Evolutionary rates of mid-Permian tetrapods from South Africa and the role of temporal resolution in turnover reconstruction

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RRH: MID-PERMIAN TETRAPOD EVOLUTIONARY RATES

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Abstract.—The Main Karoo Basin of South Africa contains a near-continuous sequence of continental deposition spanning 45 million years from the middle Permian to the Early Jurassic. The terrestrial vertebrates of this sequence provide a high-resolution stratigraphic record of regional origination and extinction, especially for the middle–late Permian. Until now, data have only been surveyed at coarse stratigraphic resolution using methods that are biased by non-uniform sampling rates, limiting our understanding of the dynamics of diversification through this important time period. Here, we apply robust methods (gap-filler and modified gap-filler rates) for the inference of patterns of species richness, origination rates and extinction rates to a subset of 1321 securely-identified fossil occurrences resolved to approximately 50 metre stratigraphic intervals. This dataset provides an approximate time resolution of 0.3-0.6 million years and shows that extinction rates increased considerably in the upper 100 metres of the mid-Permian Abrahamskraal Formation, corresponding to the latest part of the *Tapinocephalus* Assemblage Zone (AZ). Our results show that origination rates were weakly elevated in the same interval, and were not sufficient to compensate for these extinctions. Subsampled species richness estimates for the lower part of the overlying Teekloof Formation (corresponding to the *Pristerognathus* and *Tropidostoma* AZs) are low, which show that species richness remained low for at least 1.5–3 million years after the main extinction pulse. A high unevenness of the taxon abundance-frequency distribution, which is classically associated with trophically unstable post-extinction faunas, in fact developed shortly before the acme of elevated extinction rates due to the appearance and proliferation of the dicynodont *Diictodon*. Our findings provide strong support for a Capitanian ("end-Guadalupian") extinction event among terrestrial vertebrates and suggest that further high-resolution quantitative studies may help resolve the lack of consensus among palaeobiologists regarding this event.

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Introduction

The fossil record provides unique information about the history of biodiversity on Earth, yielding insights into mass extinction events and other episodes of turnover that would not be recognised solely from the study of extant species. However, inferring patterns of diversity and the dynamics of speciation and extinction from the fossil record is beset with difficulties, not least those resulting from the heterogeneous sampling of fossil specimens through time and space. This heterogeneity is caused by a diverse array of sampling biases, including the spatial and temporal architecture of the rock record itself (geological biases) and the way the rock record has been sampled by palaeontologists (anthropogenic biases) (Raup 1972; Smith 2001; Smith and McGowan 2011). Various quantitative methods have been developed to compensate for these biases that may be effective when sufficiently rich databases of fossil occurrences are available (e.g., Alroy 1996, 2009, 2014; Foote and Sepkoski 1999; Foote 2000; Silvestro et al. 2014).

The temporal resolution (i.e., the fineness of stratigraphic divisions used in discrete-time analyses) of palaeobiological studies of diversification is limited by the typical resolution at which fossil occurrences are reported in databases. For example, in the Paleobiology Database (http://paleodb.org), which is widely used in global-scale palaeobiological studies (e.g., Alroy et al. 2001; Hannisdal and Peters 2011; Mayhew et al. 2012; Wagner et al. 2006), fossil occurrences are typically assigned to the scale of Phanerozoic stages (mean 6.2 Myr) or substages (mean 3.5 Myr). Sepkoski's older, but nonetheless highly influential, databases of Phanerozoic marine macrofossils resolve over half their genera to substage-level temporal units (mean 3.51 Myr; Sepkoski 1982, 2002). However, the coarse time resolution of these global fossil databases can result in aliasing, particularly the exaggeration of standing diversity estimates due to the conflation of the ranges of non-overlapping taxa into one bin; this limits our ability to make inferences about short-lived events in the evolution of biodiversity. Such events include mass extinctions and their subsequent recovery episodes, which could potentially take place on shorter timescales (e.g., Twitchett et al. 2004; Smith and Botha-Brink 2014; Wilson 2014) or within time bins. This error is most clearly evident in studies of the Cretaceous/Palaeogene mass extinction event: although it certainly resulted in catastrophic reductions in species diversity in its immediate aftermath, subsampled richness estimates for both marine and terrestrial fossils at the level of a geological stage (4.4 Myr = earliest Palaeogene Danian stage) actually increase across this boundary (Alroy et al. 2008; Benson et al. 2016; Close et al. 2017). This illustrates how the use of data resolved only to coarse time bins allows a recovery of species richness to greater than pre-extinction levels within a few million years to entirely over-write the signal of low post-extinction richness.

High-resolution databases of fossil occurrence can provide greater temporal resolution, substantially helping to resolve the timing and magnitude of key turnover events in the history of life on Earth. The latest Cretaceous and Cenozoic fossil records of North American land mammals provide a model example of the power of this type of study (e.g., Alroy 2009; Quental and Marshall 2013), and have provided considerable insight into patterns of evolution both during, and after, the Cretaceous/Palaeogene mass extinction event (Wilson 2014; Longrich et al. 2016). However, few other examples exist, especially for the continental fossil record (which is relatively poorly sampled compared to the marine fossil record) and for pre-Cenozoic events (the relatively recent Cenozoic record is richer and stratigraphically more finely-resolved).

The Capitanian ("end-Guadalupian") mass extinction provides a second example of how coarse stratigraphic resolution can obscure the dynamics of turnover inferred from fossil data.

Initially considered part of the end-Permian mass extinction due to lack of evidence for "background" extinction rates between the Guadalupian and Lopingian [Dzhulfian] (Raup and Sepkoski 1982), a re-evaluation at higher temporal resolution recognised the "end-Guadalupian" extinction event as a separate crisis that is potentially one of the most severe in metazoan history (Stanley and Yang 1994). Subsequent quantitative analyses of turnover rates in the Phanerozoic record of marine invertebrates have mostly considered the Guadalupian (duration = ~13 Myr) as a single interval and initially supported an extinction peak in this interval (e.g., Bambach et al. 2004; Sepkoski 1996**)**. However, many more recent studies have tended to downplay Capitanian extinction intensity, especially compared to other mass extinction events (Alroy 2008 [mean interval duration = 11.3 Myr], 2010 [=10.8 My], 2014 [=10 Myr]; Clapham et al. 2009 [standardised for interval duration but 10.2 Myr for Guadalupian]; Foote 2003 [7.4 My for stages or 3.5 Myr if resolved to substage]; McGhee et al. 2013 [13.5 Myr]; Payne and Clapham 2012 [13.5 Myr]). The study of Stanley (2016) is an exception to this; by accounting for singletons and the backward smearing of extinctions due to the Signor-Lipps effect, he determined the Capitanian mass extinction (his Guadalupian crisis) to be only slightly less severe than the Cretaceous/Palaeogene mass extinction event. Stanley (2016) also suggested that the comparatively greater extinction intensity at the end-Permian event (approximately 8 Myr later) may have been exacerbated by the only partial recovery from Capitanian extinction event by this time.

This lack of consistency among appraisals of the severity of extinction in the Capitanian may be partly the result of its occurrence within a geochronological stage rather than at a stage boundary, as is suggested by several studies of fossiliferous sections in southeastern China and in Spitsbergen, at least for foraminiferans (Bond et al. 2010, 2014; Bond and Grasby 2017). This could limit the ability for some analyses at the stage level to recognise a mass extinction, as originations as part of a rapid recovery could obscure a dramatic loss of diversity. More broadly, it is a symptom of the high degree of variability in current statistical treatments of global fossil datasets; so far they have failed to reach consensus on all but the most severe ("Big Five") global diversity crises.

Despite continuing disagreement over the broader taxonomic severity of the Capitanian extinction event, field-based studies of marine sections, predominantly in China, suggest that it is closely associated with volcanism in the Emeishan Large Igneous Province (ELIP) and its timing can be constrained to the mid-to-late Capitanian within a window of perhaps 3 Myr **(**Bond and Grasby 2017; Bond and Wignall 2014; Bond et al. 2015; Huang et al. 2016**)**. Furthermore, regional and clade-specific studies suggest that the Capitanian was associated with elevated extinction rates and/or diversity loss in several higher taxa, including ammonoids, brachiopods, conodonts, benthic foraminifera, and brachiopods, as well as reef-building organisms such as sponges, rugose corals, and calcareous algae (Bond et al. 2010, 2015; Kiessling and Simpson 2011; Jin et al. 2006; Leonova 2009; Shen and Shi 1996, 2002, 2009; Weidlich 2002; Wang and Sugiyama 2000).

