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Dawn of the dinosaurs demonstrates early diversification bursts and a potential role for neutral dynamics during major evolutionary radiations

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Major radiations have given rise to huge swathes of life on Earth, and understanding their dynamics reveals the process of biodiversity generation itself. The rise of dinosaurs and other archosaurs during the Triassic was a spectacular example of such a radiation; it set the stage for Mesozoic faunas and gave rise to the largest land animals on Earth. Previous attempts to understand its dynamics have relied on phylogeny, necessitating the exclusion of much data. We use the Bayesian occurrence-based approach PyRate, allowing speciation and extinction dynamics to be estimated without recourse to phylogeny. We analyse stratigraphic range-based data for all archosauromorphs from the late Permian to the Early Jurassic, and test for association of body size with diversification using a body size proxy. We find an 'early burst' pattern of diversification, with initial high speciation giving way to increased extinction. Falling speciation is consistent with niche-filling following extinction, but increasing extinction may indicate a role for neutral dynamics during radiation. Cryptic diversification may be evidenced by a peak earlier than inferred using phylogenetic estimates. Body size is not statistically associated with diversification, but the positive direction of association potentially reflects the concurrent passive 'trend' of increasing size.

1. Introduction

Evolutionary radiations following major extinction events or climatic changes [1–4] have generated much of modern biodiversity [5,6]. Understanding their dynamics sheds light on historical biodiversity generation and post-extinction recovery [7,8]. Extinctions, thought to free 'ecospace' allowing diversification [9], are indeed one of the main triggers of evolutionary radiation alongside the acquisition of morphological innovations (see below) and colonization of completely new habitats (e.g. the colonization of land [10]). In post-extinction radiations, diversification should decline as ecospace fills—an 'early burst' pattern

of diversification [11–14]—although positive feedback between ecospace and diversity may occur in the initial recovery phase as niches are 'rebuilt' [15]. Whether early burst patterns apply at the very largest scales remains controversial, with some authors arguing that long-term diversification is exponential [16,17], whereas others suggest limits [18,19]; at smaller phylogenetic scales, there is little doubt that early bursts of taxonomic and morphological diversification occur [20,21], probably owing to niche dependence [22,23]. The role of speciation versus extinction rates in mediating early bursts is debated. Some authors suggest that increasing extinction alone could precipitate early bursts [24–26], but others reported evidence contradicting this [23,27]; the unified neutral theory of biodiversity and biogeography predicts both decreased speciation and increased extinction through time owing to fewer individuals per species [25], but empirical evidence is equivocal [28–32]. Increased extinction owing to failure to keep pace with environmental change has been implicated in the decline of many clades, but not during initial radiation [28,30,33].

Ecomorphological traits can also affect diversification, with 'key innovations' allowing decoupling of diversity dependence [34]; the development of flight [35–38], herbivory [39–41], or upright locomotion [42,43] have all opened new niches and allowed diversification beyond previous limits, although a less readily identifiable 'innovation', increased body size—typical later in radiations—can allow diversification beyond previous limits [44]. Larger size may actually reduce speciation and evolutionary rate of individual lineages [45–47] and increase extinction susceptibility [48–50], mediated by lower reproductive rate and carrying capacity [51,52]. However, quantitative evidence is rather equivocal [51,53,54]; size-frequency distributions are often right-skewed, although this may be driven by larger taxa being younger rather than higher diversification of smaller taxa [53,55]. Despite much previous attention, new approaches and ever-expanding taxonomic and temporal knowledge allow us to begin to build a more rigorous picture of the process of biodiversity generation during geological-scale evolutionary radiations.

One of the most spectacular radiations in tetrapod evolution is that of the Archosauromorpha [44,56]. This began in the Triassic following severe loss of synapsid and parareptile taxa in the end-Permian extinctions [44,57,58], and ultimately gave rise to the non-avian dinosaurs [59] and today's >10 000 bird and crocodilian species [60,61]. During the Triassic, this radiation yielded a diverse fauna of dinosaurs [59], pterosaurs [62], pseudosuchians [59], and stem-archosaurs [56], spanning a wide range of ecological and dietary niches [63–67]. Understanding this radiation is of key interest as it forms an excellent testbed for wider hypotheses regarding post-extinction evolutionary radiations. Given major expansion in body size range during this radiation [44], with sauropod dinosaurs becoming the largest terrestrial vertebrates known [68], it can also help elucidate the effects of body size on diversification.

We analyse a comprehensive dataset of fossil archosauromorph species-level occurrence and body-size proxy data, spanning the end-Permian extinctions and subsequent radiation period (late Permian–Early Jurassic), to test major hypotheses regarding the dynamics of evolutionary radiations, and their relation to body size. We apply the PyRate [69] occurrence-based Bayesian framework, which does not require explicit phylogenies, circumventing uncertainties associated with fossil phylogenetic trees (e.g. [70–73]) and allowing more taxa to be included. We test whether there is evidence for an 'early burst' of diversification, as expected in niche-limited diversification, and whether and to what extent such a pattern is mediated by speciation or extinction rate. We also test for associations between body size and diversification, specifically testing whether larger taxa are indeed at higher extinction risk and have lower diversification rates.

