Relative abundance distributions reveal constraints on tetrapod community diversity

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Abstract

Previous efforts to understand the pace of species diversification through time have disagreed over whether species diversity is unbounded or limited by a carrying capacity. Tetrapods (limbed vertebrates) have frequently been employed as a case-study in examinations of this issue, with studies of diversity being used to support both sides. Here, we examine the shape of relative abundance distributions (RADs) within terrestrial tetrapod communities between the Carboniferous and the Eocene to assess their ecological structure of tetrapod communities, assessing whether the RADs are consistent with “simple” models characteristic of finite resources distributed among species, or more “complex” models where more ecological processes permit greater functional diversity. Our results indicate that terrestrial tetrapod communities have remained consistent in the shape of their RADs since the establishment of ecological limits in the late Carboniferous, albeit with evidence of an increase in global tetrapod diversity at the Cretaceous/Paleogene boundary. Throughout much of the interval studied, the RADs of tetrapod communities best fit “simple” models indicative of finite resources. This contrasts with findings for the marine realm, where a substantial increase in community complexity is found following the end-Permian mass extinction. These results indicate that terrestrial and marine ecosystems are governed by different limits on their ecological complexity, with tetrapod communities being governed by finite ecological limits.

Introduction

A long-standing debate exists over whether species diversification is bounded; that is, whether the existence of a finite amount of ecological resources within a given region, habitat, or ecosystem limits the amount of biological diversity which can be supported within it (e.g. Etienne et al. 2012; Cornell 2013; Rabosky and Hurlbert 2015; Marshall and Quental 2016; Furness et al. 2021a). This concept is the basis of many fundamental theoretical models in ecology, such as the island biogeography model (MacArthur and Wilson 1967). However, if species diversification is unbounded, then there is potential for taxonomic richness to grow exponentially, explored in the "unified neutral theory of biodiversity" (Hubbell 2001) and sometimes referred to as the "expansionist" paradigm (Harmon and Harrison 2015). This may be the case if carrying capacities are absent or yet to be reached, when disturbances remove individuals or species, or when new ecospace is explored (Furness et al. 2021b). This latter case may include the evolution of new ecological adaptations which enable movement into previously uninhabited environments or the further subdivision of existing resources, or the introduction of new species providing opportunities for novel biotic interactions.

Tetrapoda (limbed vertebrates, including mammals, birds, amphibians and reptiles) represents a morphologically and ecologically diverse clade, including animals which exhibit a wide array of diets, locomotory modes, and body sizes. Today this group contains more than 30,000 species, descended from a common ancestor that appeared in the late Devonian, more than 350 million years ago (Benton 1995; Clack 2006, 2012; Sahney et al. 2010a). An apparent exponential increase in the number of tetrapod species between the late Devonian and the present (Benton 1995; Benton and Emerson 2007) has previously been used to support an "expansionist" model of diversification in the clade, occasionally interrupted by extreme events such as mass extinctions (Benton 1995; Benton and Emerson 2007; Sahney et al. 2010a; Harmon and Harrison 2015). However, recent analyses of the fossil record have questioned this interpretation, arguing that these seemingly unbounded diversity estimates have been heavily affected by various sampling biases, in particular uneven sampling across space, and therefore cannot be taken at face value (Benson et al. 2016; Close et al. 2017; Close et al. 2019). The rate at which tetrapod diversity has accumulated over deep time, and the timing of changes in this rate, therefore remain controversial.

The relative abundance distribution (RAD) of the species found within an ecological community can be highly informative about its structural complexity, reflecting characteristics such as richness and dominance (Wagner et al. 2006; McGill et al. 2007). Specific types of RAD can be related to theoretical models in ecology and used to make inferences about community assembly and possible bounds on diversity. Models such as the broken-stick (produced when the resources in a community are divided into a set number of non-overlapping niches, divided at random between taxa (MacArthur 1957)) and the niche pre-emption model (where adding a new species to a community pre-empts a portion of available resources without adding any (Root 1967)) are expected to be the best fit for a RAD if a community's diversity is constrained by available resources. On the other hand, models such as Zipf and Zipf-Mandelbrot (where the addition of species depends on both previous environmental conditions and species presences; pioneer species have low costs and later species have high costs (Frontier 1985)) and Lognormal (where resources are appointed sequentially to species as they are added (Sugihara 1980)) are to be expected to have the best fit if diversity is unbounded and new species create resources (Wagner et al. 2006) (Fig. 1).

Wagner et al. (2006) made the distinction between these two sets of RAD models, describing models associated with unbounded diversity as indicative of more complex ecosystems, where more ecological processes are required and greater functional diversity is permitted. The terminology of “simple” versus “complex” RADs is used hereafter following this division. Wagner et al. (2006) showed that RADs of marine ecosystems exhibited a shift from those better fitted by "simple" models in the Paleozoic to those better fitted by more "complex" models following the end-Permian mass extinction. An explanation provided for this shift was the diversification of organisms in the Mesozoic which were better suited to increasing ecospace; Paleozoic marine faunas had been dominated by sessile filter feeders (Bambach et al. 2002), but during the Mesozoic, taxa which increased ecological opportunity within an ecosystem, such as more mobile taxa and ecosystems engineers like reef-builders, became more diverse.

These results imply that, while marine diversity was bounded during the Paleozoic, these bounds were released following the end-Permian extinction, and subsequently ecosystems could follow an "expansionist" model of diversification. Conversely, however, unbounded diversification in terrestrial vertebrates (tetrapods) was rejected by recent studies investigating local species richness and spatial biases affecting global analysis of the fossil record (Close et al. 2017; Close et al. 2019). Instead, local tetrapod diversity was found to be constrained on geological timescales (Close et al. 2019).

Here, we investigate the evolution of tetrapod RADs through deep time, from the Carboniferous until the Eocene, to test whether ecosystem structure in terrestrial vertebrates supports or rejects the expansionist paradigm. We use likelihood model fitting approaches to test the fit of simple and complex ecological models to tetrapod communities, using data from the Paleobiology Database. We also use Hill numbers (Simpson's diversity) to summarise the diversity of the communities, to incorporate the relative abundances of taxa and account for sampling biases. Finally, we carry out simulation analyses to test how the model fitting approaches perform under incomplete sampling, which is prevalent in the tetrapod fossil record.