Terrestrial turnover estimates for the Permian and early Triassic have been more limited, relying mostly on ratios of within-bin extinctions and originations to assemblage or stage level tallies of taxa derived primarily from the fossil records of the Fore-Ural Basin of European Russia and the Main Karoo Basin of South Africa (Benton 1985; Maxwell 1992; Benton et al. 2004, 2013; Lucas 2009). Successive tetrapod assemblages of the mid–late Permian in these regions are well-studied, and form the basis of assemblage zones (South Africa), or simply faunal assemblages (Russia), with durations of 1–5 Myr (e.g., Rubidge 1995; Golubev 2000;

Arefiev et al. 2015; Day et al. 2015). Most previous analyses of diversity and turnover in Permo-Triassic tetrapods have used these relatively coarse stratigraphic units (but see exceptions below). They have therefore been unable to recognise patterns of extinction, diversity and origination associated with short-lived events such as the Capitanian extinction.

The exceptional continuity and density of tetrapod fossil occurrences in the Karoo Basin has occasionally been used to derive high-resolution turnover estimates from more detailed stratigraphic ranges of taxa, especially around the Permo-Triassic boundary (Modesto et al. 2003; Smith and Botha 2005; Botha and Smith 2006). Some attention has also been paid to the mid–late Permian transition (between the *Tapinocephalus* and *Pristerognathus* Assemblage Zones) (Retallack et al. 2006; Day et al. 2015), which was associated with a mass extinction among tetrapods that notably exterminated the abundant and widespread Guadalupian therapsid clade Dinocephalia (Lucas 1998, 2009). However, these preliminary appraisals have left key questions unanswered, such as the interplay of extinction and origination (evolution dynamics) surrounding the Capitanian extinction event, the duration of a possible period of low standing richness following it (see Irmis and Whiteside 2011), and especially the extent to which the apparent severity and timing of the Capitanian extinction event might be influenced by non-uniform sampling of fossils through the sequence.

This knowledge gap results from the fact that, although high-resolution analyses have considerable power to resolve the dynamics of origination and extinction on short timescales, they are still subject to the same biases as large-scale studies. In other words, bias results from uneven sampling of stratigraphic packages, even at high resolution. High-resolution studies of turnover and standing diversity in the Karoo Basin so far have not used methods that correct species richness estimates, or rates of origination and extinction, for variation in sampling rate or sample coverage. But studies at coarser time resolutions using Karoo fossil datasets or "global" datasets (of which Karoo fossils form a substantial part) have shown that sampling can strongly influence interpretations of the fossil record, necessitating quantitative approaches that specifically account for this bias (e.g., Irmis and Whiteside 2011; Fröbisch 2013, 2014).

To explore these questions, we use moving-window "gap-filler" estimates of extinction and origination rates and coverage-based subsampling methods (Alroy 2008, 2010, 2014) to elucidate evolutionary dynamics among terrestrial vertebrates through the middle–late Permian transition in the Karoo Basin. Our analyses were based on a stratigraphically high-resolution database of tetrapod occurrences modified from Day et al. (2015). This study represents the first application of robust, sample standardisation methods to high-resolution occurrence data for pre-Cenozoic tetrapods.

Materials and Methods

Tetrapod Fossil Dataset.—The starting point for the study was a dataset of 3067 fossil stratigraphic occurrences (=specimens) within the Abrahamskraal and lower Teekloof formations of the Beaufort Group (see Fig 1). This builds upon that used by Day et al. (2015) but has been expanded by over 50% and benefits from improved stratigraphic accuracy resulting from additional fieldwork (see Supplementary Table 1 for subset of data used here). Fossil taxa are entered as genera when those genera are monospecific in South Africa, and otherwise as species. The database therefore documents species-level occurrences at best. Although specifically and generically indeterminate fossil occurrences are included in the database, they were not included in most of our analyses (described below). One exception to this concerns our use of even specifically-indeterminate specimens of varanopid synapsids as a single unit of analysis. We justify this because varanopids are likely represented in South Africa by only one species: *Heleosaurus scholtzi* (Reisz and Modesto 2007). Each fossil occurrence within the Abrahamskraal Formation is assigned to one 50 m stratigraphic bin (or more when there is uncertainty about the position of the locality), over a stratigraphic distance exceeding 2000 m. Specimens from the overlying Poortjie Member of the Teekloof Formation are assigned to either the lower, middle, or upper part of that member (each of which may vary between 40–60 m across the outcrop area of the member).

The dataset incorporates most of the specimens that have been collected from the middle–late Permian boundary interval in South Africa, but is continuously expanding and so is not exhaustive. Most specimens belong to South African collections; however, important specimens, particularly holotypes, from foreign repositories are also included where possible. The original specimen occurrence list (Nicolas 2007), of which many have poorly-constrained stratigraphic origins, contained only assignments to biozone and more accurate stratigraphic provenance was only determined later as part of a second PhD thesis (Day 2013). The original occurrence list also has been substantially bolstered by recent collecting work conducted by the ESI (Evolutionary Studies Institute, Johannesburg) that, over the past decade of field expeditions, has collected over 625 further specimens (~20% of the total) with highly accurate stratigraphic provenance from the interval of interest. Specimen identifications were brought up-to-date as far as possible by incorporating re-identifications provided to collections managers by visiting researchers, from the literature, or by re-examination by one of the authors (M.O.D. or C.F.K.).

Not all of the 3067 fossil specimen occurrences were suitable for analysis. Firstly, we removed specimens for which reliable identifications were not available, which included specimens that could not be identified to the level of genus (e.g., “Therocephalia indet.”, "Scylacosauridae indet."), and those that had not been recently re-appraised by us or in the published literature. In order to observe differences when only the best quality data was considered, we also excluded all tentatively identified specimens, with the exception of "?*Glanosuchus*" and "?*Endothiodon*". These latter identifications were deemed to be likely correct, the former due to the historical tendency to assign early therocephalian fossils to the genus *Pristerognathus* (meaning that identifications as *Glanosuchus* are more than merely the "default", and generally recognize the uniquely robust cranial morphology of this taxon relative to coeval scylacosaurids), and the latter due to the ready recognisability of *Endothiodon* based on limited remains (the dental morphology of this taxon is unique among therapsids, permitting even jaw fragments to be confidently identified). The remaining 1031 specimens form our base dataset (Supplementary Table 1) and were used to produce a revised stratigraphic range chart for tetrapods during the middle–late Permian transition in the Karroo Basin (Fig. 1). Of these specimens, almost half (492) belong to a single taxon, the dicynodont *Diictodon*.

Review of the precision of stratigraphic assignments of these occurrences indicates that slightly more than half (N = 558) are assigned precisely to a single 50 m stratigraphic interval (Fig. 2). Others are assigned less precisely, and we excluded specimens that could not be constrained to 3 bins (i.e., 150 m) or fewer. Those occurrences with uncertain provenance that remained (i.e., those that could be constrained to two or three bins) were randomly assigned to one of the 50 m bins within its range of possible positions, considering only bins that fell within the known range of that taxon. We performed this 1000 times and analyses were conducted on each of these resampled datasets at thresholds of 50 m (only specimens assigned with certainty to a single interval; N = 558), 100 m (two intervals; N = 749) and 150 m (three intervals, N = 807 occurrences).

Day et al. (2015) originally divided the Main Karoo Basin into geographic “sectors”, each of which was associated with a local stratigraphic section, in order to compensate for differences in local thickness of the Abrahamskraal Formation (which varies from 100 m in the south to > 2500 m in the north; Day and Rubidge 2014). The Abrahamskraal Formation was divided into 50 m bins within each sector and was then treated separately. This was appropriate for the application of constrained optimisation (CONOP), as this considers the sequence of first- and last-appearance events of taxa from observed occurrences in multiple sections. This sequence is then used to create a composite sequence of events that is independent of any one stratigraphic section (Sadler et al. 2008). Estimates of origination and extinction rates (using boundary crossers and gap-filler methods) instead use occurrences of taxa within time bins, which in the case of the Karoo must be approximated by stratigraphic bins. For this, a single composite stratigraphic section was required. To achieve this, rates of deposition were postulated to be relatively uniform throughout the southwestern Main Karoo Basin and a composite section was created by aligning the column of stratigraphic bins from each sector down from the base of the Teekloof Formation (a broadly time-equivalent horizon throughout the basin based on radiometric tuff ages and biostratigraphy; see Day et al. [2015]).

