



Across space and time: A review of sampling, preservational, analytical, and anthropogenic biases in fossil data across macroecological scales

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ABSTRACT

Quantitative studies of fossil data have proven critical to a number of major macroevolutionary and macroecological discoveries, such as the 'Big 5' mass extinctions of the Phanerozoic. The development and easy accessibility of major meta-data sources such as the Paleobiology Database and Geobiodiversity Database have also spurred the widespread application of these data to testing ecological hypotheses at finer spatiotemporal and phylogenetic scales. However, preservational, sampling, and taxonomic issues, along with analytical decisions, can impact the degree of interpretative resolution and obscure biological 'signal' from error/bias-introduced 'noise'. The degree to which these factors can impact analytical interpretations is not well-documented in comparison to the scale of their application. Here, we review many forms of systematic bias that can creep into a paleoecological study, from the stage of data collection to the interpretation of analytical results. We provide two case studies where we artificially introduce such biases to previously-published datasets to illustrate their varying impacts on otherwise well-constrained data. The first case study focuses on the Cambrian Burgess Shale (*konservat lagerstätte*), and the second on bonebeds of the Cretaceous Belly River Group (*konzentrat lagerstätte*), with both representing highly-sampled, taphonomically-characterized, and spatiotemporally-constrained datasets developed through multiple years of sustained field collecting. In the former, we illustrate the impacts of collecting bias through quantitative comparisons of collected vs. discarded specimens over multiple field seasons and the impact of the loss of these data on ecological reconstructions and analysis. In the latter case study, we review the impact of preservational biases, differing approaches to their mitigation, and the impact of analytical decisions on ecological resolution. Lastly, we synthesize these case studies with our review of past approaches to propose a series of recommendations for future paleoecological and macroecological studies, emphasizing the continued importance of high-quality primary data and ongoing need for a first-principles approach to address existing issues of missing data.

1. Introduction

Macroecology refers to the ecology of large scales in terms of space, time, and number of species considered (McGill, 2019). While this definition seems to lack rigidity, its very flexibility is a strength, allowing the field to encompass topics that share an underlying theme of major change across three separate but related axes. Along the axis of space, macroecology concerns the distribution of organisms across landscapes, continents, or even the entire globe, and how these distributions are structured. The influence of environmental parameters,

species traits such as dispersal ability, and the role of competition are some of the major components which dictate the gradients and mosaics that define modern biodiversity (Connell, 1961; Paine, 1974; McCook et al., 2001; Darling et al., 2012; Markey et al., 2016). The recognition of metacommunity dynamics (Leibold et al., 2004) and the role of neutral processes in community structure (Hubbell, 2001; Holland and Sclafani, 2015; McGill et al., 2016) can be seen as some of the major insights from the spatial axis of macroecology. From a temporal standpoint, macroecology concerns how species interactions and distributions have changed over geologic timescales. Extinction, speciation, range shifts

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and fluctuations in community structure across thousands to millions to hundreds of millions of years are the causative factors behind modern day species distributions (Benzie, 1999; Klaus et al., 2012). Species ranges and community composition as dictated by major allopatric barriers, such as the formation of the Panama isthmus (McCartney et al., 2000; Rocha et al., 2008) or the complex events involved in the formation of mountain ranges (Hazzi et al., 2018), are obvious results of processes that can only be appreciated from a macrotemporal perspective.

The axes that define the scope of macroecology by their own nature underscore the relevance of paleoecology to robustly understanding the principles that govern species interactions and distributions. Most species that have ever existed are now extinct. Therefore, the only direct way to observe major changes in species distributions and interactions over a macroecological timescale is through an investigation of the fossil record. These reconstructions have revealed fundamental macroecological patterns that would be otherwise impossible to predict. Notable examples include the 5 major mass extinctions (Raup and Sepkoski, 1982) that have occurred throughout the Phanerozoic (in addition to another 13 other major extinctions which may meet the same criteria; (Bambach, 2006)), explosive patterns of diversification (Servais et al., 2010; Erwin et al., 2011), the relatively recent development of the modern latitudinal diversity gradient (Fenton et al., 2023), and continent-scale biogeographic distribution events such as the Great American Faunal Interchange (Marshall et al., 1982).