Methods

Data

A dataset of tetrapod occurrences from the Carboniferous (including the oldest crown-group fossils) until the end of the Eocene was downloaded from the Paleobiology Database (PBDB; https://paleobiodb.org/) in November 2020 (Supplementary Table 1). These data consist of lists of taxa present within “collections”: spatially and temporally restricted sets of occurrences representing taxa which are likely to have interacted with one another in life. Marine collections were discarded, including those that contained occurrences of terrestrial taxa, since terrestrial tetrapods in marine sediments have almost certainly been transported from their original habitat, and so are not representative of a community (Supplementary Table 2). Efforts were made to make abundance data more complete: where abundance counts were not included within collection data, the “occurrence comments” were checked for information regarding taxon abundance. These data were manually added to the abundance records employing the following rules: a) if the notes mentioned the number of specimens of a particular taxon found, this was the number used; b) if museum catalogue numbers of the specimens were listed, these were counted; and c) if a list of museum catalogue numbers of the specimens was included but acknowledged as not being complete e.g. with a statement such as “and other specimens”, the abundance count was left empty. Collections without abundance data or palaeo-coordinates (as outputted by the GPlates palaeorotation models implemented within the PBDB (Wright et al. 2013)) were then discarded.

Analyses were conducted at the species level, but attempts were made to include occurrences that were not identified to that taxonomic resolution. If an occurrence was assigned to a higher taxon, and no occurrences of species within that higher taxon were known from its bioregion, the higher taxon was considered a unique species within that collection and retained within the dataset. To ensure the included collections were sufficiently well-sampled to provide a robust set of results, collections were rejected if they contained fewer than three taxa, or if they had a Good's U of less than 0.4. Good's U is a measure of coverage, indicating the percentage of individuals in the original population belonging to the species sampled (Good 1953; Chao and Jost 2012). Good's U was calculated in R v3.6.1 (R Core Team 2020) using custom code (Supplementary Data 1).

The remaining 863 tetrapod-bearing collections, containing a total of 4048 species, were assigned to time bins representing geological stages (as defined by the International Commission on Stratigraphy [v. 2020/03]). Within each time bin, collections were grouped into "bioregions" (contiguous areas of land with distinct endemic faunas) in R using the method of Brocklehurst & Fröbisch (2018), with an updated version of the code provided in that paper (Supplementary Data 1). This method groups collections based on two cluster analyses, the first based on geographic distances and the second based on taxonomic distances. Great circle distances between palaeo-coordinates were used as a metric of geographic distance, calculated using the rdist.earth() function in the R package fields (Nychka et al. 2017). Taxonomic distances were represented by the modified Forbes Metric (Alroy 2015). The original Forbes index represents the expected number of species found in two random samples divided into the observed number, with the modified version amended to allow for uncertainty in sample size. Taxonomic distances were transformed using the relative abundance corrected procedure (Brocklehurst et al. 2018). These metrics were chosen because they perform well when taxon samples are incomplete, and sampling is unequal between pairs of localities (Brocklehurst et al. 2018). To ensure that bioregions represented local communities, only collections within 100km of each other were grouped (Brocklehurst and Fröbisch 2018). The number of bioregions in each stage varied from three (Asselian [early Permian], Sinemurian [Early Jurassic], and Hauterivian [Early Cretaceous]) to 301 (Ypresian [Eocene]), with a median of 11.

Analysis of Relative Abundance Distribution

Within each bioregion, five models were fit to the observed relative abundance distribution (RAD) using likelihood model fitting approaches: Null (or Broken-Stick), Pre-emption (or log series), Lognormal, Zipf, and Mandelbrot. The model fitting was carried out using the function radfit() in the R package vegan (Oksanen et al. 2019). The strength of fit of each model to the RAD was assessed using Akaike weights, calculated from the Akaike information criterion (AICc; Hurvich and Tsai 1995). The summed Akaike weights of the Lognormal, Zipf and Mandelbrot models were used as a proxy for the "complexity" of an ecosystem (Wagner et al. 2006). The median and standard error of the Akaike weights for all bioregions within a time bin were used to examine variation in ecosystem complexity through time (Supplementary Data 1).

Simpson Diversity

Inverse Simpson Concentration (or Simpson's Diversity, as it is referred to throughout this paper) is a measure of diversity belonging to the family of indices known as Hill numbers (Hill 1973; Chao et al. 2014a, 2014b). These indices aim to summarise the diversity of an assemblage in a way that incorporates the relative abundances of species. Species richness as a metric, whether incorporating sampling correction or not, considers common and rare species equally, and so does not account for the fact that rare species make smaller contributions to ecosystem function (Pielou 1975; Chao et al. 2014a). Hill numbers downweight rare species by an order q, producing greater diversity estimates for more even abundance distributions (Chao et al. 2014a). A Hill number of order q=0 represents raw species richness. If q=1, species are weighted in proportion to their relative abundance (Shannon entropy), and if q=2 (Simpson's diversity), more abundant species are weighted higher than rare species. Simpson's diversity therefore represents the effective number of dominant species in an assemblage, taking greater account of the species that make the greatest contributions to an ecosystem, and therefore of more relevance to ecological structure of a community.

The Simpson's diversity of each bioregion was calculated using the R package iNEXT (Hsieh et al. 2016). To account for heterogeneous sampling, the assemblages were subsampled to a coverage of 0.4. As above, the median and standard error of all bioregions within a time bin were used to examine variation through time (Supplementary Data 1).

Quantification of Sampling

Sampling heterogeneity through time and between bioregions was quantified using three approaches. The first is Good's U, as described above, quantifying the sampling coverage within each bioregion. The median U value and standard error of all bioregions within a time bin were used to compare variation in taxonomic sampling completeness through time within each bioregion. The second is the number of tetrapod-bearing collections sampled within each time bin, as a proxy for global sampling effort (Alroy et al. 2001, 2008; Crampton et al. 2003; Butler et al. 2011). Finally, the minimum spanning tree length between all collections within each time bin provides a quantification of the spatial coverage of sampling, indicating to what extent the observed signal is likely to represent local variation or a regional signal (Close et al. 2017).