This assumption could be challenged, because the Main Karoo Basin is a flexural foreland basin in which areas at different distances from the orogen experienced different rates of deposition (see Catuneanu et al. 1998), and the Abrahamskraal Formation is known to become considerably thinner distally (Day and Rubidge 2014; Cole and Wipplinger 2001). However, the base of the Abrahamskraal Formation has been shown to be diachronous in the southwest of the basin, so much of the difference in thickness is likely due to the later onset of non-marine deposition in distal areas (e.g., Rubidge et al. 1999). Furthermore, the vast majority of specimens from the northern Fraserburg and Victoria West districts are from the *Pristerognathus* and *Tropidostoma* AZs, which crop out in the southern portion of those districts in a relatively narrow band. Thus, the effect of variable depositional rates is likely to be limited for these zones. Error from differential rates of deposition may result when incorporating occurrences from the northwestern-most *Tapinocephalus* AZ, away from the exposure of the Teekloof Formation, but these are relatively few (<10 specimens). The presence of the dicynodont *Diictodon* (SAM-PK-K5838) close to the base of the Abrahamskraal Formation 45 km northeast of core QU1/65 (Abrahamskraal Fm = 500 m; Day and Rubidge 2014) suggests that these strata all fall within the upper 450 m of the Abrahamskraal Formation as exposed further south (the range of *Diictodon* there) and thus, even with continued thinning, the difference in time represented by each 50 m bin does not exceed one or two bins for the informative part of the stratigraphic sequence. Any specimens from the Philippolis and Fauresmith districts of the Free State Province were excluded, as these areas are situated in the mid-basin region, much further north and more distal than other mid-Permian occurrences. Not only has it not been possible to trace lithostratigraphic units this far, but the faunal assemblage displays a unique character and therefore cannot at present be reliably correlated with the southwestern sequences (MD personal observation).

Our dataset is restricted to the Abrahamskraal Formation and lower Teekloof Formation (Poortjie Member). However, data from at least two stratigraphic bins above the final interval of interest are required to estimate origination and extinction rates using the gap-filler method. This requirement could be very limiting on the duration of the informative upper part of the data series (Alroy 2014; this is also true for "three-timer" rate estimates). Therefore, to extend the upper range of the data series, we added data from three additional stratigraphic bins above the Poortjie Member: the lower, middle and upper parts of the overlying Hoedemaker Member of the

Teekloof Formation. Because the Hoedemaker Member is similar in thickness to the Poortjie Member, these bins also reflect ~40–60 m of stratigraphic thickness. These data were based on the counts of occurrences provided by Smith et al. (2012) for the *Tropidostoma* AZ, which corresponds in the most part with the Hoedemaker Member. In total, this resulted in the addition of 2649 specimens to the effective dataset.

The distribution of taxa within the three bins was determined by retrieving more specific stratigraphic information from publications (for recently revised taxa) and by inference from geological maps and field observation. For common taxa where no observation exists in the literature (e.g., *Tropidostoma*), we assumed an even distribution of occurrences across the three bins (see Supplementary Table 1). Although this treatment is less thorough than our treatment of the underlying stratigraphic units, this mainly affects only common taxa. Most occurrences of rarer taxa are from localities that are described in the literature, and for which good stratigraphic provenance data is available. We consider that the assignments sufficiently represent the occurrence of taxa within the Hoedemaker Member to determine the patterns of taxon survival (from preceding bins) that are used to infer extinction rates, and patterns of taxon appearance in the Hoedemaker Member that are used to infer origination. Indeed, the uncertain taxonomy and the possibility of unrecognised taxa in the large collection of unevaluated specimens from the Hoedemaker Member is likely a much greater bias on our findings regarding the *Tropidostoma* AZ. The subset of occurrences used in the final analysis, through the entire studies interval, is provided in .txt format as Supplementary Data 1.

Calculating Macroevolutionary Rates.—We used the gap-filler (GF) method of Alroy (2014) and modified gap-filler method of Alroy (2015), to estimate origination and extinction proportions through the informative portions of our stratigraphic series (upper Abrahamskraal

Formation, Poortjie Member and lower Hoedemaker Member of the Teekloof Formation). Both sets of results are essentially congruent with each other.

The gap-filler method calculates turnover rates using a form of cohort analysis and then adjusts these using sampling probabilities derived from taxon occurrences within a moving-window of four intervals. This approach uses several different sets of taxa with different distributions across a moving window comprising, for estimates of extinction rate, a focal interval i, the preceding interval (i-1) and the following two intervals (i+1 and i+2). The equations for gap-filler origination rates are just the extinction rate equations in reversed-time and make use of intervals i, i+1, i-1 and i-2.

Counts of forward two-timers (t_2; used for extinction rate estimates) represent those taxa that occur in the focal interval (i) and the preceding interval (i-1), and provide an estimate of the number of taxa that crossed the lower boundary of the focal interval. Three-timers (t_3), occur in the focal interval (i), and the preceding (i-1) and following (i+1) intervals, representing those taxa that crossed both the lower and upper interval boundary. Broadly speaking, extinction rates are estimated using information on the proportion of two-timers that are not also three-timers (i.e., the number of lower boundary-crossers that did not survive to cross the upper boundary). However, extinction is not the only process that can cause t_2 taxa to be absent from interval i+1 (and therefore not also be t_3 taxa). Incomplete sampling in i+1 can also cause this to occur; the gap filler method (and the "three-timer" method of Alroy [2008]) therefore uses estimates of the taxon sampling rate in interval i+1 to adjust the apparent extinction rate for sampling failure. Sampling rate (s) is calculated using counts of part-timers (p), which are taxa that were not sampled in an interval (in this case, in i+1), but that were sampled in the preceding (i) and following (i+2) intervals. Part-timers therefore represent the set of taxa that must have been present in an interval but were not sampled, and the sampling rate is the ratio of part-timers to part-timers plus three-timers. Counts of gap-fillers (g) are unique to the "gap-filler" method. Forward gap-fillers (used to estimate extinction rates) are those taxa that occur in intervals i-1 and i+2 and help to distinguish genuine extinction from sampling failure in i+1 using information about the presence of taxa in i+2.

The gap-filler extinction rate equation is:

$$\mu = \ln[t_2 + p/t_3 + p + g]$$

This yields an instantaneous, per-interval extinction rate. The derivation of the gap-filler equation was given by Alroy (2014), who also demonstrated under a variety of simulated cases that the gap-filler method performs substantially better than face-value "boundary crosser" (Foote 1999, 2000; Alroy 1996) proportions of taxa making their last- (or first-, in the case of origination) appearances in a given time interval, and also better than the three-timer rate equations of Alroy (2008).

The modified gap-filler method (Alroy 2015) yields a per-taxon, per-interval extinction proportion, denoted as E. It is based on a reformulation of the gap-filler equation that substitutes a calculation using various indices (including g, the count of gap-fillers) with one that makes use of first-interval taxa (s_1), the count of taxa sampled in i-1 and i but not i+1 or i+1, and third-interval taxa (s_3), the count of taxa sampled in i-1 and i+2 but not i or i+1. These provide an estimate of the turnover rate because s_3 converges on zero as turnover rates increase.

The modified gap-filler equation is:

$$E = (s_1 - s_3)/(t_2 + p)$$

Furthermore, the true values of s_1, s_2, and s_3 should be arranged in decreasing magnitude, and the modified gap-filler method replaces s_3 with the second-lowest of s_1, s_2, and s_3 when this condition is not met. This represents an improvement on the gap-filler method because, among other reasons, it rarely gives rise to highly negative (and nonsensical) extinction proportions, though it is slightly upward-biased (Alroy 2015). Alroy (2015) did not present an equation for modified gap-filler origination proportions. We compute these by applying the extinction proportion equation in reversed-time.