These paleoecological reconstructions hinge on large, quantitative studies of fossil databases tailored to uncovering specific biotic patterns in Earth's history. Before meaningful and accurate analyses can be performed, such databases must be carefully vetted to accommodate the many forms of common bias that affect any paleontological study. Some of these biases impact the fossil record at large scales, and others at the scale of individual localities or specimens (which themselves can then accumulate and impact at larger scales). At the broadest scales are common biases in the fossil record such as the temporal bias towards more complete fossil records in younger vs. older rocks (the 'Pull of the Recent'; Raup, 1972; Jablonski et al., 2003), and the related effects of major differences in the amount of fossil-bearing rocks preserved through time and across environments ('geological megabiases'; Barrett et al., 2009). Related to these factors are the wide range of sources of bias that impact the preservation of individuals, assemblages, and communities. These can include taphonomic factors such as the selective decay of soft-tissue organisms from communities (Sansom et al., 2010; O'Brien et al., 2014; Nanglu et al., 2015), as well as differential rates of preservation based on composition, shape, or type of fossil and its relation to the depositional setting (Dodson, 1971; Brinkman et al., 2004). Other taphonomic factors include the effects of time-averaging, transport distances, and local environmental effects impacting preservation potential (Behrensmeyer et al., 2000; Bath Enright et al., 2021), and substantial (as much as 10-fold) size-biases that can vary in impact across depositional settings (Benson, 2018; Brown et al., 2013a, 2013b; Brown et al., 2021). Harder to quantify, but potentially as significant, are the anthropogenically-induced biases introduced by collections methods which may be optimized for goals other than a robust paleo-community reconstruction (Whitaker and Kimmig, 2020), and the cumulative effects that these sorts of sampling biases can have when combined with the spatial and temporal heterogeneity of the fossil record (Benson et al., 2022).

It may be argued that the potential confounding effects of these biases are mitigated over large spatiotemporal scales, and in general that sufficiently large datasets may overcome minor errors in their constituent sources (Fan et al., 2014). Indeed, the advent of meta-databases such as the Paleobiology Database have made such studies more approachable than ever, and have yielded significant insights into the macroecological trends and their drivers. However, great care must be exercised when using these types of datasets that aggregate data from multiple sources. Factors ranging from depositional setting to species

identification to sampling methodology can significantly impact our attempts to infer important ecological patterns such as species turnover, ecological structure and niche partitioning (Brown et al., 2013b, a). This is particularly true when the uploading and vetting of data to meta-databases is on a voluntary basis, which may lead to uneven representation of taxa, localities, or time periods. Analyzing such data without relevant expert collaborators on specific localities or taxa requires caution in order to disentangle genuine biological or geological signal from unrecognized database bias. Further complicating matters is the difficulty in quantifying the magnitude and directionality of bias in our reconstructions without accurate baseline models or datasets. To that end, there is a growing consensus among many researchers that in order to meaningfully test paleoecological hypotheses relevant to our understanding of biodiversity change, biotic-abiotic interactions, and community dynamics, we require: 1) quantitative datasets with high temporal and spatial resolution, 2) good stratigraphic control, and 3) constrained or homogeneous biases, which 4) have undergone rigorous taxonomic evaluation (Zhao et al., 2013; Price, 2018; Chiarenza et al., 2019; Cullen et al., 2020; Dean et al., 2020; Nanglu et al., 2020; Maidment et al., 2021).

While a number of these issues have been raised in individual studies or systems (e.g. Badgley, 1986; Bartels et al., 1992; Brinkman, 1990; Cleary et al., 2015; Sakamoto et al., 2017; Plotnick et al., 1988; Plotnick et al., 2016; Kosnik et al., 2011; Tomašových and Kidwell, 2010a; Valentine et al., 2006; etc.), or in other broad reviews in decades past (e.g. Behrensmeyer et al., 2005; Kidwell, 1985; Kidwell and Flessa, 1995; Kidwell and Behrensmeyer, 1993, etc.), a renewed review and discussion of these myriad sources of bias is necessary. The vast expansion of analytical options in recent years, and increasingly easy access to massive databases for meta-analyses, represent critical tools to expand the possibilities of hypothesis testing, but they also come with drawbacks. Chief among these is that a researcher can now perform a methodologically sophisticated paleobiological study of a given time, location, or taxonomic group without any particular expertise on the system in question, the biases associated with the assemblages from where those fossils were collected, how to mitigate these biases, or the pre-existing literature for that system/sub-field. This can lead to analyses suffering from a series of critical biases which impact the results, but which may not be known to or noticed by the researcher.