Simulations

Since our approach does not incorporate an explicit correction for incomplete sampling, a set of simulations were designed to investigate our ability to assess model fit to abundance distributions influenced by sampling bias. Assemblages were randomly generated using abundances drawn from either a broken-stick (simple) or lognormal (complex) distribution using the R package *mobsim* (May et al. 2018). The assemblages all contained 200 species and at least 5000 individuals; these values were chosen to produce mean abundances of species consistent with values found in modern ecosystems, whilst also allowing simulations to run in a reasonable amount of time (Matthews & Whitakker 2014; Yin & He 2014). Subsamples were created by drawing Individuals from the assemblages until a specified level of coverage was reached (measured, as described above, by Good's U), to imitate the incomplete sampling present in the known fossil record. Levels of coverage between 0.4 and 0.9 at intervals of 0.1 were tested. The RAD models were fit to the complete and subsampled datasets as described above, with summed Akaike weights being used to determine whether models indicative of complex or simple ecosystems better fit the incomplete datasets.

Results

The relative fit of the different models to the relative abundance distributions (RADs) of tetrapods demonstrates two intervals of long-term stability in RAD shape (Fig. 2a): from the early Permian (Artinskian) until the late Triassic (Norian), and from the middle of the Cretaceous (Aptian) until the end of the study interval (end of the Eocene). During both of these intervals, RADs for the majority of tetrapod faunas were best fitted by the "simple" models (Broken-Stick or Pre-emption). In both intervals, the median of summed Akaike weights of the complex models remained between 0.15 and 0.35. Variation across bioregions in these stages mostly remained within 95% confidence intervals, even across the two largest mass extinctions sampled (the end-Permian and end-Cretaceous extinction events). The Permian–Late Triassic is also an interval of relative stability in Simpson's diversity (Fig. 2b). There is more variability in Simpson's diversity during the mid Cretaceous–Eocene interval, including an increase across the Cretaceous/Paleogene boundary that persisted until at least the end of the study interval.

Between these two intervals of stability, during the Jurassic and earliest Cretaceous, poorer sampling means that very few tetrapod-bearing collections met the limits we imposed. Although there appears to be increased support for more complex ecosystems during this interval, the error margins surrounding the median Akaike weights estimates are too broad to make robust assertions. A similar breadth of error margins hampers interpretation of Simpson’s index during this interval.

A more significant increase in support of complex ecosystems is observed in the latest Carboniferous (Kasimovian). This coincides with a significant decrease in median Simpson’s index, from its highest level throughout the study interval (3.8), to a level that is maintained throughout the Permian and Triassic, between 1 and 1.8.

Simulations were used to test how the model-fitting analyses perform under incomplete sampling, as is present in the fossil record. Incompletely sampled RADs simulated using simple models were found to more frequently be better fit by complex RAD models, even at relatively high levels of coverage; the median summed Akaike weights of complex models only fell lower than 0.5 when coverage was greater than 0.9 (Fig. 4). However, incomplete sampling of the simulated RADs did not hinder the ability of model-fitting analyses to infer them as being complex; even at low levels of coverage, the median summed Akaike weights of complex models did not fall below 0.8. This simulation therefore suggests that overall, our method tends towards identifying incompletely sampled RADs as complex in shape, regardless of whether their true RAD is simple or complex.

Discussion

An apparently continuous increase in the number of tetrapod species through deep time, and an increase in the number of ecological "categories" they occupy, has previously been used to support an "expansionist" model of diversification in the clade (Benton 1995; Benton and Emerson 2007; Kalmar and Currie 2010; Sahney et al. 2010a). In this case, we expected to see more "complex" relative abundance distributions (RADs) within tetrapod communities over time, with a higher proportion having shapes more consistent with Zipf and lognormal distributions towards the present (Frontier 1985; Laland et al. 1999). However, consistently since the Carboniferous, the RADs of terrestrial tetrapods are instead better fit by the Broken-Stick and Niche Pre-emption models. Such models are more indicative of simpler ecosystems, where species divide a limited number of resources between individuals (Root 1967). This finding supports an equilibrium model of diversification, or carrying capacity, where tetrapod diversity is subjected to ecological limits which were established during the late Carboniferous (Fig. 2).

The late Carboniferous was an interval of substantial change in terrestrial ecosystems. A transition to a warmer, drier climate, that would continue through much of the Permian, began at this time: the substantial polar icecaps present since the Devonian began to shrink, the equatorial rainforests collapsed to be replaced by more open seasonal woodland, and the arid zones surrounding them expanded (Rees et al. 2002; Tabor and Poulsen 2008; Cleal et al. 2012). This transition coincided with substantial evolutionary changes in terrestrial tetrapods, including the radiation of amniotes, extinctions among amphibians, the origin of herbivory, and the evolution of large body size (Carroll 1964; Sues & Reisz 1998; Sahney et al. 2010b; Brocklehurst & Brink 2017; Brocklehurst & Fröbisch 2018; Dunne et al. 2018). The analyses presented here indicate a substantial restructuring of ecosystems at this time. We observe a shift during the Kasimovian (latest Carboniferous) towards ecosystems with lower entropy, which is subsequently maintained throughout the Permian and Triassic. There is also a brief shift in relative abundance distributions at this time, towards shapes that indicate greater ecosystem complexity, before the return of those supporting simpler ecosystem processes, which also persist through the Permian and Triassic.

These patterns in the Carboniferous should be interpreted with caution due to the relative incompleteness of the fossil record at this time. Only the most well-sampled collections were analysed, but the fitting of RAD models does not make any further correction for incomplete sampling. The median coverage of tetrapods within bioregions, as measured by Good's U, is lower during the Carboniferous than at any other time in the study interval (Fig. 3a). Simulations show that incomplete sampling can, even under relatively good coverage, make 'simple' Broken-Stick abundance distributions appear closer to more complex models (Fig. 4a). Under the broken-stick model, there are large numbers of rare taxa which are difficult to sample. When sampling is incomplete, the tail of the RAD is removed, and the more easily-sampled common taxa receive greater emphasis (Fig. 4a). The RADs of the Garnett Quarry and Mazon Creek localities, Kasimovian communities which best fit the Zipf model, show a similar appearance to simulated RADs produced when a Broken-Stick distribution is incompletely sampled (Fig. 5). One might argue that, were the support for more complex RADs during the Carboniferous driven by poor coverage, the same would be seen in other Carboniferous intervals rather than just the Kasimovian. Moreover, the calculation of Simpson's index does explicitly correct for incomplete sampling via coverage-based subsampling, and indicates a significant decrease at this time, supporting a general shift in ecosystem structure. However, it should also be noted that the Carboniferous is an interval where the spatial extent of sampling (minimum spanning tree length between occurrences) and global sampling effort (number of occurrences) is also poor (Fig. 4b). Almost all tetrapod-bearing formations analysed from this interval are from palaeo-equatorial latitudes in North America and Europe (Kemp 2006; Brocklehurst et al. 2013; Benson & Upchurch 2013), and it is possible that the results represent local variation rather than a global signal.