2. Material and methods

(a) Data collection

We expanded the late Permian–Early Jurassic section of the archosauromorph dataset of Sookias *et al.* [44], merging it with the dataset compiled by Pradelli *et al.* [74], to create a comprehensive dataset, including all valid archosauromorph species currently known for that time range. The dataset consisted of 410 taxa, with estimated maximum femoral lengths for 331 (81%) of the taxa from the literature or directly from specimens. First appearance and last appearance dates (FADs and LADs) were based on true multiple occurrences or on stratigraphic uncertainty, with the majority based on the latter. Stage-level dates were from the 2023 International Commission on Stratigraphy [75].

(b) Data subsetting

We partitioned the dataset for the separate analysis of subsets of taxa of interest, in addition to studying Archosauromorpha as a whole. The taxon sets correspond to stem-Archosauria, Archosauria, Pseudosuchia, Avemetatarsalia, Dinosauria, Sauropodomorpha, Theropoda, and Ornithischia. Stem-Archosauria is non-monophyletic, but relevant to compare patterns with the crown group. Assignment to these groups was largely uncontroversial and was based on the most recent literature.

(c) PyRate analyses

PyRate is an occurrence-based Bayesian framework [69] to infer origination, extinction, and preservation rates, without phylogenetic information. PyRate uses process-based speciation and extinction models and can incorporate preservation process and age uncertainties [30,76,77]. It has been tested under varied conditions [30,77] and is less prone to edge effects than other approaches [76]. It also allows testing for trait covariance with speciation and extinction rates [69]. We conducted Bayesian analyses under trait-dependent birth–death models with PyRate v3.0 [69]. Trait dependency was modelled as the covariance between

Table 1. Changes in diversification, speciation, and extinction rates for all different taxonomic groups across their entire occurrence interval.

group	diversification	speciation	extinction
Archosauromorpha	−0.097	−0.059 (−43.454%)	0.010 (10.113%)
stem-Archosauria	−0.085	−0.051 (−30.263%)	0.006 (4.319%)
Archosauria	−0.09	−0.049 (−41.121%)	0.016 (19.665%)
Pseudosuchia	−0.071	−0.042 (−38.699%)	0.012 (15.134%)
Avemetatarsalia	−0.051	−0.021 (−24.213%)	0.010 (13.190%)
Dinosauria	−0.062	−0.028 (−30.262%)	0.010 (13.376%)
Sauropodomorpha	−0.038	−0.015 (−19.725%)	0.007 (9.884%)
Theropoda	−0.016	−0.005 (−5.138%)	0.004 (5.215%)
Ornithischia	−0.015	−0.006 (−5.707%)	0.003 (2.464%)

$\log_{10}$-transformed femoral length estimates (body size proxy) and speciation and extinction rates [69]. The prior on the covariance parameters was a normal distribution centred on 0 with a standard deviation of 1. Missing femoral length observations were imputed during parameter estimation based on a simple linear regression. We analysed the dataset and all subsets under a homogeneous Poisson process (HPP), where the rate of preservation is constant. For comparison, we analysed the entire dataset (but not subsets) with a more complex model that uses a time-variable Poisson process (TPP), where the base rate of preservation varied across pre-defined time bins corresponding to major geological time units: Capitanian–Changhsingian (late Permian), Lower Triassic, Middle Triassic, Upper Triassic, and Lower Jurassic.

To account for age uncertainty, we randomly resampled the ages of each taxon occurrence from their respective temporal intervals with uniform probability, generating 20 replicates for analyses with HPP. These were sufficient to stabilize the incremental change of variance of the posterior probability below a 5% threshold. Throughout this paper, we report the pooled results of analyses of those replicates, drawing 250 samples from each replicate. The posterior distributions of model parameters were estimated with reversible jump Markov chain Monte Carlo (RJMCMC) with a Gibbs sampler for speciation and extinction times. We used Tracer v1.7.2 [78] to track chain stationarity and effective sample sizes with a burn-in of 10%. In practice, 1 million generations were sufficient for HPP analyses and 2.75 million generations for the TPP analyses. Batch analyses were managed with GNU Parallel v.20230622 [79].

The preservation and diversification models of PyRate are intended for analysing occurrence data, differing from our data in that they include additional occurrences between the first and last appearance. To evaluate the impact of the absence of occurrence data beyond first and last appearances, we ran additional analyses of simulated datasets. Specifically, we re-analysed two sets of 100 simulated datasets from Silvestro *et al.* [76]. These were generated under time-variable birth–death models and a homogeneous preservation process with a rate randomly drawn from a uniform distribution $\mathcal{U}(0.5, 1.5)$. The simulations in the first set were generated under a piece-wise constant birth–death model with time of origin set to 35 Ma and origination rates starting at 0.4 and decreasing to 0.1 and 0.01 at 20 and 10 Ma, respectively. The extinction rates were set to 0.05, 0.3, and 0.01, with rate shifts at 15 and 10 Ma. The second set of simulations was generated under a piece-wise constant birth–death model with time of origin set to 40 Ma, with times of rate shifts set to 30, 18, 15, and 7 Ma for both origination and extinction rates. The origination rates were 0.3, 0.07, 0.6, 0.05, and 0.3, respectively. The extinction rates were set to 0.02, 0.6, 0.05, 0.2, and 0.5. We analysed the datasets after removing all occurrences except for the first and last appearances, running 10 million RJMCMC iterations and assuming a homogeneous Poisson sampling model. We compared the combined results across simulations with those obtained, including all occurrences (benchmarked in Silvestro *et al.* [76]).