Simulations suggest that the gap-filler methods perform best for small datasets when they are uniformly sampled (Alroy 2014). Although it is large compared to some other stratigraphically well-resolved databases of fossil tetrapod occurrences, our dataset is in fact small compared to many of the richest fossil record datasets. We achieved uniform sampling by randomly drawing a fixed number of occurrences from each interval in our stratigraphic series prior to estimation of extinction and origination rates (i.e., by application of classical rarefaction recommended by Alroy [2014] to satisfy the assumption of uniform sampling). This was done over 1,000 iterations in each case and the interquartile ranges and median values of our results are reported in our summary figures. Due to the different number of occurrences available at different thresholds of stratigraphic precision (50 m, 100 m, 150 m), our subsampling quota differed among analyses ($N_{1bin} = 8$, $N_{2bin} = 14$ and $N_{3bin} = 16$).

Like other cohort analyses and range-based methods, the gap-filler method omits information from taxa that occur only in a single-bin (one-timers: t_1) because of their susceptibility to fluctuations in sampling. Although this practice has been questioned at the stage level (Stanley 2016), it is appropriate at the high stratigraphic resolution considered here, where single occurrences of rare taxa are likely heavily influenced by sampling. Nevertheless, we recognise that the omission of rare taxa that occur as singletons may lead us to underestimate absolute extinction/origination rates; this is in any case a phenomenon inherent in any analysis of empirical data due to the preservation bias against rare taxa (e.g., Raup 1988; Sepkoski 1994; McKinney 1997a), combined with their greater susceptibility to extinction (Stanley 1986; McKinney 1997b; Johnson 1998; Jablonski 2008; Harnik et al. 2012) and the likelihood that new species are likely to be rare (Glazier 1987; Vrba and DaGusta 2004).

Estimating Standing Diversity.—Estimates of standing diversity can also be highly sensitive to variation in sample completeness among intervals (e.g., Raup 1976; Alroy 2010a; Smith and McGowan 2011; Benson and Upchurch 2013), and we demonstrate below that sampling is highly non-uniform through the mid–late Permian boundary interval in the Karoo Basin. To accommodate this, we used equal-coverage (shareholder quorum) subsampling (SQS; Alroy 2010a,b). SQS draws taxon occurrences until a quorum value of coverage is met, which is the summed estimated frequency (as proportions of 1, the total occurrence pool) contributed by each taxon that has been drawn. This approach performs substantially better than classical rarefaction for estimating standing diversity, as it samples harder in cases where an underlying species pool is actually richer. By doing so, SQS preserves underlying differences in diversity rather than smoothing out variation in richness by imposing a fixed quota of data items, as done by classical rarefaction (Alroy 2010a, b).

The proportional abundance of the most common species varies among bins, meaning that some bins have substantially more uneven abundance-frequency distributions than others (see below). Variation in evenness influences richness estimates from most methods, including subsampling methods, although SQS is relatively robust compared to other approaches (Close et al. 2018). We addressed this by excluding the most abundant taxon prior to subsampling (recommended by Alroy 2010a, 2010b, 2010c). This considerably reduced variation in evenness, allowing better estimates of species richness. Note that the application of SQS to estimate standing diversity differs from the application of classical rarefaction described above when standardising data prior to estimating extinction and origination rates using the GF equations; this difference is appropriate based on the assumptions of different methods (Alroy 2014).

Results

Data Description.—Our dataset provides insights into sampling of fossil specimens through the mid–late Permian boundary interval of the Karoo Basin, indicating that few specimens have been collected from the lowermost 2000 m of the succession (Fig. 3). This lower portion of the succession has yielded important early therapsid specimens of the *Eodicynodon* Assemblage Zone (Rubidge 1995; Rubidge and Hopson 1996). However, these are few in number, and individual 50 m stratigraphic bins have yielded generally fewer than ten specimens. Furthermore, these specimens have been collected predominantly from an interval of approximately 450 m (nine stratigraphic bins in our analysis). A prominent gap exceeding 1000 m (20 stratigraphic intervals), from which only a handful of specimens has been recovered, separates this richer portion of the *Eodicynodon* AZ from the upper 600 m of the Abrahamskraal Formation (upper *Tapinocephalus* AZ, Capitanian). Fifty metre intervals in this latter portion of the succession have each yielded up to 30 specimens, which marks the beginning of continuous and well-sampled deposits extending into the late Permian. Because the lower deposits are not sufficiently rich or continuously-sampled to provide information about species richness, extinction, or origination, our analyses focus on the upper portion of the succession.

Specimen occurrence densities are greater still in the uppermost 50 metres of the Abrahamskraal Formation and equivalent thicknesses of the lower Teekloof Formation (>45 specimens per interval). Despite this increase in counts of sampled specimens, species counts are typically similar to or lower than those of the preceding 450 m of upper Abrahamskraal

Formation (Fig. 3). Two alternative possibilities could explain why the observed increase in numbers of specimens sampled through the upper part of the succession does not result in an increase in species counted: (1) Sampling of the preceding parts of the Abrahamskraal Formation, although less intensive, was already sufficient to recover most or all species that existed, so increasing the intensity of sampling does not increase the count of observed species; or (2) species richness was actually lower at the top of the Abrahamskraal Formation and in the Teekloof Formation, so much greater sampling intensity yields only similar species counts to those from the preceding intervals. These alternatives are tested below using equal-coverage subsampling (SQS). A decrease in the evenness of that assemblage, and particularly an increase in the relative abundance of the dominant taxon (*Diictodon*), could not explain this pattern: fewer taxa are counted in the first two bins of the Teekloof Formation even when the dominant taxon is excluded, even though (non-dominant) specimen counts in these bins are similar to those of the upper 50 metres of the Abrahamskraal Formation. This occurs because a large proportion of the increase in specimen counts is due to an increase in the abundance of the most common taxon, the dicynodont *Diictodon* (Figs. 3,4A). In fact, the relative abundance of *Diictodon* in the uppermost 50 metres of the Abrahamskraal Formation is around 40%. This is more than twice the abundance of the preceding stratigraphic bin (100–50 metres below the top of the Abrahamskraal Formation), and specimen counts from the uppermost 50 metres of the Abrahamskraal Formation are similar to those in lower intervals when *Diictodon* is excluded (Fig. 3).

We were concerned that the onset of the increase in the abundance of *Diictodon* might be artefactual in the Abrahamskraal Formation, where it overlaps with the range of dinocephalians and basal pareiasaurs. This is because *Diictodon* is readily recognizable from unprepared specimens (mostly skulls), whereas dinocephalians and pareiasaurs are difficult to identify even with good material; in most cases, dinocephalian finds consist of fragmentary skeletons dominated by postcranial elements that cannot be identified beyond family level. Both dinocephalians and pareiasaurs also suffer from problematic taxonomy, exacerbating the problem. Consequently, it is possible that at least some, if not most, dinocephalian and /or pareiasaur genera may have survived later and at higher relative abundances than is reflected by our database and stratigraphic chart, thereby exaggerating the dominance of *Diictodon* (Fig. 1).

To control for this, we calculated the proportion of specimens in each interval belonging to *Diictodon* counting even generically/specifically indeterminate occurrences of dinocephalians and other non-dicynodont tetrapods, allowing far more specimens (representing genuine individuals of unknown genus) to be included. The relative abundance of *Diictodon* could thus be compared more fairly across the bins in which it occurs. This approach (not shown) suggests that "diagnosability" is unlikely to explain the increased abundance of *Diictodon* near the top of the Abrahamskraal Formation, because lower intervals of the Abrahamskraal Formation also contain abundant indeterminate tetrapods and should be affected in an identical way by this possible bias.

To examine variation in dominance or evenness, regardless of the identity of the dominant taxon, it is necessary to use only the occurrences of specimens that are diagnostic to a particular taxon. When this is done, most bins of the Abrahamskraal Formation, excluding bins containing fewer than ten specimens, exhibit low dominance (the most abundant taxon has a relative abundance of 20%) and high evenness (Fig. 4B,C; Pielou's J). The increases in *Diictodon* abundance described above are associated with large reductions in evenness and an increase to relative abundance of the dominant taxon to 60%. This shows that the evenness of the species abundance-frequency distribution is lower (i.e., more uneven) at the top of the Abrahamskraal Formation and in the Teekloof Formation than it is further down in the stratigraphy, and this occurs specifically because of a step-wise increase in the dominance of *Diictodon*.