If we interpret the results as a true biological signal, it appears that the late Carboniferous was an interval of reorganisation of tetrapod communities, producing a structure which persisted until the Cenozoic. The changes in terrestrial ecosystems at this time include the radiation of amniotes and the evolution of tetrapod herbivory. During the Carboniferous, a greater proportion of non-amniote tetrapods (amphibians) were spending the bulk of their adult life on land relative to today, even though their reproduction and larval stages were still tied to the water (Schoch 2009, 2014; Bazzana et al. 2020). This provided a means of shifting primary productivity between aquatic and terrestrial ecosystems, allowing a greater variety of organisms to occupy terrestrial ecosystems and potentially allowing amphibians to develop biotic interactions in ecosystems containing both them and the fully terrestrial amniotes, but no tetrapod herbivores to serve as primary consumers. The latter stages of the Carboniferous, where there is support for increased complexity of ecosystems, represents an interval before the diversification of herbivores, but when amniotes were beginning to increase in diversity and abundance relative to amphibians. The greater radiation of fully terrestrial amniotes at the end of the Carboniferous (Benson & Upchurch 2013; Dunne et al. 2018), and the diversification of amniote herbivores (Pearson et al. 2013; Brocklehurst et al. 2020), lead to terrestrial tetrapod ecosystems being more completely separated from aquatic ecosystems, particularly in uplands where amphibians were rare (Eberth et al. 2000; Martens et al. 2005; MacDougall et al. 2017). This radiation and diversification also led to the establishment of the ecological limits that were maintained through the Permian and Triassic.

A second restructuring of tetrapod ecosystems appears to have occurred across the Cretaceous/Paleogene boundary. While there is no increase in the complexity of ecosystems at this time, Simpson’s diversity is significantly higher in the early Paleogene than through the Permian, Triassic and much of the Cretaceous. This fits with recent suggestions of a shift in absolute species richness at this time (Close et al. 2017; 2019). This shift in equilibrium may be related to ecological upheaval following the end-Cretaceous mass extinction, particularly the extinction of non-avian dinosaurs and subsequent radiation of mammals. Alternatively, it may be related to the easier diagnosability of mammalian fossils, particularly their teeth, relative to other tetrapods (Gingerich 1974; Szalay et al. 1987; Rowe 1988), which could be inflating observed mammalian diversity within communities.

The long-term stability and simplicity of terrestrial tetrapod communities contrasts with results seen in the marine realm, where a major shift towards more complex ecosystems occurred following the end-Permian mass extinction (Wagner et al. 2006). Although the simulation results obtained here imply caution should be taken in the inference of more complex RADs when sampling is sparse, there is no evidence for a reduction in sampling effort coinciding with the end-Permian extinction and persisting throughout the Mesozoic and Cenozoic (e.g. Benson et al. 2021). The shift towards more complex marine ecosystems at the end of the Paleozoic was attributed either to an increase in the diversity of ecological guilds (although there was very little change in the ecological guilds occupied before and after the extinction (Foster & Twitchett 2014)), or an increase in the diversity of organisms which contributed to building complex RADs. Mesozoic and Cenozoic marine ecosystems include a greater diversity of motile organisms, and reef-building organisms such as corals, which are more predisposed to structuring ecosystems and generating additional ecological opportunities (Bambach et al. 2002; Clapham et al. 2006; Wagner et al. 2006). Terrestrial vertebrate diversity, on the other hand, appears to be constrained by external limits, which would imply that tetrapod taxa generally cannot generate additional ecospace in the same manner as marine invertebrates.

It seems unlikely that the apparently consistent simplicity of terrestrial tetrapod communities relative to marine communities is due to lower sampling completeness of the tetrapod fossil record relative to the marine. Our simulations show that while incompletely sampling a community can result in a RAD from a simple ecosystem resembling one more indicative of a complex ecosystem, the inverse does not appear to be true. Incompletely sampling lognormal distributions, even to a coverage of 0.4 (the minimum cut-off for including a collection in our analysis), still predominantly fits models indicative of complex ecosystems (Fig. 4b). We may therefore take the apparent simplicity of tetrapod ecosystems relative to their marine counterparts as a biological signal.

Terrestrial tetrapod ecosystems appear to have been structured differently to post-Paleozoic marine ecosystems. There has been much discussion of how ecological processes contrast between the terrestrial and marine realms. For example, there is a greater diversity of species in terrestrial ecosystems (Vermeij & Grosberg 2010; Mora et al. 2011), a greater diversity of higher taxa in marine ecosystems (May 1994), a greater size-structuring of communities in the marine realm (an individual's size is a greater indicator of its ecological role (Webb et al. 2011)), and a greater abundance of herbivores in the marine realm (Hairston & Hairston 1997; Cyr & Pace 1993). A potentially important factor in the context of the results observed here is the shorter food chains found in terrestrial tetrapod ecosystems, with fewer secondary consumers feeding directly on each other (Hairston & Hairston 1993, 1997). There is a very distinct separation between small carnivores feeding predominantly on invertebrates and large macro-predators feeding on large-bodied prey (Carbone et al. 2007; Meachen-Samuels & Van Valkenburg 2009; Purwandana et al. 2016). Shorter food chains mean that species are less likely to be generators of ecospace in the same way that marine species can be.