In addition to the simulations, we also performed sensitivity analyses on the Archosauromorpha set in which we fixed speciation and extinction times. In this analysis, the speciation and extinction times were drawn from the resampled temporal ranges of the same 20 replicates of the main analysis. The results from the replicates were also pooled as in the main analysis.

3. Results

Using the HPP model, a downward trend in diversification rate characterizes the first 90 million years of evolutionary history of Archosauromorpha (figure 1). This trend is largely driven by declining speciation rates, but also by—to a lesser extent—increasing extinction rates through time (table 1). There is evidence for strongly supported downshifts (SSDs) in speciation rates in the Early, Middle, and Late Triassic and the Early Jurassic, and an upshift in extinction rates close to the end of the studied time interval. Speciation rate goes through a first period of decline spanning the Olenekian and the Anisian, with four SSDs (Bayes factors >2; shown as points on the rate curve), and after which the mean diversification rate is about 50% of its initial value in the

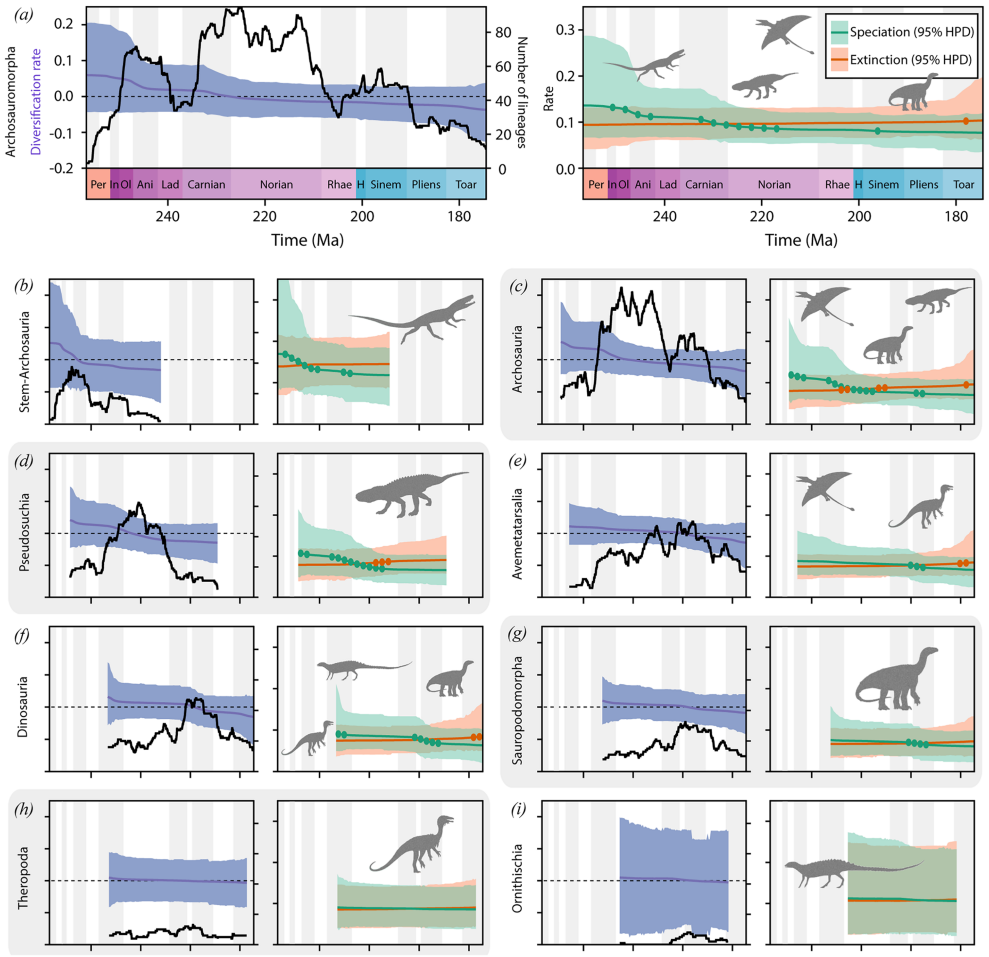

Figure 1. Mean estimates of diversification dynamics parameters (with 95% highest posterior density (HPD)) in (*a*) all Archosauromorpha, (*b*) stem archosaur taxa only, (*c*) crown taxa only, and the focal crown subgroups (*d*) Pseudosuchia, (*e*) Avemetatarsalia, (*f*) Dinosauria, (*g*) Sauropodomorpha, (*h*) Theropoda, and (*i*) Ornithischia. Speciation (green) and extinction (red) rates are per lineage per Myr, and the diversification rate (purple) is the difference between speciation and extinction rates. Filled circles on the lines indicate speciation and extinction rate shifts supported by Bayes factors above a threshold of 2.0. Curves of lineage diversity through time are plotted in black. Axis scales are identical in all the plots. Silhouettes adapted from Phylopic: *Euparkeria capensis* by Taenadoman (CC BY-SA 3.0), *Postosuchus* by Wani2Y (CC BY 4.0), *Eudimorphodon ranzii* by Steven Traver (public domain), *Liliensternus liliensterni* and *Melanorosaurus readi* by Tasman Dixon (CC BY 4.0), *Scutellosaurus lawleri* by Robert Gay (public domain).