The proportional abundance of *Diictodon* continues to increase through the Poortjie Member of the Teekloof Formation (*Pristerognathus* AZ), reaching an acme in the Hoedemaker Member (*Tropidostoma* AZ); in this unit around 80% of specimens belong to *Diictodon* using conservative calculation (Fig. 4A). The overall pattern is one in which *Diictodon* occurred at low proportional frequencies for 400–500 metres (~3 Myr, based on an age of ca. 264 Ma for the mid-Abrahamskraal Formation and of 260.3 Ma for the top; Lanci et al. 2013; Day et al. 2015a) following its first occurrence, but subsequently underwent stepwise and cumulative increases in proportional abundance from the uppermost 50 metres of the Abrahamskraal Formation onwards.

No bins of the *Eodicynodon* AZ, in the lower part of the study interval, contain enough specimens to make confident estimates of dominance (arbitrarily designated as > 10 specimens here). However, the combined data for 250–950 metres from the bottom of our section contain in total 36 specimens, of which 31 belong to *Eodicynodon*, indicating a highly uneven abundance-frequency distribution here too.

Subsampled Species Richness.—Subsampled species richness through the uppermost 450 m of the Abrahamskraal Formation is relatively high compared to that in the Teekloof Formation. This is found consistently at multiple quorum levels (q = 0.4 is reported in Fig. 5) when occurrences with stratigraphic precision of two or three bins are used. When only strictly constrained stratigraphic occurrences are considered (one bin of stratigraphic precision), many fewer intervals have sufficiently high coverage to subsample effectively. Results therefore become uninformative. In fact, in this case richness within the Abrahamskraal Formation can only be estimated for a few intervals low in the formation, which apparently have similar richness to the better-sampled boundary interval. This result is, however, based on a relatively small amount of data. We therefore favour the results of analysis using greater numbers of specimen occurrences with less precise stratigraphic data. It is unlikely that this introduces aliasing (= time averaging) bias because species turnover through the uppermost 500 metres of the Abrahamskraal Formation is remarkably low (described below).

Extinction and Origination Rates.—Gap-filler estimates of extinction rates are consistently found in all our analyses as being elevated to around 0.5 interval^{-1} in the penultimate 50 m of the Abrahamskraal Formation, and to around 0.75 interval^{-1} in the uppermost 50 m of the Abrahamskraal Formation (Fig. 6A). Modified gap-filler estimates of extinction proportion are similar, around 0.5 interval^{-1} for the final two bins (= top 100 m) of the Abrahamskraal Formation (Fig. 6C). Other stratigraphic intervals have distributions of estimated extinction rates whose interquartile ranges include zero, and median estimated extinction rates are typically positive (both methods). The lower interval of the Hoedemaker Member is the highest stratigraphic interval for which we were able to estimate extinction rates (using data from the preceding and two following stratigraphic intervals: the middle and upper portions of the Hoedemaker Member), which has a median estimated extinction rate of zero across all our analyses, except when using only precisely-dated specimen occurrences.

Dinocephalians make a large contribution to the occurrence of extinctions in the upper portions of the Abrahamskraal Formation (i.e., dinocephalian species disproportionately become extinct). The presence of rare dinocephalians in the lower portion of the Poortjie Member (Fig. 1; Day et al. 2015b) is therefore curious, and raises questions about whether a small number of dinocephalian lineages survived a short time after the extinction event. Alternatively, an abrupt extinction of all dinocephalians during a brief interval of time equivalent to the upper Abrahamskraal Formation could still occur if the base of the Poortjie was slightly diachronous. In fact, radiometric and biostratigraphic data suggest that the base of the Poortjie is among the most isochronous time-lines within the lower Beaufort Group (Rubidge et al. 2013; Day et al. 2015a). We therefore suggest that the evidence is consistent with the survival of at least one dinocephalian species beyond the main extinction pulse in the upper Abrahamskraal Formation. This is comparable to observed therapsid turnover during the end-Permian extinction event, in which several therapsid groups survive as “dead clades walking” (Jablonski 2002) following the main extinction pulse but disappear from the record shortly thereafter (e.g., akidnognathid therocephalians; Smith and Botha 2005).

Origination rates show a background pattern of generally low median values, with inter-quartile ranges that include zero. Median origination rate estimates are high in the upper 50 m of the Abrahamskraal Formation, and elevated (although less so) in the lower 50 m of the overlying Poortjie Member based on the gap-filler method (Fig. 6B). They are not elevated according to the modified gap-filler method, although their confidence intervals exclude zero, suggesting a weak pulse of origination compared to background (Fig. 6D). This latter result is more consistent with patterns of subsampled richness, which is low from the start of the Poortjie Member, in turn suggesting that post-extinction origination rates were not sufficient to recover substantive standing diversity (Fig. 5).

Discussion

The boundary between the Abrahamskraal Formation and Poortjie Member of the Teekloof Formation is a near-isochronous horizon in the Karoo Basin, possibly related to basin-wide tectonic influence (see Paiva 2016). Using robust estimates of patterns of species richness, extinction rates, and origination rates we find evidence of strongly elevated extinction rates in the upper 100 m of the Abrahamskraal Formation. This coincides with a reduction of species richness that persisted through the Poortjie and Hoedemaker Members of the Teekloof Formation. Origination rates were only weakly elevated in the upper Abrahamskraal Formation and lower Poortjie Member. Although the gap-filler method suggests that origination rates reached similar levels to extinction rates in the last interval of the Abrahamskraal Formation (Fig. 6A–B), this was not obtained using the modified gap-filler method (and is the largest discrepancy between these two modes of analysis). Furthermore, even if the gap-filler result is correct, origination rates are based on the number of taxa crossing the upper boundary of the interval, whereas extinction rates are based on the proportion of taxa crossing the lower boundary. Because more taxa cross the lower boundary, as a result of high extinction within the interval, the number of lineages crossing into the following bin is much lower. Thus, even relatively few absolute originations would appear as an apparently high origination rate. Our results demonstrate that the late Capitanian-aged upper *Tapinocephalus* AZ of the Main Karoo Basin represents a high diversity tetrapod assemblage, whereas the assemblages of the *Pristerognathus* AZ and early Wuchiapingian (early Lopingian) lower *Tropidostoma* AZ had low richness.

The finding of low species richness in the early late Permian of the Karoo Basin is consistent with a previous study that used rarefaction to estimate species richness at coarse stratigraphic resolution (Irmis and Whiteside 2011). Using high-resolution stratigraphic data divided into approximately 50 m stratigraphic intervals, we find consistent estimates of species richness in multiple successive bins on intermediate timescales, providing greater confidence in this conclusion. By accounting for sampling differences, this demonstrates that the *Pristerognathus* AZ and at least the lower part of the *Tropidostoma* AZ document a taxonomically impoverished, post-extinction tetrapod assemblage spanning approximately 2 Myr between the late Capitanian and early Wuchiapingian (Rubidge et al. 2013; Day et al. 2015a). Although the *Tapinocephalus* AZ has yielded more fossils from a greater number of localities, these are spread over a much greater stratigraphic thickness and the precision with which fossils can be placed within it is much lower. Fossil occurrences per unit thickness in the *Tapinocephalus* AZ are also low (Fig. 3). Nevertheless, many genera have been sampled in the upper few hundred metres of the Abrahamskraal Formation. Conversely, the *Pristerognathus* AZ has produced a relatively large number of fossils given its lesser thickness, and fossil occurrences in that biozone have better stratigraphic precision. Our analysis therefore cannot attribute its lower diversity to lower sampling, and this is especially true given that we use equal-coverage subsampling to estimate richness while accounting for differences in sample coverage through the stratigraphy.

Previous work has documented low evenness in the abundance frequency distribution of tetrapod species in the *Tropidostoma* AZ (Irmis and Whiteside 2011). Low evenness (= high dominance) is often associated with ecosystem instability, and is a characteristic of post-extinction “recovery” faunas. Our high resolution stratigraphic data indicates that the transition from high to low evenness results from the increase in abundance of the dicynodont *Diictodon*, which began below the upper 50 m of the Abrahamskraal Formation and, therefore, before the peak of Capitanian extinction rates. Although the increasing dominance of *Diictodon* leads to low evenness in genus frequency distributions in the uppermost bins of the Abrahamskraal Formation, the magnitude of this unevenness continues to grow into the succeeding Poortjie and

Hoedemaker members of the Teekloof Formation. We therefore suggest that the increasingly exceptional dominance of *Diictodon* during the latest Capitanian and early Wuchiapingian represents opportunistic expansion in an unstable ecosystem, beginning prior to the acme of species extinctions and continuing after them.