Conclusions

The expansionist view of diversity accumulation posits that as species accumulate in a community, they create new niches that further species may “exploit” in a variety of ways. This hypothesis has been used to explain the apparent exponential increase in species richness through time. However, recent research is beginning to suggest that, in terrestrial tetrapods at least, the observed increase in species richness through time is likely an artefact of sampling and preservation biases. Instead, tetrapod diversity is characterised by extended intervals of stasis, indicative of ecological limits placed on species richness. The analysis of ecosystem structure presented here supports long-term ecological constraints on terrestrial tetrapod diversity. The relative abundance distributions of species are characteristic of ecosystems where limited ecological resources are divided between individuals, and these patterns remain consistent through most of tetrapod evolutionary history. There is a resetting of ecological limits across the Cretaceous/Paleogene boundary, but the structure of the relative abundance distributions does not shift at this time. These results reject an expansionist view of diversity accumulation, and instead indicate that ecological limits on terrestrial tetrapod diversity were established in the Carboniferous and remained in place through to the Cenozoic.

Acknowledgements

We sincerely thank all those who have contributed occurrence data to the Paleobiology Database. This is Paleobiology Database official publication number XXX. [Thanks to reviewers to be added]. B.J.A was supported by ETH+ grant (BECCY) funded by ETH Zurich. E.M.D was supported by a Leverhulme Research Project Grant (RPG-2019-365).

Competing Interests

We have no competing interests.

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Figures

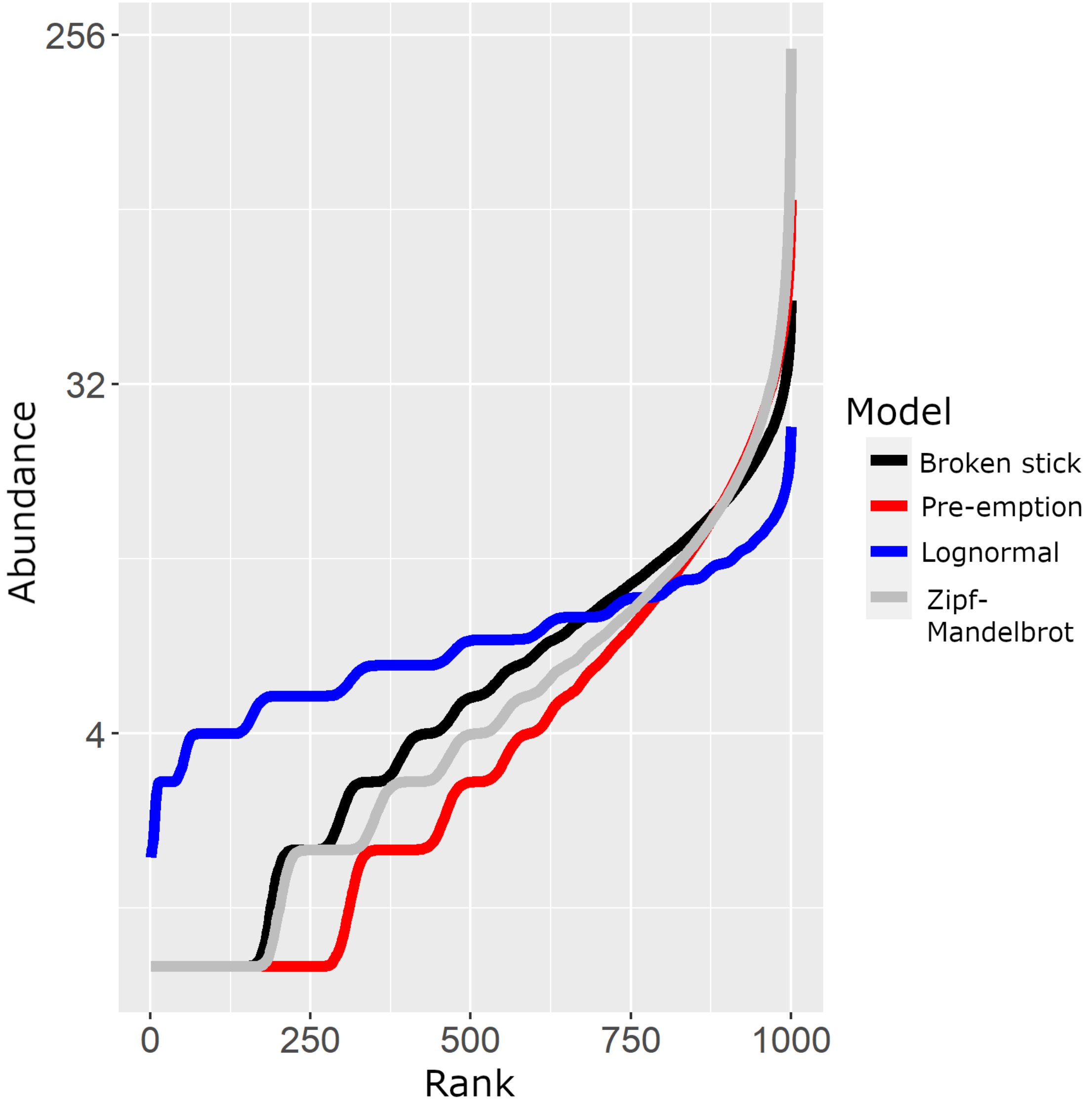


Figure 1 – Models of relative abundance distributions. Each line represents the mean of 1000 abundance distributions simulated using the R package mobsim, each with 1000 species and up to 7000 individuals.