Wuchiapingian (figure 1*a*). A second period of decline of speciation rate extends from the middle Carnian to the middle Norian, with seven SSDs; in the early Norian, diversification rate becomes negative. Another single SSD is found in the Sinemurian, but the mean diversification rate declines less strongly. The extinction rate, by contrast, remains much more constant, with a single strongly supported upshift in the Toarcian, also reflected as a kink in the diversification rate curve.

All taxon subsets display overall downward diversification and speciation rates and relatively constant, but increasing, extinction rates, mirroring major extinction events (figure 1*b–i*; table 1). Subclade trajectories highlight their additive contributions to the broader archosauromorph pattern; for instance, the Carnian dip in the archosauromorph diversification rate reflects a swift fall below zero in stem-archosaurs. Pseudosuchians and the surviving stem-archosaur lineages drove the Norian diversity peak, even though pseudosuchian diversification became negative by the early Norian owing to concurrent speciation declines and extinction upshifts.

Avemetatarsalia and Dinosauria follow similar trajectories. Unambiguous avemetarsalians appear in the Anisian and dinosaurs in the Carnian, but in the studied time bins, the diversification rate of avemetatarsalians is essentially constant, while dinosaurs start off with downward speciation rate shifts. Avemetatarsalians and dinosaurs possess a small extinction rate bump in the Toarcian, as seen in Achorsauromorpha, but no dinosaur subclade replicates this feature. The diversification dynamics of Dinosauria are clearly dominated by Sauropodomorpha, which displays the most marked downward speciation shifts from the Rhaetian to the Sinemurian. There is barely a negative slope in the diversification rate of Theropoda and Ornithischia, with no evidence of distinct shifts in speciation or extinction rates. However, the net diversification for all three major dinosaur clades becomes negative close to the Triassic–Jurassic (Tr–J) boundary (roughly synchronous given age uncertainties), probably associated with the end-Triassic mass extinction and the Toarcian faunal turnover.

With the TPP model applied to Archosauromorpha as a whole, the recovered preservation rate is the lowest (below 0.1) in the late Permian and the highest (around 0.23) in the Middle Triassic, while staying around 0.175 in the remaining time bins. Otherwise, the TPP model yields very similar results, qualitatively and quantitatively (supplementary material, figure S1 [80]).

Table 2. Estimated covariances between body size and speciation or extinction rate for all taxonomic groups examined.

group	speciation rate	extinction rate
Archosauromorpha	0.086 (−0.215 to 0.404)	−0.129 (−0.394 to 0.129)
stem-Archosauria	0.120 (−0.544 to 0.792)	0.094 (−0.537 to 0.738)
Archosauria	0.029 (−0.291 to 0.362)	−0.109 (−0.392 to 0.191)
Pseudosuchia	−0.115 (−0.706 to 0.468)	0.007 (−0.608 to 0.612)
Avemetatarsalia	0.024 (−0.322 to 0.391)	−0.098 (−0.433 to 0.245)
Dinosauria	0.043 (−0.480 to 0.569)	−0.103 (−0.586 to 0.377)
Sauropodomorpha	0.097 (−0.586 to 0.821)	−0.071 (−0.774 to 0.618)
Theropoda	−0.022 (−0.943 to 0.901)	−0.086 (−1.009 to 0.848)
Ornithischia	0.008 (−1.305 to 1.333)	0.020 (−1.288 to 1.334)

Values are given as means with 95% credibility intervals.

The most marked difference is a delayed and less pronounced fall of the diversification rate in the Anisian, which is an effect of a slower decline of the speciation rate and a bump in the extinction rate during this age. The upward extinction rate shift of the Toarcian in the HPP model is not supported by Bayes factors in the TPP model, but this shift is so modest that the diversification rate trajectories under both models remain almost identical. We take the strong similarities of the results of both analyses as an indication that our results are robust to preservation rate modelling and that the HPP model is sufficient to characterize the diversification dynamics of the taxon subsets.

We found no evidence of a strong relationship between body size and speciation or extinction rates in any of the studied groups (table 2; supplementary material, figure S2). Although most clades (e.g. Archosauromorpha, Dinosauria) show weakly positive covariance with speciation and weakly negative covariance with extinction, Pseudosuchia, stem-archosaurs, and Theropoda deviate slightly from these trends. However, the spread of the covariance estimated is large, and our results remain consistent with no real effect of body size on diversification dynamics across all groups.