Together with the observation of low levels of dinocephalian survival into the lower 50 m of the Poortjie Member, this suggests that the Capitanian extinction event among tetrapods in the Karoo Basin was a dynamic process occurring over an interval of more than 100 m of stratigraphy. Estimates of depositional rates for the upper Abrahamskraal Formation exist from the eastern Karoo Basin, based on rock thickness between dated tuff horizons (Day et al. 2015a: Supplementary Information 1.C). These suggest that about 130-150 Kyr is represented per 50 m. Alternatively, if we assume a constant rate of deposition between the top of the Abrahamskraal Formation (260.3 Ma; Day et al. 2015) and the mid-Abrahamskraal Formation (~264 Ma; Lanci et al. 2013; but see Day and Rubidge 2014), then 50 m of rock would represent 138–250 Kyr. Dates from a single locality in the western margin of the basin alone suggest approximately 330 Kyr per 50 m (Lanci et al. 2013). Thus, although depositional rates were no doubt variable and these estimates to be treated very tentatively, we propose that the extinction event took place over 0.3–0.6 Myr.

Comparison with Previous Sampling-Corrected Diversity Estimates for Tetrapods.—Our results contrast with several previous studies of tetrapod taxonomic richness during the mid-to-late Permian. Reasons for this include differences in methodologies used to estimate (or count) species richness), whether and how those methods attempt to standardize variation in sample size/coverage, the quality of the datasets used, and the geographic and temporal scale at which they were conducted. For instance, in a study of global palaeodiversity patterns among Permian tetrapods, Benton et al. (2013) found that a number of diversity crises appear to have occurred in the late Palaeozoic but failed to find any crisis in the Capitanian. Instead, they identified a diversity decline in the Wordian (early Guadalupian, 5–8.5 Myr before the event documented here), and another in the early Wuchiapingian (1–6 Myr after the event documented here their study). To this latter event they attributed an 81% loss of genera (92 out of 113) but this appears to be based erroneously on ratios of originations rather than extinctions (Benton et al. 2013: Table S1). When this is corrected the early Wuchiapingian has a ~58% proportional extinction (as a proportion of total diversity within the substage) and extinction rate peaks stand out in the late Kungurian (i.e., early/middle Permian transition; 91%), lower (early) Capitanian (77%) and Changhsingian (i.e., Permian/Triassic transition; 89%), much more in line with expectations. Furthermore, the extinction peak in their "lower Capitanian" corresponded to the loss of diversity between the *Tapinocephalus* AZ and the *Pristerognathus*/*Tropidostoma* AZs, which radiometric ages published subsequently have shown to actually be within the late Capitanian (Day et al. 2015a). When per-taxon extinction rates are calculated for the same dataset, but taking into account stage duration, the same peaks remain. Benton et al. (2013) did not generate sampling-corrected global diversity estimates, due to the difficulty of accounting for the plethora of factors that bias the fossil record on a global scale.

Regional studies suffer from fewer distinct types of biases. In particular, regional scale studies are not affected by temporal fluctuations in the number of sampled regions (i.e., areas of the Earth that have yielded fossils) that occurs in "global" studies. Because sampling a new region is likely to produce greater numbers of species, this is arguably the largest bias on apparently "global" palaeodiversity assessments (e.g., Alroy 2010c). For instance, Benson et al. (2016) showed that the palaeogeographic extent of global fossil localities explained at least 60%

of the variance in species and genus counts for Mesozoic tetrapods. On the other hand, whilst the Main Karoo Basin is a fine natural laboratory, it is not necessarily representative of global patterns of diversity change. Regional studies in other basins, particularly at different latitudes, may therefore differ in their results but by limiting a study to a single region, as done here, we provide one solution to the problem of "geographic sensitivity" experienced at a global level (see Close et al. 2017 for a broader method).

Studies of the Main Karoo Basin and the fore-Ural region of the Russian platform have attempted to standardize for sample availability using residual diversity estimates, derived from differences between modelled diversity assuming complete dependence on a sampling proxy and observed diversity (Fröbisch 2013, 2014). Such proxies have included the number of localities, number of specimens and, in the case of the Karoo, total outcrop area. This approach found positive residuals for the *Pristerognathus* AZ, suggesting higher species richness than could be explained by the sampling proxy (outcrop area; Fröbisch 2013). In other words, it provided little support for a Capitanian extinction in terms of taxic diversity loss, because richness appeared to be higher after this event than before it.

Fröbisch (2013) primarily used outcrop area to correct face-value taxon counts but this and other "rock amount" measurements only influence sampling intensity indirectly, by providing rock from which to sample fossils. Fröbisch (2013, 2014) also considered the number of specimens actually collected as a sampling proxy; we consider this to be preferable given that it more accurately reflects the high intensity of collecting in the *Pristerognathus* AZ (e.g., Fig. 3). When species counts were corrected for counts of specimens sampled, the residual diversity was negative for synapsids, more similar to our findings here (Fröbisch 2013: Fig. S2), although the same was not true of other tetrapods (Fröbisch 2013: Figs. S3–S5). The positive diversity residuals for non-synapsid tetrapods found by Fröbisch (2013) may be partly due to the presence in the *Pristerognathus* AZ (in his dataset) of the pareiasaurs *Bradysaurus* and *Embrithosaurus*, the biarmosuchian *Hipposaurus*, and the rhinesuchid temnospondyl *Rhinesuchoides*, taxa that we do not consider to occur in that AZ. Inspection of our specimen counts suggests that face-value species counts in the *Pristerognathus* AZ are in fact low in comparison to the number of specimens sampled (Fig. 3), consistent with our relatively low subsampled richness estimates.

An alternative method for estimating global richness is a form of range-through diversity estimate that uses information from phylogeny in addition to taxon ranges, known as phylogenetic diversity estimation (Norell 1992; Smith 1994). So far this has been applied to datasets for parareptiles (including pareiasaurs) and anomodonts (including dicynodonts) through the mid-late Permian (Ruta et al. 2011; Ruta et al. 2013), amniotes from the Carboniferous to the Triassic (Brocklehurst et al. 2015), and for temnospondyls at family level (Ruta and Benton 2008); these studies have indicated an increase in richness above the Capitanian, in direct contrast to our findings. However, their conclusions are partly attributable to the coarse time resolution of these studies: for instance, Ruta et al. (2013) observed an increase in richness between the Capitanian and Wuchiapingian but use the sum of ranges within these extended time intervals, which both exceed 5 Myr in duration (i.e., approximately one-tenth of the temporal precision of our analyses).

Overall, our finding of an elevated extinction rate for the tetrapod community in the upper 100 m of the Abrahamskraal Formation is consistent with the stratigraphic ranges of taxa (Fig. 1), and with counts of last appearances derived from constrained optimisation of range-end events that was performed on an older (smaller) version of this same dataset (Day et al. 2015a). This latter used minimum stratigraphic range lengths alone and was not so well tied to the lithostratigraphy, with some uncertainty remaining over the exact position of the extinction peak. The reason for this is because the CONOP algorithm considers only the relative positions of events, regardless of lithostratigraphic provenance, so that such contacts can only be projected onto the optimal sequences of first- and last-appearance events when considered as events themselves; their position relative to the sequence of last appearances is therefore variable. By using stratigraphic bins measured from a relatively isochronous lithostratigraphic horizon, i.e., the base of the Poortjie Member, our analyses assign this contact an *a priori* fixed position, and so the distance from the contact can be more accurately observed.