In this paper, we provide a review of many of the most common and serious biases impacting paleocommunity and macroecological data from the fossil record. We do so by first taking two recently published datasets of well-preserved and carefully curated fossil assemblages and simulating the effect of common paleontological biases (ie. collection biases, sampling biases). We then analyze these datasets using standard paleoecological methods (ie. multivariate ordination) and compare our results with the original studies in which they were published. These case studies underscore how relatively small decisions in sampling regime and analytical method can result in major changes to pattern inference.

Both datasets for our case studies are drawn from fossil localities of exceptional, albeit differing forms, of preservation. The first is the middle Cambrian Burgess Shale of Canada, a world-famous example of a *konserverat lagerstätte* (Caron and Jackson, 2008), which preserves a nearly unparalleled richness of articulated soft- and hard-bodied fossils in extremely fine detail. The second case study dataset comes from a series of vertebrate microfossil bonebeds sampled from the Late Cretaceous Belly River Group of Alberta, and in contrast represents *konzentrat lagerstätte* (Rudkin and Young, 2011), preserving high abundances of disassociated skeletal remains from a range of fossil groups across a spatiotemporal and environmental gradient.

Finally, we provide suggestions for best practices for making robust and generally applicable conclusions about macroecological patterns and processes in terms of data assembly, appropriateness of scale, and analytical method. Often the simplest and most effective remedy to insufficient data is to collect more until the hypotheses of interest can be

meaningfully tested at scales relevant to those at which these ecological/evolutionary/environmental processes operate. This may seem somewhat glib as a solution, or unsatisfactory for those wishing to analyze a particular question immediately, but it may also be the unfortunate reality that certain hypotheses in certain systems cannot be robustly tested until more primary data are collected. Despite these limitations, it is true that simulations and extrapolations can help to frame predictions for eventual direct testing when more robust primary data are available (further outlined in Box 1).

Overall, we hope that these case studies, reviews, and subsequent discussion will serve as a guide for paleontologists and ecologists to thoroughly consider the potential sources of bias in data, and how to mitigate them, before drawing broad conclusions when incorporating fossil data into their analyses. More broadly, we hope that it will spur discussion and collaboration between both groups, as a comprehensive macroecological picture can only be developed through a robust integration of both types of data. This latter point is of particular relevance given the increasingly common overlap between fossil and modern data in research programs (Dos Reis and Yang, 2013; Nanglu et al., 2015; Pyron, 2015; Cullen et al., 2020; Fabre et al., 2021), with conservation paleobiology being a particularly relevant example (Dietl and Flessa, 2011).

2. Case Study #1: the Burgess Shale

2.1. Preservation biases and the Burgess Shale

The majority of fossil localities in the paleontological record are dominated by biomineralizing taxa, whether typical marine “shelly assemblages” of animals like brachiopods, crinoids and molluscs, or the bones and teeth of vertebrates. This most readily fossilizable record of diversity through deep time is most tractable for assessing macroecological and macroevolutionary patterns at large, coarse temporal scales, and it remains foundational for understanding the fundamental structure of life’s evolution on the planet (Raup and Sepkoski, 1982; Sepkoski, 1988; Alroy et al., 2008). However, this fact does not detract from the importance of *lagerstätte*, exceptional localities which often include soft tissue preservation, which are often excluded by design from such studies in order to not bias general trends. Instead, such sites provide a more complete picture of the total biodiversity and paleoecological structure of ancient communities than would otherwise be possible.

