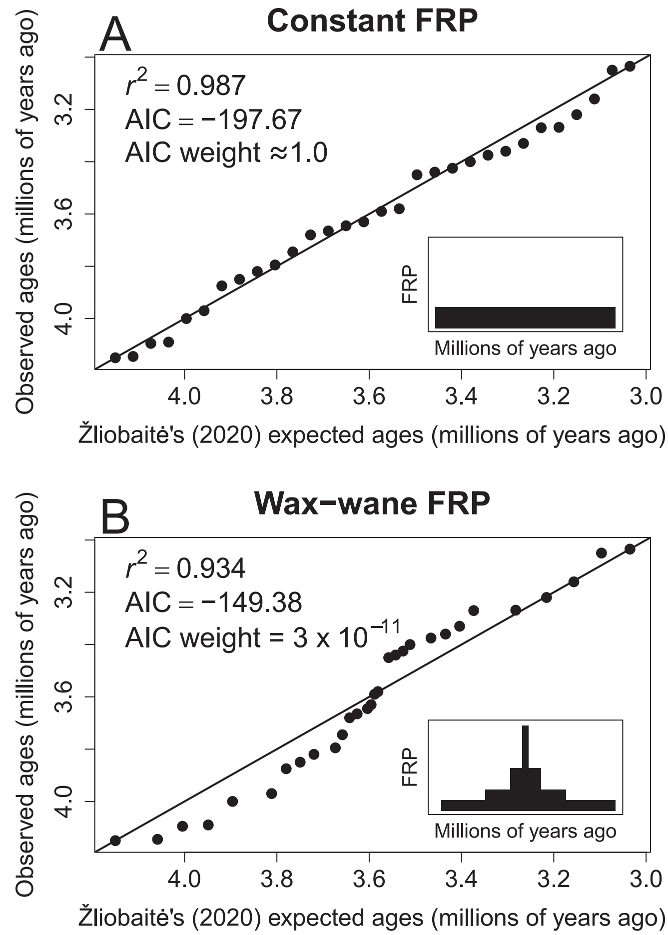

Figure 2. Observed ages of *A. anamensis–afarensis* fossil horizons plotted as a function of expected ages from A) Žliobaitė's constant fossil recovery potential (FRP) model and B) Žliobaitė's wax–wane FRP model. Expected ages are estimated following Žliobaitė (2020), using code from https://github.com/zliobaite/Australopithecus-hat/blob/master/run_uniformity.R, wherein fossil horizon ages are sampled from prespecified FRP distributions (insets). Lines represent the line of unity. A) is similar to a uniform probability plot (cf. Fig. 5 in Du et al., 2020).

Nevertheless, it is possible that the temporal distribution of *A. anamensis–afarensis* fossil horizons exhibits weak waxing and waning: the observed horizons are slightly younger than expected between 3.9 and 3.7 Ma, slightly older than expected between 3.4 and 3.1 Ma (Fig. 2A), and there is a paucity of age gaps greater than 0.05 million years between 3.6 and 3.4 Ma (Fig. 1). The reason why the wax–wane model fits poorly then is because we modeled wax–wane dynamics using Žliobaitė's (2020) specific, predetermined FRP trajectory (Fig. 2B inset). A more rigorous analysis would model wax–wane FRP using a continuous, unimodal distribution (e.g., beta distribution) that is fit to the data, but such an undertaking is not trivial and is therefore outside the scope of our response. Nonetheless, we predict that the larger number of free parameters in the more complicated distribution of the wax–wane FRP model will not result in an appreciable increase in goodness of fit, such that the constant FRP model will 'win out' (when AIC is used to assess models, goodness of fit is penalized by the number of free parameters [Burnham and Anderson, 2002]). Furthermore, the wax–wane signal in *A. anamensis–afarensis* is so weak that Du et al.'s (2020) estimated origination and extinction dates are unlikely to change much, even if one did incorporate wax–wane into the analysis.

4. Why is wax–wane not seen in *A. anamensis–afarensis*, and how does this affect estimated origination and extinction dates?

We suggest that the distribution of *A. anamensis–afarensis* fossil horizons sufficiently follows a uniform distribution (Du et al., 2020, Section 3), implying that this taxon's FRP is constant through time. As mentioned in Section 1.1, this is curious, given that many other taxa wax and wane in their occupancy, geographic range size, and thus inferred abundance (Jernvall and Fortelius, 2004; Foote, 2007; Foote et al., 2007; Liow and Stenseth, 2007; Liow et al., 2010; Quental and Marshall, 2013; Bibi and Kiessling, 2015; Raia et al., 2016). Why then is waxing and waning not seen in the temporal distribution of *A. anamensis–afarensis* fossil horizons?