Time Standardisation.—The comparison between our results and the studies above suggest that the temporal resolution of datasets used in the determination of richness and of turnover rates can be influential. Shen and Shi (2002) were aware that long time bins (i.e., for the Lopingian) may have masked diversity loss in brachiopods, while this possibility was also recognised more generally by Bambach et al. (2004). This poses a problem because analytically adjusting species richness estimates, turnover rates, or other metrics using information on time bin duration will not be sufficient to correct the findings from databases with coarse stratigraphic resolution, and in fact can introduce substantial error. The reason is that if a rapid extinction event occurs in a long time bin, then its apparent severity will be diluted across the whole interval, though this is also dependent on the magnitude of background rates both absolutely and relative to the mass extinction. Conversely, if it occurs in a very short bin then it will be divided by a lesser amount of time and appear greater. An extinction event of the same magnitude would thus appear much less severe if it occurred in a 5.5 Myr bin than if it occurred in a 1 my bin, even if background rates were constant. This would make comparisons of the mid-Permian

(Capitanian=5.5 Myr; Wuchiapingian=5 Myr) and Permo-Triassic (Changhsingian=2.2 Myr; Induan=0.7 Myr) mass extinctions unfair. Time-standardised rates may be especially problematic in the Karoo because the *Tapinocephalus* AZ is mostly sampled from the upper part of the zone; time corrections assuming it spans the length of the Capitanian may thus underestimate extinction rates.

A rate metric that is better able to quantify mass extinction intensity at this stage resolution involves identifying mass extinctions *a priori* and then accounting for background extinction as calculated from intervals in which such events do not occur (Stanley 2016). Of course this requires recognition of these events in the first place, which may only be apparent at the regional level. Indeed, our results show that at high stratigraphic resolution a distinct increase in extinction rates and corresponding drop in richness is apparent in the late Capitanian, which eluded previous studies at coarser, standardized timescales. Furthermore, evolutionary rates appear to be multidimensional, so are unlikely to be reliably described by single metrics employed at different temporal scales. This remains a problem when trying to understand "background" extinction rates and elevated, mass extinction rates simultaneously. The best approach could be to combine low-resolution trends with high-resolution studies at focal intervals, isolating rate anomalies and, ultimately, to adjust long-term trend lines accordingly.

Conclusions

Global datasets may be unable to identify rapid turnover or extinction events, especially when they occur in longer time bins. This may be true even when such events had a profound effect on an ecosystem, particularly if the extinction occurs only at lower taxonomic levels. When such cases arise, regional stratigraphic studies must be relied on to correctly interpret the fossil record. We applied probabilistic methods to a high-resolution fossil dataset to constrain the timing of evolutionary events among terrestrial tetrapods in the mid-late Permian boundary interval of the Main Karoo Basin. This differs from previous approaches that used coarsely resolved occurrence data and taxon counts (rather than subsampled richness estimates), or that considered first- and last-occurrences to represent literal originations and extinctions.

Sampling across most of the *Tapinocephalus* and *Eodicynodon* AZs is insufficient to infer patterns of diversification, but sampling is generally good over the upper *Tapinocephalus* and *Pristerognathus* AZs when using specimen occurrences and when the thickness of the zones is taken into account. These assemblage zones document the middle–late Permian transition in South Africa, including turnover associated with the Capitanian mass extinction. The peak of extinction rate occurs predominantly at the top of the *Tapinocephalus* AZ (uppermost Abrahamskraal Formation), despite the occurrence of at least one dinocephalian genus in the lower Poortjie, which likely represents a "dead clade walking" (sensu Jablonski 2002).

An increase in the unevenness of taxon abundance frequency distributions is also associated with the Capitanian extinction event. This is caused by the increasing dominance of the dicynodont *Diictodon*, a robust finding even when accounting for taphonomic biases. A large increase in *Diictodon* abundance, and the resulting decrease in evenness, presages the peak of extinction rates by one 50-metre bin; it was therefore not caused directly by the disappearance of other species, although it may reflect a reaction to ecosystem perturbation in advance of the Capitanian extinction peak.

Our results are broadly congruent with those reported by Day et al. (2015a) using constrained optimisation of range-end events (75-80% diversity loss), but go further in that 1) they more precisely constrain the lithostratigraphic position of the extinctions and 2) they show that the post-extinction *Pristerognathus* AZ represents an interval of low diversity compared with the *Tapinocephalus* AZ, which cannot be explained by poor sampling. This relatively low richness continues into the lower part of the overlying, late Permian (early Wuchiapingian) *Tropidostoma* AZ and suggests that recovery of species richness in the Main Karoo Basin was delayed for several million years after the Capitanian extinction event. Although the *Pristerognathus* AZ does exhibit elevated origination rates, these were not sufficient to balance the loss of richness resulting from the extinction event. At larger scales, the loss of biodiversity in the Main Karoo Basin may have been greater than in other parts of Gondwana, perhaps because of its higher latitude, but data on regions outside the basin remain inadequate to examine at the resolution used here. Nevertheless, in key areas such as the Main Karoo Basin, the Capitanian extinction event precipitated a long period of low species richness that paved the way for the late Permian tetrapod radiation.

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Figure captions

Figure 1. Stratigraphic range chart (black lines) with occurrences (grey discs) of tetrapod species (mostly as monotypic genera) for the *Eodicynodon–Tropidostoma* assemblage zones (AZ) in the Karoo Basin of South Africa. This range chart makes use of all non-questionable species occurrences (i.e., those not marked with “?”), plus all occurrences of *Endothiodon* and *Glanosuchus* (even those marked with “?”, explained in text) for which the stratigraphic position had been checked by M.O.D., either at outcrop or by investigation using geological maps. Uncertainty over the stratigraphic ranges of individual specimens was resolved by placing specimens randomly into one bin in its range of possible positions, as long as this overlapped with the known range of that taxon as determined by better constrained occurrences. If its range of possible positions fell entirely outside the known range, then it was determined to occur in the

most proximal bin and the known range of the taxon was extended to this point. This figure shows only one such iteration but others are highly similar. Taxa occurring above the studied interval (continuers) are indicated with an ascending grey arrow. Ci., *Cistecephalus*; Pr., *Pristerognathus*; Tr., *Tropidostoma*; Wuchiapin., Wuchiapingian.

Figure 2. Precision of stratigraphic assignment to 50 m bins, displayed cumulatively from most accurate (1 bin certainty [= 50 metres]) to least accurate (50 bins [=2500 metres]). Numbers above bars indicate total occurrences within bins, both with and without *Diictodon*. Dark grey portion of bar indicates proportion of cumulative occurrences that are *Diictodon*.

Figure 3. Raw specimen (A, C, E) and species (B, D, F) counts for each 50 m stratigraphic bin in the Abrahamskraal Formation and lower Teekloof Formation at three levels of stratigraphic precision: Using only specimens constrained to occur in a single bin (A, B), one of two bins (C, D), and one of three bins (E, F). Specimen counts increase from the upper Abrahamskraal Formation into the Poortjie and Hoedemaker members of the Teekloof Formation but species counts are universally lower in the lower two bins of the Poortjie Member than either before or after. Stratigraphy labelled in A and B only. P., Poortjie Member; H., Hoedemaker Member.

Figure 4. Dominance in the taxon abundance-frequency distribution in the Karoo Basin. (A) Relative abundance of *Diictodon* from its first appearance datum (FAD) between 550–500 metres below the top of the Abrahamskraal Formation in the northwest quadrant of the basin (the second appearance being 450–400 metres below the top of the Abrahamskraal Formation). This was calculated conservatively by including only specimens identified definitively as *Diictodon*

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Figure 5. Mean subsampled species richness for stratigraphic bins using specimens constrained to one bin (white circles) and specimens constrained to two (grey circles) or three (black circles) bins and randomly assigned to one of them. Results are smeared over all 1000 iterations of random assignment and whiskers indicate interquartile ranges of the results from these iterations. Few bins contained sufficient occurrences to be subsampled when using only the best constrained occurrences (white circles).

Figure 6. Gap-filler estimates of extinction (A) and origination (B) rates, and modified gap-filler estimates of extinction (C) and origination (D) proportions for three levels of stratigraphic precision. White symbols indicate analysis only using occurrences that are assigned with certainty to a single 50 metre stratigraphic interval; grey symbols show the results of analyses using occurrences with up to 2 bins of uncertainty; black symbols show the results of analyses using occurrences with up to 3 bins of uncertainty. Stars indicate rates for which the interquartile

range did not include 0. Whiskers show standard interquartile ranges of results recovered from 1000 iterations, in which occurrences were randomly assigned to a single 50 metre stratigraphic bin within the range of their uncertainty. Per-bin occurrence counts were standardised using classical rarefaction prior to rate estimation. Box marked “EXT” shows interval associated with the Capitanian mass extinction.