Few periods record such an abundance of *konsevat lagerstätte* as the Cambrian (Butterfield, 1995; Gaines, 2014; Van Roy et al., 2015), with the possible exception of the Ediacaran which presents a unique taphonomic mode due to the widespread microbial mats of the period (Lafamme et al., 2013). Consequently, they have had a disproportionately large impact on understanding Cambrian diversity than is true of most periods. This fact becomes ever truer each year, as more Cambrian *lagerstätte* are discovered (ie. Du et al., 2020), increasing the geographic and temporal scope of our window into Cambrian paleoecology. However, the most holistically analyzed Cambrian *lagerstätte* remains the Burgess Shale of Canada, which has remained unrivaled in intensity of study since its discovery over 100 years ago (Caron and Jackson, 2008; O’Brien and Caron, 2015; Nanglu et al., 2020). Further returns to the Burgess Shale have underscored its vast untapped potential, as new localities such as the Marble Canyon are discovered, yielding thousands of new specimens and potentially dozens of new species (Caron et al., 2014; Nanglu et al., 2020). However, in order to fully appreciate the magnitude of insight which sites such as the Burgess Shale can provide, a robust, quantitative understanding of how it differs from more common, shelly-fossil-only-preservation conditions is necessary.

In his seminal work on the community structure of the “Phyllopod Bed” of the original Walcott Quarry, Conway Morris estimated that shelly taxa which would be preserved in typical conditions constituted only 14% of the site’s total generic diversity (Conway Morris, 1986).

Such a reduced fauna, representative of the vast majority of Cambrian sites, is dominated by animals such as brachiopods, hyoliths and a diversity of trilobites. This value has continued to be cited in considerations of the taphonomic bias implicit in studying paleocommunities (Shaw et al., 2020), but significant updates have been made to our understanding of the Burgess Shale beyond the Phyllopod Bed. Caron and Jackson (2008) expanded the scope of the Walcott Quarry from a 2 m sampling of strata to a 7 m sub-section with centimetre-scale stratigraphic data collected for all specimens. Additional robustly sampled localities have since been described, including the Tulip Beds (O’Brien and Caron, 2015), the Raymond Quarry located 20 m directly above the Walcott Quarry, and the aforementioned Marble Canyon (Nanglu et al., 2020). Together, these 4 localities, which share a broadly similar preservational setting (Butterfield, 1995; Gaines et al., 2012; Gaines, 2014) include a total of 77,179 specimens representing 234 species-level taxa, and were recently analyzed together to produce the most comprehensive paleoecological study of middle Cambrian ecological dynamics (Nanglu et al., 2020).

Our first goal was to investigate the extent to which these data might differ from those under which only shelly fossils are preserved, and by proxy the magnitude of difference in the ecological conclusions we would draw from a Cambrian soft-tissue *lagerstätte* versus other fossil assemblages. To do so, we removed all species from the Nanglu et al. (2020) dataset that are unlikely to preserve without the exceptional conditions of Burgess Shale type preservation. This includes vermiform taxa such as polychaetes, priapulids, and hemichordates, as well as lightly sclerotized arthropods like radiodonts. While the latter groups may preserve in *lagerstätte* with lower preservational quality than the Burgess Shale, such as the Spence Shale or Weeks Formation (Lerosey-Aubril et al., 2018; Whitaker and Kimmig, 2020), they are still uncommon in the vast majority of Cambrian sites.

The result of these analyses is a reduction in species number from 234 to 37, and of specimen abundance from 77,179 to 18,581; proportional reductions of species diversity and abundance by approximately 84% and 76%, respectively (Fig. 1; supplemental file 1). This reduction in diversity incorporating taxa from all 4 sites roughly mirrors the