Theoretically speaking, all lineages must wax and wane (Liow and Stenseth, 2007). Each lineage originates as a single population (i.e., via cladogenesis) that occupies only one site and is therefore geographically restricted. A lineage eventually goes extinct when all its populations die out, and occupancy and geographic range size correspondingly drop to zero. Therefore, it is almost certain that a lineage's abundance, occupancy, and geographic range size will be larger at some point between origination and extinction, the two times when these measures are at their lowest. Where in the lineage these measures peak and for how long are all variations on the wax–wane pattern (see Fig. 4 in Jernvall and Fortelius [2004], Fig. 1 in Foote et al., [2007], and Fig. 3 in Liow et al., [2010]). As a result, it is highly likely that *A. anamensis–afarensis* waxed and waned in reality, and we do not dispute this point. What is relevant for the accurate estimation of origination and extinction dates, however, is the form of the wax–wane pattern.

Waxing and waning in *A. anamensis–afarensis* would cause the estimated origination and extinction dates of Du et al. (2020)—and the corresponding confidence intervals—to be too young and old, respectively (Marshall, 1997; Žliobaitė, 2020). However, if waxing and waning were a smooth, gradual process (e.g., Fig. 2B inset; the curve in Fig. 3C), one would expect to detect signatures of wax–wane in the older and younger *A. anamensis–afarensis* fossil horizons (e.g., Žliobaitė's [2020] Fig. 1d and g), but this is not clearly seen (Fig. 1; compare Žliobaitė's [2020] Fig. 1f and g). The only way a wax–wane dynamic would result in a uniform distribution of fossil horizons is if waxing and waning occurred extremely rapidly (Fig. 3A and B). For example, it could be that waxing and waning each finished within 10^4 years in *A. anamensis–afarensis*, such that these processes would be unobservable given the resolution of the current fossil record (i.e., they are geologically invisible). If true, the FRP of *A. anamensis–afarensis* would be effectively constant on geological time scales (Fig. 3B). And because there would be only a negligible amount of time between origination and the end of waxing and between the beginning of waning and extinction (Fig. 3A), Du et al.'s (2020) estimated origination and extinction dates—and their confidence intervals—would be minimally