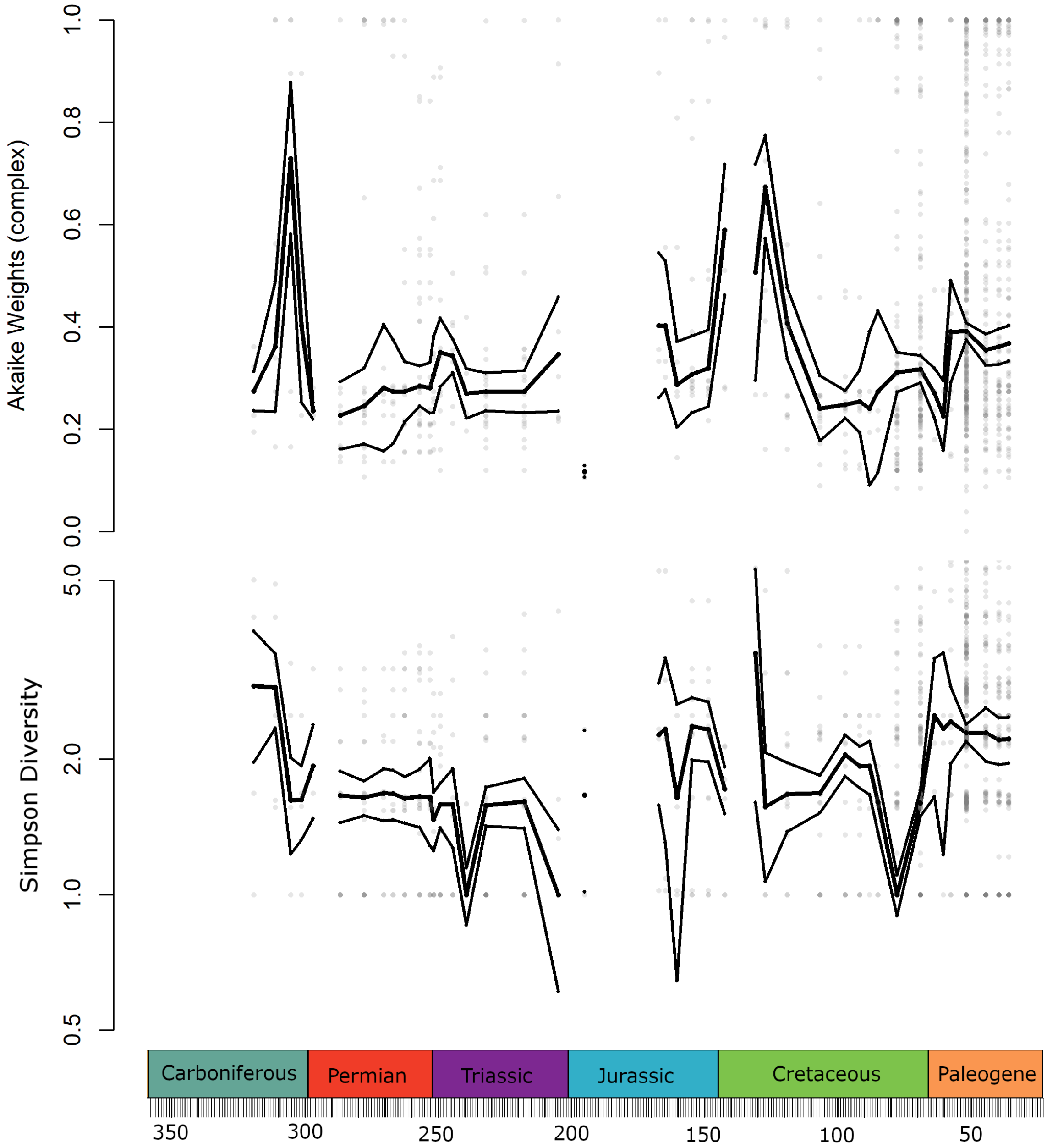


Figure 2 – A) The summed Akaike weights support for models indicative of "Complex" ecosystems (as defined in the main text) from each bioregion in each time bin. B) Simpsons diversity of bioregions in each stage. In both panels, each grey dot represents the value of a bioregion. The thick black line represents the median values in each stage, and the thin black lines represent one standard error around the median.