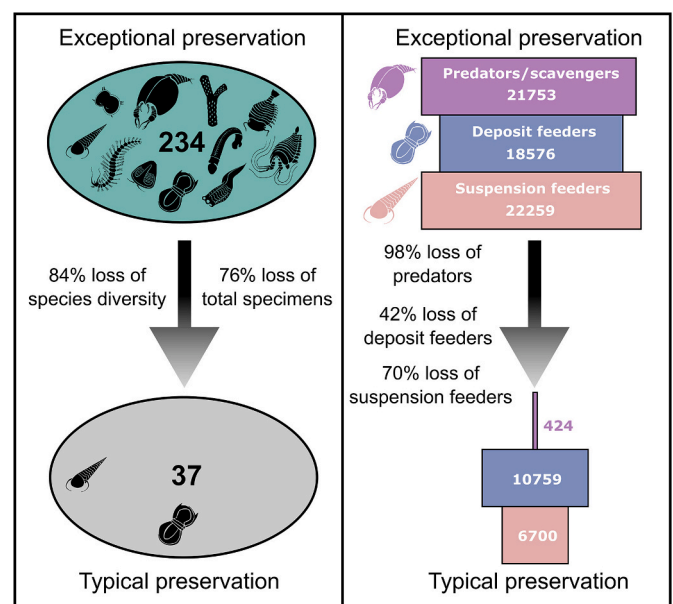


Fig. 1. A comparison of how the diversity and trophic structure of the Burgess Shale would differ in conditions of typical shelly preservation. The total species richness from (Nanglu et al., 2020) reduces from 234 species to 37, a roughly six-fold drop in diversity. A reduction in the abundance of predatory, lightly skeletonized (ie. non-trilobite) arthropods results in a community composition more heavily weighted towards epibenthic suspension and deposit feeders.

estimate made by Conway Morris based on a limited sampling of the Walcott Quarry. This lends further credence to a consistency across the most studied Burgess Shale sites in terms of preservation quality. It is notable, but not surprising, that the total loss of diversity exceeds that of specimens, reflecting the selective loss of rare taxa.

From an ecological viewpoint, macrofaunal predators and scavengers see the biggest loss in total abundance. This drop is largely driven by small arthropods, which are generally inferred have a predatory or scavenging trophic mode based on limb morphology, such as *Liangshanella* (Nanglu et al., 2020). Deposit feeders are least impacted, reflecting the large variety of benthic taxa with robust exoskeletons, such as trilobites, inferred to be deposit feeders.

2.2. Collections bias – the Marble Canyon case study

Marble Canyon is the most significant major fossil locality discovered from the Burgess Shale in decades (Caron et al., 2014). Field collection of fossils from Marble Canyon were conducted by Royal Ontario Museum teams in 2012, 2014, and 2016, yielding a total of 21,661 specimens from strata 0.98 m below the Eldon Formation-Stephen Formation contact point to 5.20 m below the contact point. This makes Marble Canyon the second most comprehensively sampled Burgess Shale locality, after the original Walcott Quarry (Caron and Jackson, 2008). Most crucially for this current study is that detailed data were taken on all non-collected specimens (including stratigraphic occurrence information) before they were discarded, allowing for a case-study investigation of the effects of anthropogenic selection bias on a museum collection.

In the description of the Marble Canyon fauna, Nanglu et al. (2020) divided the Marble Canyon quarry into 10 cm thick intervals of strata, termed bedding assemblages, in order to assess patterns of temporal change in the community. In essence, these bedding assemblages constitute mixtures of communities over the course of hundreds of years; a snapshot in time from a geological perspective. To further remove potential sources of bias, bedding assemblages with fewer than 299 specimens observed were removed from all analyses, yielding a dataset of 16,438 specimens across 10 cm thick bedding assemblages. This dataset can be thought of as the closest view we can get to the “true” diversity and temporal dynamics of the Marble Canyon paleo-community, considering: 1) the relatively low potential for specimen loss due to decay (Caron and Jackson, 2006; Nanglu et al., 2015); 2) the comprehensive sampling of both “museum-worthy” and discarded material; and 3) the removal of undersampled bedding strata from the dataset to mitigate potential sources of sampling bias when analyzing turnover patterns.

This dataset also allows us to explore how anthropogenically induced sampling bias might influence paleocommunity analyses based solely on already collected museum specimens by creating a matrix exclusively using the non-collected specimens from the Marble Canyon bedding assemblages already analyzed in Nanglu et al. (2020). This resulted in a final not-collected species occurrence matrix of 10,111 specimens, representing 24 unique taxa (‘sampling bias dataset’ tab in supplemental file 2). We then subtracted this matrix from the “true” community dataset (published in (Nanglu et al., 2020) to yield a new dataset that simulates typical sampling bias that might be present in a paleontological collection (‘comparison’ tab in supplemental file 2). We then performed cluster analyses on the “true” matrix and the “biased” matrix using both abundance (Morisita-Horn) and presence/absence (Jaccard) indices, to compare how the effects of sampling bias influence our conclusions regarding temporal ecological dynamics. In essence, what these sets of data treatments and analyses allow us to do is compare how a typical museum collection from a given locality might differ from the total diversity of specimens that were originally at that site but not exhaustively sampled.