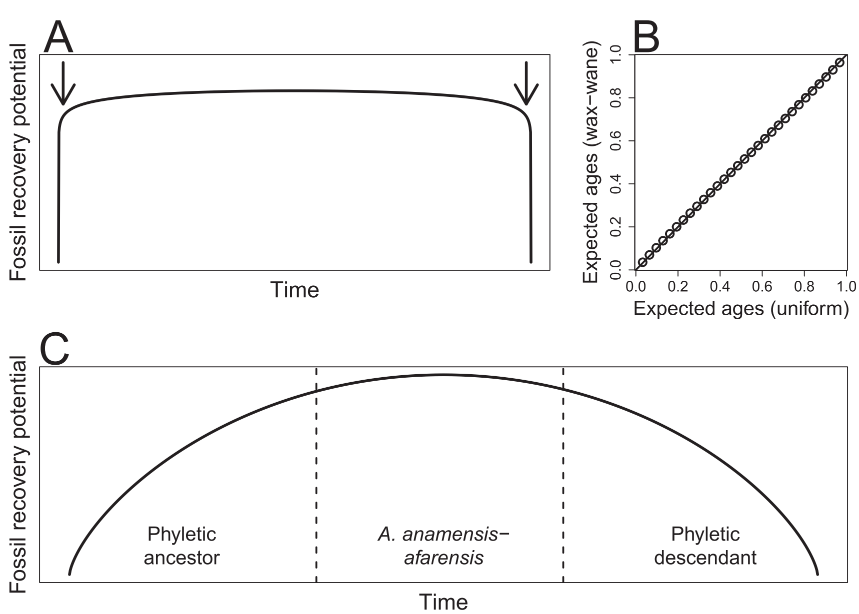

Figure 3. A) Hypothetical wax–wane pattern through time for the fossil recovery potential (FRP) of *Australopithecus anamensis–afarensis*, wherein waxing and waning happened extremely rapidly on geological time scales (e.g., within 10^4 years). As a result, there is a negligible amount of time between the origination date and the end of waxing (left arrow) and between the beginning of waning (right arrow) and the extinction date. The curve was generated from a beta distribution, whose shape is determined by two parameters, which here are 1.05 and 1.05. B) Expected fossil horizon ages sampled from the wax–wane FRP distribution in A), plotted as a function of expected ages from a uniform FRP. Expected wax–wane ages are averaged over 10,000 iterations, each one a sorted, random sample of 30 points (i.e., the number of observed *A. anamensis–afarensis* fossil horizons) from the distribution in A). Expected uniform ages are 30 points evenly distributed between 0 and 1, noninclusive (Du et al., 2020). Line represents the line of unity. C) Hypothetical wax–wane pattern through time for *A. anamensis–afarensis* along with its phyletic ancestor and descendant. The phyletic ancestor and descendant respectively show the waxing and waning portions, while *A. anamensis–afarensis* exhibits a weak wax–wane pattern. This pattern holds, even if phyletic transformations are gradual (i.e., the vertical dashed lines are replaced by wider, 'fuzzy' zones). The curve was generated from a beta distribution with shape parameters 1.7 and 1.7. See SOM for R code used to run these analyses and make these plots.

affected. To quantitatively demonstrate this, and focusing just on the extinction date for simplicity, we randomly sampled 30 fossil horizons (i.e., the number of observed *A. anamensis–afarensis* horizons) from the FRP distribution in Figure 3A and estimated the extinction date and its 95% confidence interval using Strauss and Sadler's (1989) Equations 8 and 20, respectively. After repeating this 10,000 times, the estimated extinction date is, on average, too old by 0.4% of the true range duration, and 93.8% of calculated confidence intervals cover the true extinction date, just shy of the nominal 95%. This exercise demonstrates that estimated origination/extinction dates and their confidence intervals (Strauss and Sadler, 1989) are negligibly biased with a rapid wax–wane FRP as in Figure 3A.

There is one situation, however, where *A. anamensis–afarensis* might not have waxed and waned in reality. Imagine that *A. anamensis–afarensis* occupies the middle portion of a larger lineage, which as a whole exhibited waxing and waning (Fig. 3C). If true, the phyletic ancestor and descendant should respectively display the waxing and waning segments of the complete wax–wane pattern. This might also explain why *A. anamensis–afarensis* exhibits a weak wax–wane pattern (Section 3; Fig. 3C), although the degree of waxing and waning in this lineage remains an open question. In this scenario, estimated origination and extinction dates would represent the timing of phyletic origination and extinction (i.e., pseudoextinction), and Du et al.'s (2020) estimated dates would be unbiased because FRP is relatively constant within the lineage's middle segment (Fig. 3C).

5. Conclusions

Estimating origination and extinction dates for hominin taxa is an important and necessary undertaking in human origins research. These dates are unknown quantities that can never be known from fossil discoveries alone because the fossil record will never be perfectly preserved and sampled. As a result, we must depend on models to estimate these dates, but model results are only as sound as their assumptions.

Du et al. (2020) estimated origination and extinction dates for the *A. anamensis–afarensis* lineage, using a model that assumes fossil recovery potential is uniform through time (Strauss and Sadler, 1989). When they assessed this assumption with the data, they concluded that the temporal distribution of *A. anamensis–afarensis* fossil horizons is consistent with a uniform distribution. In response, Žliobaitė (2020)—who suggested that the uniform distribution of *A. anamensis–afarensis* horizons would make it an outlier among the many fossil taxa that exhibit waxing and waning—conducted simulations and concluded that the *A. anamensis–afarensis* fossil horizons are consistent with either a uniform or a wax–wane distribution. In this response, we argue that abundance is only one of many factors that influences FRP, so the two do not have to be closely related. We quantitatively demonstrate that the uniform FRP model fits the *A. anamensis–afarensis* horizon data better than the wax–wane model, as specified by Žliobaitė (2020). We conclude with some thoughts, exploring why *A. anamensis–afarensis* does not exhibit a wax–wane pattern and how this does not bias its estimated origination and extinction dates.

We thank Žliobaitė for the opportunity to engage in this interesting discussion. This is certainly an exciting time to be thinking about the dynamics and patterns of hominin lineages and their implications for estimating origination and extinction dates.

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Supplementary Online Material

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