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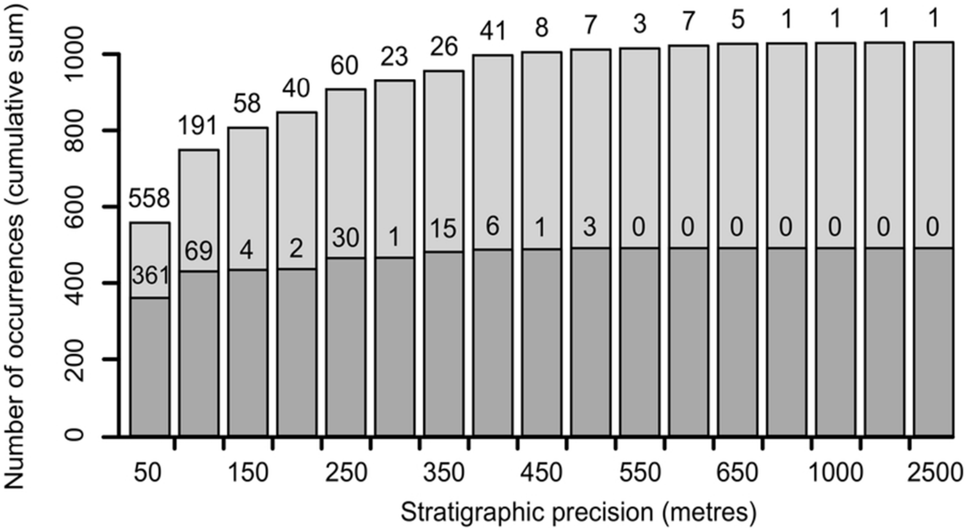

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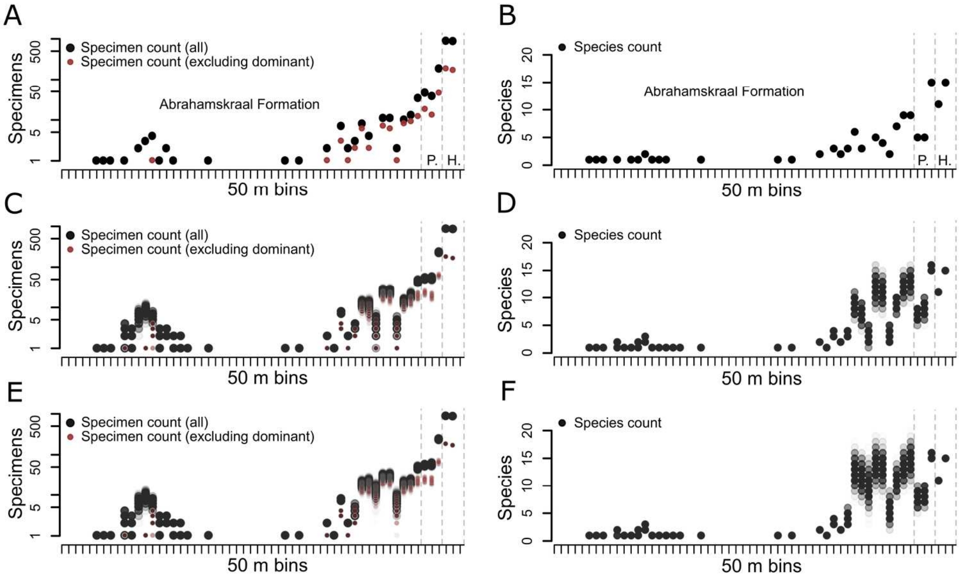

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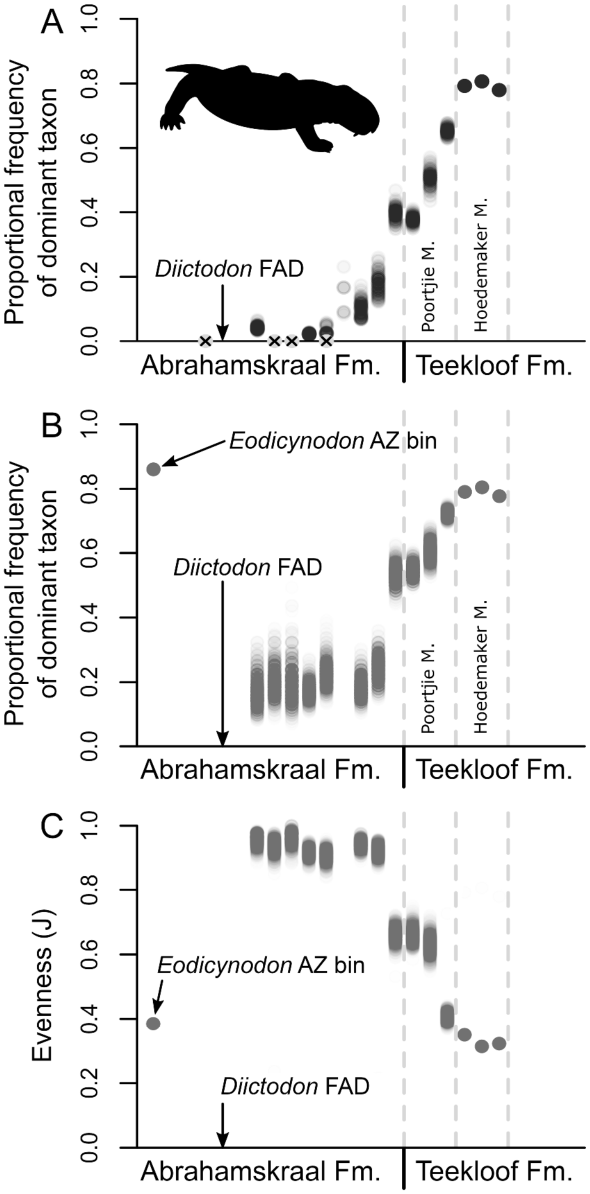

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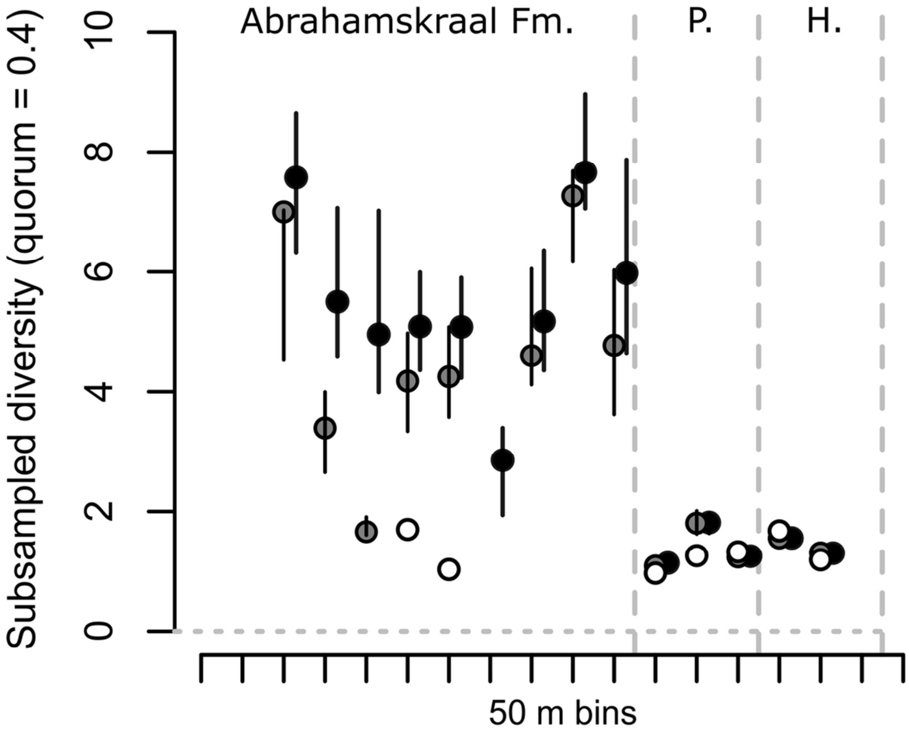

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