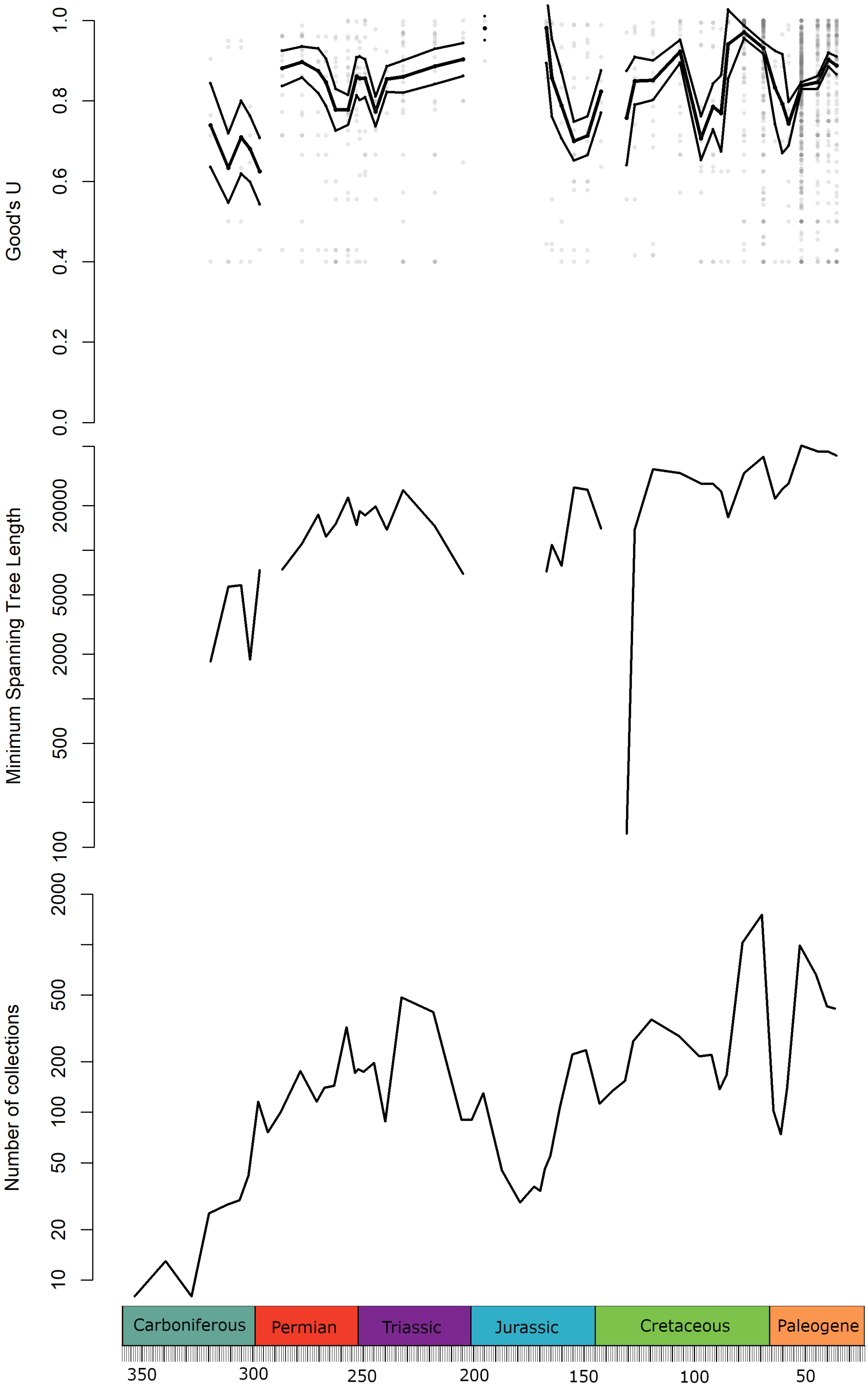
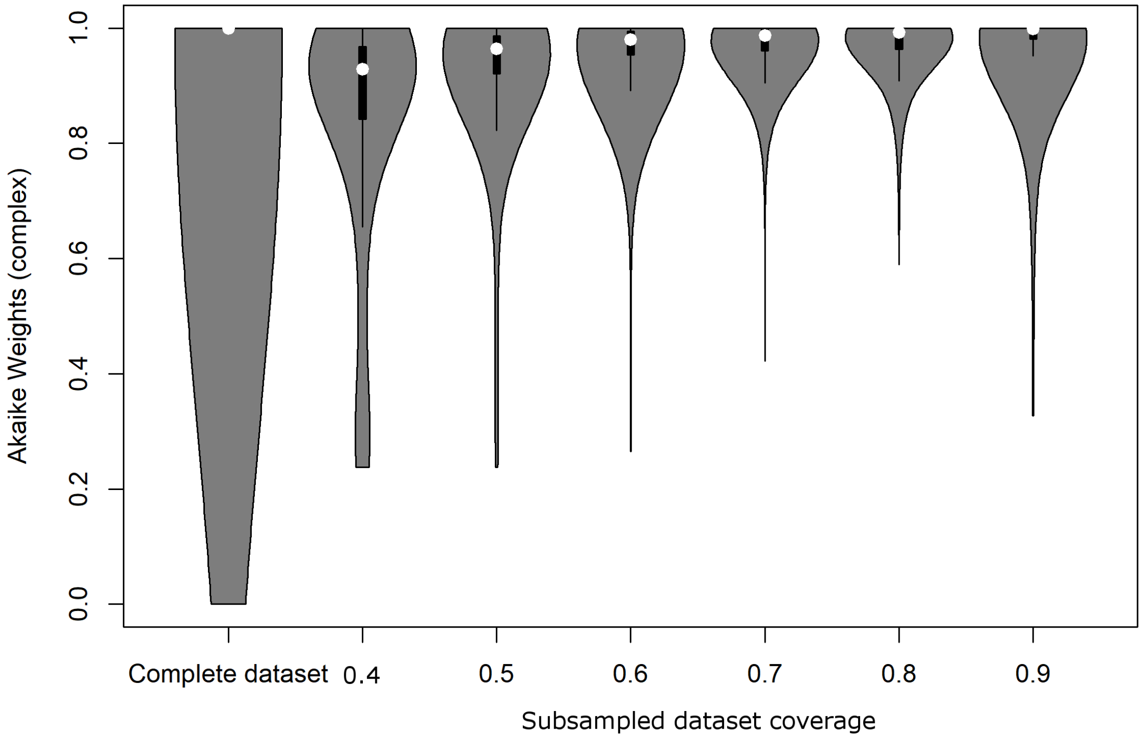
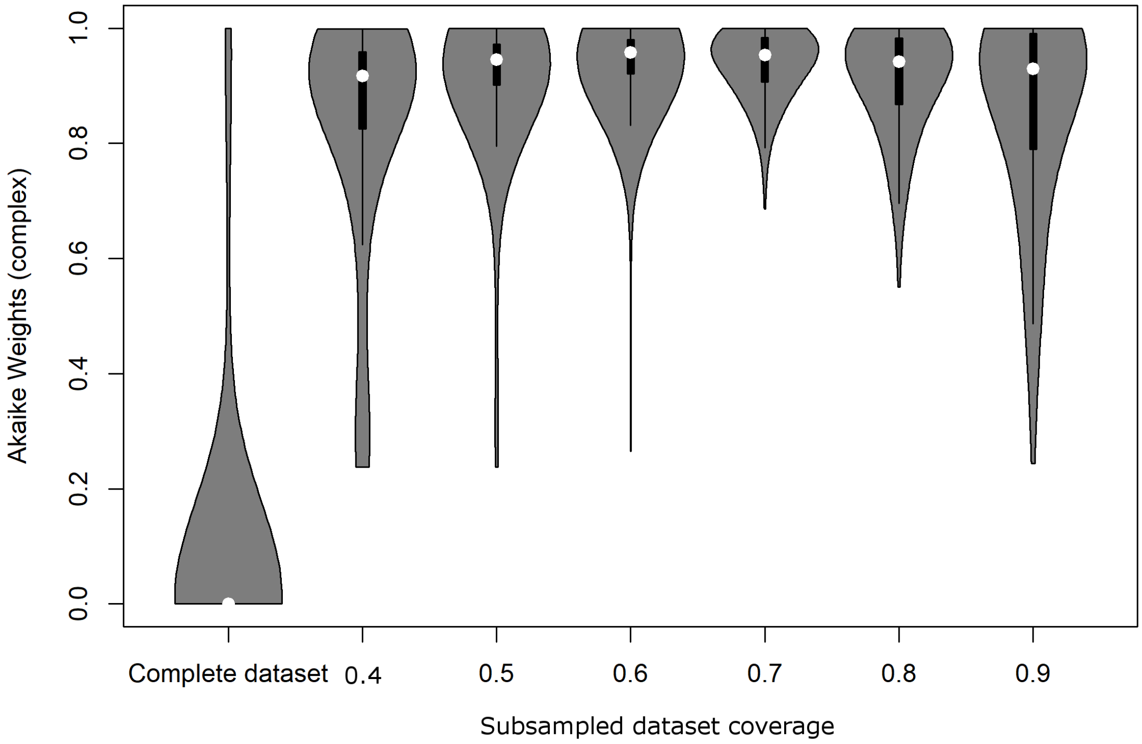