In our simulations, the rates estimated after removing the internal fossil occurrences were generally consistent with those inferred using the full datasets. For the first set of simulations, the mean absolute percentage error (MAPE) between the full data and the first and last appearance data was 0.63 for speciation rates ($R^2 = 0.90$) and 1.18 for extinction rates ($R^2 = 0.21$). The R^2 for net diversification was 0.80. For the second set of simulations, the MAPEs were 0.59 for speciation and 0.66 for extinction ($R^2 =$ 0.75 and 0.36, respectively). For the net diversification, the R^2 was 0.67. Although the times of shifts appear to be less accurately estimated than with the full fossil sampling, the general trends in rate variation are reasonably well inferred, even in the absence of internal fossil occurrence data.

The sensitivity analyses on the Archosauromorpha dataset reveal the smoothing effects of fossil interval replication and the Bayesian estimation of speciation and extinction times. The speciation and extinction times were fixed in the same manner over the 20 replicates, and the diversification dynamics were estimated from the pooled results. The three curves from the sensitivity analysis reach rate magnitudes about 10 times that of their counterparts in the main analysis (supplementary material, figure S12). Up until the Norian, the speciation rate trajectory roughly resembles that of the main analysis, but with much steeper downward shifts. The extinction rate features a trajectory similar to the speciation rate curve, but not perfectly matched, resulting in a diversification rate trajectory characterized by irregular oscillations instead of the slow stepwise decline seen in the main analysis. Furthermore, this analysis retrieves an important rapid event of extinction followed by speciation occurring between the Rhaetian and the Sinemurian. This event was not detected in our main analysis of Archosauromorpha, although we did find downward speciation shifts around the same period for Sauropodomopha, which were also reflected in Dinosauria and Avemetatarsalia. Despite a final up-tick in the extinction rate starting by the Pliensbachian–Toarcian, the extinction rate follows a marked downward trend (about 50% decrease), instead of the slight overall increase found in the main analysis. The femoral length covariances from this sensitivity analysis are close to the values estimated in the main analysis: speciation rate covariance of 0.01 (95% CI: −0.3427 to 0.3858) and extinction rate covariance of −0.16 (95% CI: −0.512 to 0.196).

4. Discussion

Our results strongly support the occurrence of initial high rates of taxonomic diversification followed by declining speciation through time during the Triassic evolutionary radiation of Archosauromorpha, with significant declines in speciation in the Early

and Middle Triassic (figure 1). Similar 'early burst' diversification patterns have been documented in numerous other taxonomic groups [20,81–83], but not previously quantitatively evidenced in the radiation of archosaurs or dinosaurs. Cretaceous dinosaurs also evidenced declining speciation through time [28], but the time interval examined did not bracket the initial diversification of the clades, preventing interpretation of those results in the context of evolutionary radiations. Such patterns of decreasing speciation following radiation have long been hypothesized to be caused by radiation into 'vacant' niches followed by gradual saturation of niche space through time, and are often observed in the wake of extinction events or after entry into new niche space [11–13]. However, demonstrating such niche filling as being the only or even the main cause of such patterns is challenging. Other potential explanations do exist, such as the unified neutral theory of biodiversity and biogeography, which predicts that post-extinction ecospace desaturation elevates individual birth rate above death rate so that speciation is more likely, but that subsequently declining population sizes per species (precipitated by speciation itself) in turn reduce speciation rate [25]. Although the pattern is more pronounced in Archosauromorpha as a whole (figure 1*a*), declining diversification rates are also found in the mean trends of all individual subclades investigated (figure 1*b–i*); although no significant declines in speciation are identified in Theropoda and Ornithischia. The fact that the same pattern is also seen within subclades, potentially indicates that the development of new 'morphotypes' and their accompanying novel ecomorphologies (e.g. the sauropod dinosaur body plan and herbivory) opened new areas of ecospace, which were then in turn gradually filled; this would support a model analogous to that of decoupling following 'key innovations' [34], but occurring more broadly at the base of most major clades. However, these initial high speciation rates might not have been entirely adaptive, but rather partially driven by non-adaptive radiations [84]. In a non-adaptive scenario, rapid taxonomic diversification occurs primarily through geographic isolation (allopatric speciation) without immediate, large-scale ecomorphological divergence. Although the current-day continents formed the contiguous landmass of Pangaea, extreme thermal gradients [85] and severe ecological instability following the end-Permian extinction [86] acted as effective biogeographical barriers. This environmental structuring would have restricted gene flow and facilitated allopatric speciation, making initial bursts of non-adaptive radiation a compelling mechanism. This is consistent with previous work on the Triassic archosauromorph radiation that found a decoupling of morphological disparity and taxonomic diversity and showed bursts of morphological diversification at the base of major clades [15,37], and strongly aligns with the evidence for cryptic early diversification and delayed disparity peaks discussed further below. Our results are broadly consistent with patterns previously recovered from studies using phylogenetic data (e.g. [56]), which demonstrated high rates of lineage increase and morphological change across the Permian–Triassic boundary, with a gradual falloff in diversification through time across the Triassic. This shows the concordance of the PyRate analyses with alternative approaches and its utility in achieving similar inferences without recourse to explicit phylogenetic methods.