Using Morisita-Horn, our true dataset recovers three major clusters, representing three major faunal types in Marble Canyon: a suspension

feeding, lophophorate and hemichordate dominated upper fauna (cluster F1); a predatory arthropod dominated middle fauna (cluster F2); and a deposit feeding arthropod dominated lower fauna (cluster F3) (Nanglu et al., 2020; Fig. 2A). Notably, these three clusters contiguously recapitulate the stratigraphy of the quarry, and each cluster is mutually exclusive on any non-adjacent strata. This pattern shifts subtly but importantly when performing the same analysis with our sampling-biased dataset. First, F1 incorporates more assemblages in total, representing an additional 30 cm of strata, one of which is disjunct from the others (level 370; Fig. 2B). Second, level 480 is now included in F2, where before it was the uppermost level of F3 (Fig. 2B). These two differences appear minor, but can easily change how we interpret temporal gradients of species turnover in Marble Canyon. First, the sampling-biased dataset homogenizes the community overall, resulting in a greater imbalance in the sizes of the three clusters. Second, by introducing non-adjacent strata into F1, we may interpret community assembly as more temporally variable, rather than the initial interpretation of largely stable community structure with rare but major perturbation. Third, there is a large area of undersampling between strata 430–480, which led to these strata not being included in the originally published multivariate analyses (Nanglu et al., 2020). The true dataset recovers the strata above and below this boundary to be significantly different in composition, an intuitive result as we cannot discriminate what ecological dynamics occurred throughout the 50 cm of undersampled strata. Using the sampling-biased dataset, we instead recover strata 480–490 as being similar in composition to F2, which may prompt an interpretation of the undersampled intervening strata as also being consistent in composition with a typical F2 assemblage.

Using Jaccard, our true dataset cluster analysis is broadly similar to that of the Morisita-Horn cluster analysis (Fig. 2C). The only significant difference is the clustering of strata 360–370 in F1 rather than F2. Presence/absence metrics are more sensitive to the distribution of rare taxa, thus a slightly less stratigraphically cohesive result is unsurprising. When we perform this analysis using the sampling-biased dataset, F1 also includes the significantly disjunct strata between 420 and 430 and 480–490. This is a marked difference from the “true” pattern, and may logically prompt an inference of repeated returns to an F1 community structure over long timescales. Knowing that this pattern is not supported based on both the Jaccard and Morisita-Horn analysis of the true dataset underscores that sampling bias not only effects our interpretation of turnover patterns in a paleocommunity study, but can have differential and more significant impacts depending on the choice of ecological metric. These ideas are further expanded after our second case study below, specifically in the Discussion sub-sections concerning the importance of data vetting and the choice of appropriate metrics.

3. Case Study #2: vertebrate microfossil bonebeds in the Belly River Group

3.1. Preservational biases in vertebrate fossils and the utility of microfossil bonebeds

There are multiple types of vertebrate fossil assemblages in terrestrial fluvio-deltaic settings, with varying preservational conditions, ranging from isolated fossils to vast bonebeds, with the latter representing a form of *konzentrat laggestätte*.

Isolated fossils and skeletons, and in particular well-preserved and/or complete specimens, have the potential to provide critical anatomical information useful for testing phylogenetic, biomechanical, life history, and other hypotheses. However, isolated specimens are effectively point samples, temporally, as other isolated specimens collected even a few metres above or below another in fluvial strata may be from tens to hundreds of thousands of years apart in time (Kidwell and Flessa, 1995; Behrensmeyer et al., 2000; Mallon et al., 2012; Brown, 2013). In contrast, bonebed assemblages, whether formed via sudden mass-death events or time-averaged attritional accumulation, can provide the