Good's U
0.0
0.2
0.4
0.6
0.8
1.0
Minimum Spanning Tree Length
100
500
2000
5000
20000
Number of collections
10
20
50
100
200
500
2000
Carboniferous
Permian
Triassic
Jurassic
Cretaceous
Paleogene
350
300
250
200
150
100
50

Figure 3 – Estimates of the quality of sampling of terrestrial tetrapods. A) The Good's U of each bioregion included in the analyses, estimating the coverage. Each grey dot represents the value of a bioregion. The thick black line represents the median values in each stage, and the thin black lines represent one standard error around the median. B) The minimum spanning tree length between each collection included in the analyses in each time bin, estimating the spatial extent of sampling. C) The number of terrestrial tetrapod-bearing collections in each time bin, estimating sampling effort.


Akaike Weights (complex)
0.0
0.2
0.4
0.6
0.8
1.0
Complete dataset
0.4
0.5
0.6
0.7
0.8
0.9
Subsampled dataset coverage


Akaike Weights (complex)
0.0
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Complete dataset
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0.6
0.7
0.8
0.9
Subsampled dataset coverage

Figure 4 – Simulation results showing the ability of model fitting analyses to distinguish between simple and complex models under incomplete sampling. A) Violin plots showing the summed Akaike weights of “complex” models when data is simulated under a lognormal (complex) model and then subsampled to different levels of coverage; B) Violin plots showing the summed Akaike weights of “complex” models when data is simulated under a Broken Stick (simple) model and then subsampled to different levels of coverage. Each violin plot represents results of 1000 simulated datasets.

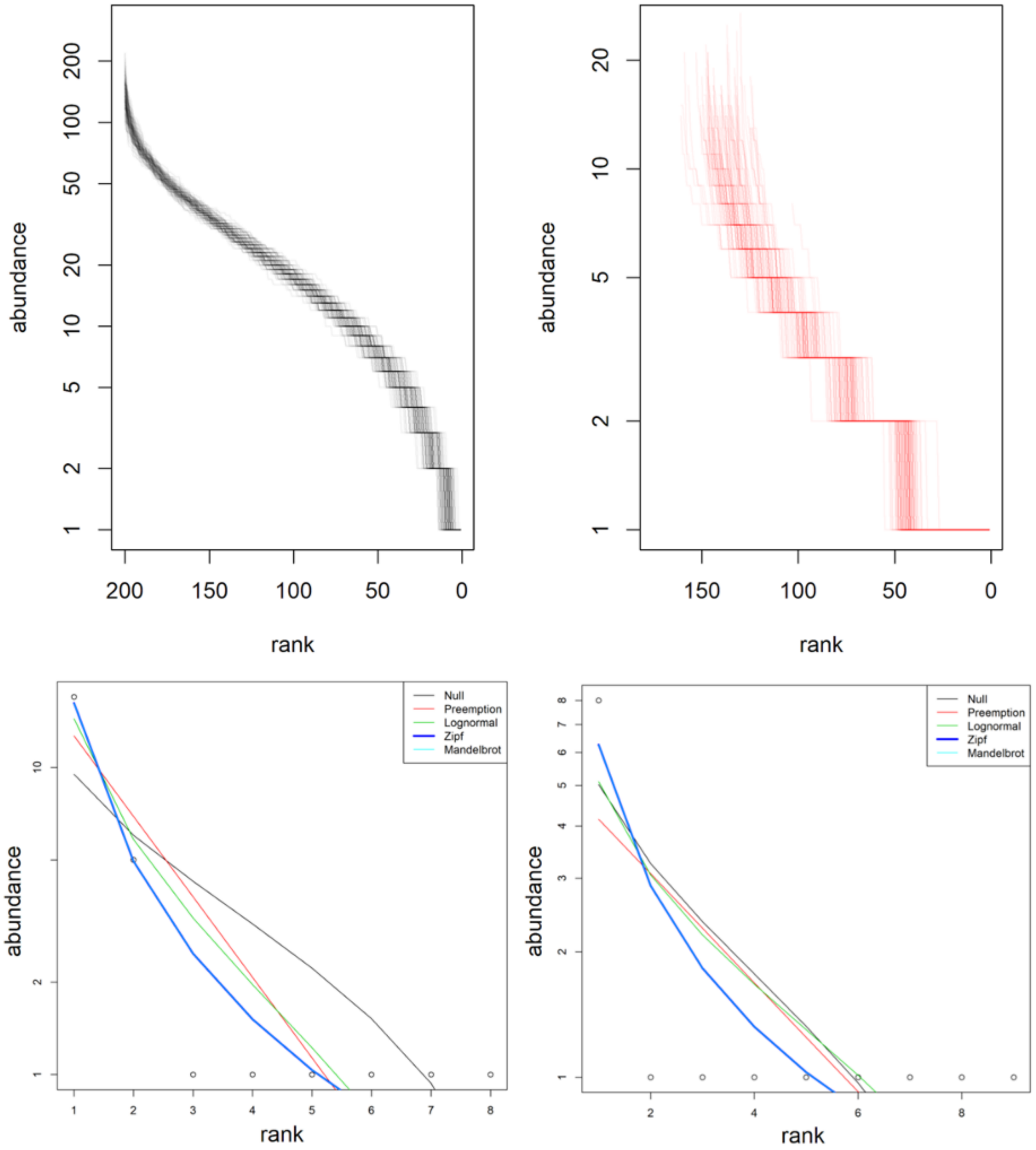

Figure 5 – A) 1000 relative abundance distributions (RADs) simulated using the broken-stick model (simple). B) The same RADs subsampled to a coverage of 0.9. C/D) The RAD of tetrapods from two Kasimovian localities, the Garnett Quarry (C) and Mazon Creek (D) and the curves representing the fit of different models to these distributions. The bold curve represents the best-fitting model (Zipf in both cases).