When interpreting the initial phases of the radiation, it is important to consider the nature of post-extinction survivors [86]. Although diversification models implicitly assume all survivors had an equal probability of speciating, many represented short-lived 'disaster taxa' or 'dead clades walking' (DCWs) [87]. Consequently, rather than a broad-based recovery, a minority of lineages were probably responsible for the 'early burst' in speciation [86]. By contrast, DCWs failed to capitalize on the emptied ecospace, terminating shortly after the crisis without a diversity rebound. This indicates that the massive Early Triassic speciation rates were driven by a restricted subset of the archosauromorph lineages that crossed the Permian–Triassic boundary.

In contrast with these speciation patterns, our results also reveal a consistent pattern of gradually increasing extinction rates through time. However, this is much less pronounced than the decrease in speciation, and significant shifts in extinction appear localized around known extinction events (figure 1). Such a pattern of gradually increasing extinction has not been widely demonstrated in other clades, possibly owing to methodological (e.g. BAMM versus PyRate [88]) or study scope (ordinal versus specific diversity [89]) differences, but this potentially may also represent biological differences, with, for example, some major insect groups eliciting diversification in positive feedback with angiosperms (e.g. [29,90]). One example of similar findings is the case of eutherian mammals over the course of the Cenozoic, where extinction rates are estimated to have increased gradually [31], despite heterogeneity between clades. Such patterns of increasing extinction tend to occur in the later stages of the 'lifespan' of clades, as evidenced in other mammalian clades [33] and potentially in Cretaceous non-avian dinosaurs (although the latter also show a sudden, probably environmentally driven elevation in extinction from the middle Campanian) [28]. These patterns are hypothesized to represent a failure to keep pace with a changing environment (i.e. the 'Red Queen' effect [33]). However, although turnover is certainly seen in some groups showing especially pronounced increases in extinction rates in our dataset (pseudosuchians during the Late Triassic; dinosaurs during the Early Jurassic; figure 1*d*,*f*), our observed increases in extinction rates do not appear to relate only to what have been considered to be already declining groups during the interval (e.g. stem-archosaurs, pseudosuchians following the Tr–J extinctions), and thus a Red Queen-based hypothesis may not be fully satisfactory in explaining the pattern seen. An alternative explanation for a pattern of increasing extinction even before clade decline may be provided by the unified neutral theory via the mechanism that—with a set number of individuals—average population size of each species will decrease as taxonomic diversity increases, leading to a greater probability of extinction per species via stochastic processes [25] (figure 2). Because of the universality of this process, predicted to occur in at least all ecologically comparable groups of taxa, it is concordant with our observation of increasing extinction rate over time in nearly all subclades examined. Although the full conditions of the neutral model may not apply in our data (the taxa vary in their ecology and extinction events, meaning there is not a permanent state of saturation), it is still plausible that aspects of neutral dynamics still apply, specifically the positive causal relationship between taxic diversity and extinction rate mediated by population size.

Other potential explanations for increased extinction rates through time exist, although they are arguably less plausible than neutral dynamics. Increasing niche saturation might render ecosystems less hospitable for 'newcomers' [91], requiring more complex ecological assumptions. Additionally, following an 'Out of the Tropics' model [92], lineages that predominantly originated in

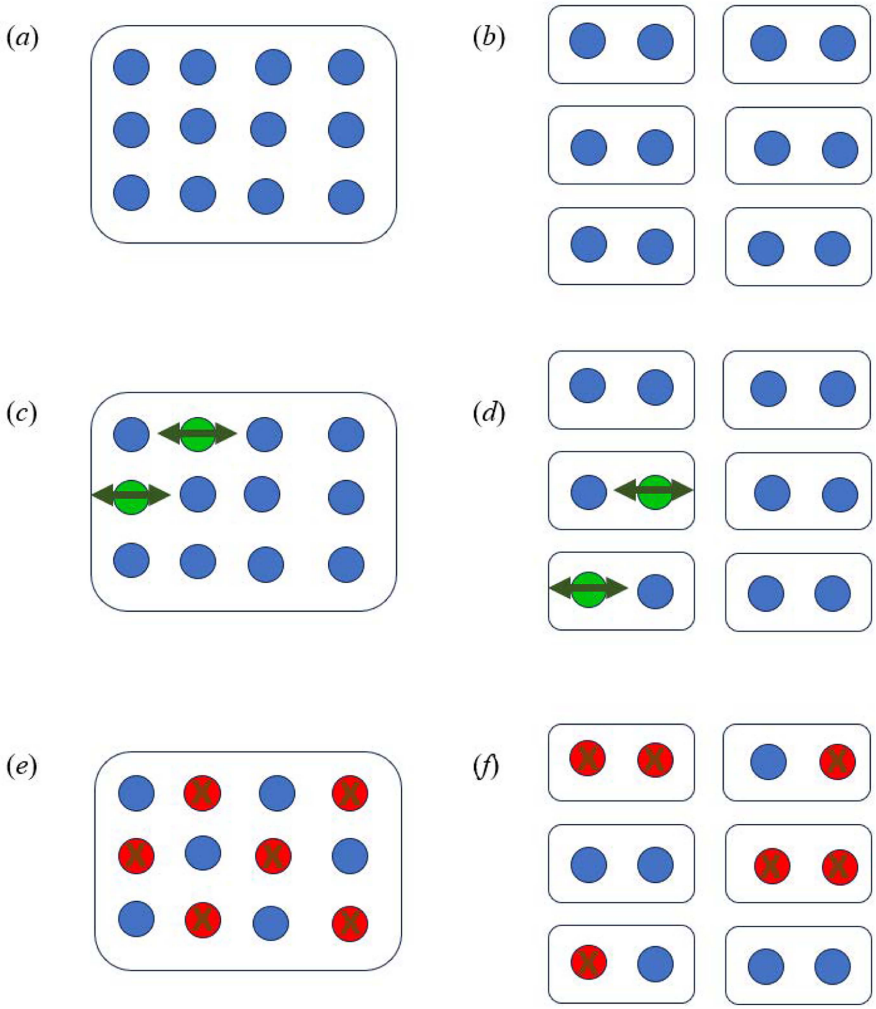

Figure 2. Schematic diagram demonstrating how the unified neutral theory of biodiversity and biogeography potentially precipitates increasing extinction and decreasing speciation through time. Blue circles are individuals, and boxes are species. Green circles with arrows are speciating individuals, and red circles with crosses are individuals that die. During initial radiation, population size per species is high and the number of species low (*a*,*c*,*e*). If a certain number of speciation events per individual occurs, a species is likely to speciate (*c*), and if a certain number of deaths occur per individual, a species is unlikely to go extinct (*e*). Later in a radiation (*b*,*d*,*f*), the number of species is higher and population sizes per species lower, meaning that with the same number of speciation (*d*) or death (*f*) events per individual, at least some species are likely to fail to speciate or to go extinct.

equatorial regions and subsequently expanded—or were passively displaced by plate tectonics—towards higher latitudes could experience a latitudinal gradient in age-dependent extinction [11], which would naturally contribute to an overall increase in extinction rates as the lineages aged and the radiation progressed. Another explanation could be that earlier taxa tend to be more resilient 'disaster taxa', with more extinction-prone, specialized taxa appearing only once ecosystems stabilized; this would fit the pattern of Archosauromorpha taken as a whole, but for the other subclades—in which increasing extinction rates are equally evidenced—this is less plausible because even early members of these lineages are relatively specialized and ecosystems were already relatively stable. Furthermore, although larger-bodied, younger taxa are often more extinction-prone [48–50], we found no correspondence between body size and extinction rate. Finally, artefactual biases—such as higher later diversity leading to rarity and lower sampling, or better-constrained later temporal ranges—are unlikely to drive this trend, as PyRate models preservation frequency and our time-binned analyses yielded congruent results. Thus, neutral dynamics remain the most plausible explanation.

Overall, the pattern we observe of decreasing diversification conflicts with hypotheses of continuous macroscale diversity increases [16], although this remains disputed [18,19]. Nevertheless, even models proposing exponential biodiversity growth [93] acknowledge that individual clades follow distinct evolutionary trajectories [20–23]. Thus, our clade-specific, temporally constrained results do not contradict these broader macroevolutionary frameworks.

Our results also lend weight to previous work, indicating a 'diversity-first' scenario during the archosauromorph radiation, with initial taxonomic diversification of major clades only subsequently followed by major expansion in morphospace [56,86]. Not only this, but our results appear to evidence a morphologically cryptic or near-cryptic initial diversification, similar to that probably documented in both larger radiations such as crown-mammals [94], angiosperms [32], or lissamphibians [95], and some smaller radiations (e.g. anoles [96]), based on comparison between molecular and morphological data, although potentially contrasting with some other groups [97]. Such cryptic early diversification would not be unexpected because interpreting the

group affiliation of early fossils can be challenging [32]. The early fossil record of a group may be poor owing to low abundance, and geographic separation may precipitate lineage divergence before major evolutionary radiations [98,99]. Our simulations suggest that FAD/LAD sampling and the absence of internal fossil occurrences can theoretically shift the inferred rate curves back in time. Consequently, this data limitation and methodological constraint might obscure the precise timing of critical speciation and extinction shifts, particularly concerning abrupt turnover events like those at the Tr–J boundary. Thus, although this constraint represents a potential factor influencing the timing of the observed peak, if representing a true pattern, these results agree with previous work, indicating the presence of a delayed disparity peak in the archosauromorph radiation [60,100], with full morphological diversification perhaps only occurring once environmental conditions became stable following the mass extinctions. Delayed disparity peaks have also been documented in several other major reptile clades [101–103], but are often seemingly less apparent in smaller radiations [104].

Although all subgroups show a broadly similar pattern of decreasing speciation and increasing extinction, each one displays a trajectory specific to its own evolutionary history. Pseudosuchians show an initially high diversification, but this declines and is almost stationary even by the Late Triassic, before their major decline in diversity and disparity at the Tr–J boundary [2,59] (figure 1*d*). Extinction rates significantly elevate towards the Tr–J boundary and remain very high during the Early Jurassic. These results reflect much previous work demonstrating their decline in the wake of the Tr–J extinction, but indicate that these processes may have begun earlier than previously thought, perhaps reflecting major environmental changes already by the Late Triassic and the concurrent rise of dinosaurs. However, avemetatarsalians also show a trajectory of declining speciation and increasing extinction through time, with a clear downturn in speciation at the Tr–J boundary (probably driven by the sauropodomorph pattern—see below; figure 1*e*,*g*), but with stabilization by the end of the interval. Sauropodomorphs have high initial diversification rates, but also appear to have been relatively strongly affected by the Tr–J events, with a significantly declining speciation (and elevated extinction, although not significant). Sauropodomorphs in particular were also strongly affected by environmental changes at the Pliensbachian–Toarcian boundary and during the Toarcian [105,106]. An atmospheric warming event precipitated by magmatism-induced methane emission and melting ice [107–109] had major impacts on multiple groups, including the terrestrial flora [106,108,109]. This is thought to have led to the loss of many non-eusauropod taxa and, ultimately, the radiation of Eusauropoda [105]. Theropods, on the other hand, show a relatively more stable diversification pattern through time with no significant changes (figure 1*h*); this may reflect their continued diversity and expansion over the younger time span of the study interval, but is also probably indicative of their relatively low diversity during the interval as a whole. Ornithischians indeed show an almost flat diversification trajectory and no significant shifts, which is undoubtedly a reflection of their low sample size (especially given silesaurids are not here considered successive sister taxa to 'core-ornithischians' following recent works [110,111], which disagrees with some other recent, although controversial, works [112,113]; figure 1*i*). Owing to this uneven sampling, the lack of clear shifts within Ornithischia should not be interpreted as a definitive evolutionary pattern for the clade, as it may simply be the result of limited data rather than a true lack of conspicuous diversification during the study interval. Dinosaurs, as a whole, possess a pattern that reflects each subgroup (figure 1*f*), and, in particular, a more tempered version of the sauropodomorph curve, but interestingly showing significant extinctions at the end of the interval, indicating that not only sauropodomorphs were affected by these events. Stem-archosaurs unsurprisingly show a high initial diversification, followed by major declines in speciation, with diversification approaching and then reaching zero (figure 1*b*). Interestingly, though, they show no significant shifts in extinction rate before their final disappearance, indicating that their demise was quite abrupt and corresponding to what we know about their relatively high taxonomic diversity remaining until their extinction [60,100].

No significant association is found between body size (femoral length) and extinction rate, in contrast with the existing evidence for higher extinction in larger taxa [48–50]. In fact, the direction of the relationship found was opposite to the expectation that body size increases extinction rate. The probable passive nature of body size increase (see [44]) may be part of the reason for the weakness of the association. The only exceptions to this trend were Pseudosuchia and Ornithischia (supplementary material, figures S2D and S2I); drawing any conclusion for the latter is difficult owing to the small sample size, but for the former, this pattern is consistent with previous findings of a marked reduction in body size across the Tr–J boundary [74,114].

It must be noted, however, that relying solely on femoral length as a body size proxy might oversimplify the morphological diversity of such disparate groups. Archosauromorphs encompass clades with highly diverse body plans and locomotor and postural adaptations (e.g. small-headed versus big-headed taxa, bipedal versus quadrupedal, erect versus sprawling postures [115]), meaning femoral length may not uniformly capture body mass or volume across all taxa. This morphological limitation, combined with the fact that a portion of the body size data was supplemented with imputation and that our lack of significant association is accompanied by high uncertainty of the covariance estimates, renders these negative results slightly ambiguous. Future analyses incorporating alternative or multiple body size proxies could potentially yield different signals and provide a more nuanced picture of trait-dependent diversification in clades with diverse body plans and postural adaptations.

Ultimately, notwithstanding these methodological considerations, our results, spanning over 80 million years and two major mass extinctions, provide an expanded understanding of the archosauromorph radiation and evolutionary radiations broadly. We demonstrate that widespread 'early burst' diversification and cryptic diversification probably occurred in the archosauromorph radiation, similar to other major radiations. Across Archosauromorpha and its major subclades, we observe increasing extinction rates through time, possibly mediated by neutral biodiversity dynamics. Furthermore, our results clarify the impact of body size on diversification, supporting passive processes in body size evolution. Finally, these findings provide a robust methodological test of the applicability of occurrence-based Bayesian approaches to stratigraphic range-based datasets, which may promise to help our understanding of other major radiation events in Earth's history.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.
Data accessibility. Data are available in the supplementary material and also archived on Dryad [80].

Supplementary material is available online [116].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.
Authors' contributions. R.B.S.: conceptualization, data curation, investigation, methodology, writing—original draft, writing—review and editing; L.A.P.: conceptualization, data curation, investigation, writing—review and editing; E.A.: formal analysis, investigation, methodology, writing—review and editing; D.S.: formal analysis, investigation, methodology, validation, writing—review and editing; M.D.E.: data curation, investigation, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.
Conflict of interest declaration. We declare we have no competing interests.
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