sample sizes, and often the temporal resolution, necessary to examine ecological and evolutionary hypotheses within extinct species at a scale approximating the population- or community-level (Eberth and Getty, 2005; Brinkman, 2014; Chiba et al., 2015; Eberth, 2015). A sub-type of these assemblages, and the primary focus of discussion of this section, are vertebrate microfossil bonebeds (VMBs). These sites represent concentrations of hundreds, often thousands, of individual bones, teeth, and scales deposited attritionally over geologically-brief periods of time (i.e. 100 s – 1000s of years) in low energy wetland, pond, or lake settings (Eberth, 1990; Rogers and Brady, 2010; Rogers et al., 2017). Due to their differing preservational conditions, VMBs lack the substantial (often 10-fold) taphonomic bias against the preservation of small specimens (Brown et al., 2013a; Benson, 2018) present in many other terrestrial fossil assemblages, and have played a critical role in our understanding of small-bodied taxa in coastal-floodplain paleocommunities, often being the main source of fossil biodiversity data for small mammals, lizards, amphibians, and fish, while also still containing fossil materials from larger taxa (Brinkman, 1990, 2014; Peng et al., 2001; Brinkman et al., 2004, 2005, 2017; Neuman et al., 2005; Brown, 2013; Gates et al., 2015, 2019; Carrano et al., 2016; Cullen et al., 2016). VMBs have played a crucial role understanding paleocommunity structure and dynamics (eg. Brinkman, 1990; Brinkman et al., 2004; Sankey, 2008; Gates et al., 2010; Carrano et al., 2016; Cullen and Evans, 2016). and have been used in paleoecological analyses using stable isotopes (e.g. Fricke and Pearson, 2008; Fricke et al., 2008; Cullen et al., 2020, 2022, 2023).

While VMB assemblages do not represent a single point in time, as an individual skeleton or a catastrophic mass-death assemblage would, and while a time-averaging on the order of hundreds to perhaps thousands of years is not ideal if attempting to reconstruct a community that is directly comparable to ‘snapshot’ biodiversity measures of modern ecosystems, this type of assemblage provides appropriate resolution for inter-community comparisons. In contrast, biostratigraphic faunal assemblage zones of dinosaurs in the Dinosaur Park Formation (a formation within the Belly River Group, and one of the best sampled units of dinosaur-bearing rocks in the world) each typically span hundreds of thousands of years, with ~5–20 dinosaur species per bin represented by one to several dozen specimens each (Mallon et al., 2012; Cullen et al., 2021). Most database-derived studies of tetrapod biodiversity patterns are performed at the sub-Stage- to Stage-level (i.e. time bins of varying durations, typically ~1–10 million years each) despite frequently possessing levels of standardized species diversity per Stage bin that are similar to those present at the level of a single assemblage zone (~600 k year duration) in the Dinosaur Park Formation example (e.g. Brusatte et al., 2015; Mannion et al., 2015; Dunhill et al., 2016; Close et al., 2019; Condamine et al., 2021). This is not mentioned as a criticism of these coarser studies, but rather to underscore the considerably finer temporal resolution and larger sample sizes afforded by VMBs, a degree of resolution generally only exceeded by rare *konserverat-lagerstätte* such as the Cambrian-aged Burgess Shale (as mentioned above) or, in terms of vertebrate- or dinosaur-hosting sites, localities such as the Jurassic-aged Solnhofen Limestone or Cretaceous-aged Jehol Biota (Sankey, 2008; Oreska et al., 2013; Gilbert et al., 2018). Nonetheless, systematic sources of error and preservational artefacts discovered when analyzing such sites might reasonably be expected to increase in magnitude as data compilations increase in spatiotemporal scale (Tomašových and Kidwell, 2010b).

3.2. Preservational, data-treatment, and analytical biases – case study of Belly River Group VMBs

A critical consideration when using VMB data are the various biases that exist favouring or opposing the preservation of particular taxa and/or elements in these sites. Due to a suite of taphonomic and other preservational biases, the taxonomic and abundance makeup of a given VMB cannot necessarily be assumed to be a faithful sample of the biotic community from which it was derived (Fig. 3) (Hadly, 1999; Terry,

2010; Behrensmeier and Miller, 2012), and thus the raw number of specimens per taxon (NISP) will provide a distorted view of community structure that often over-inflates the abundance of taxa based on their relative rates of fragmentation (Badgley, 1986; Brinkman, 1990). However, the attritional nature of these bonebeds and the broad diversity of species and elements being preserved can lead to an over-representation of rare-taxa and introduce subjectivity when applying ‘minimum number of individuals’ (MNI) approach to quantification (Badgley, 1986). Data processing approaches designed to account for the greater likelihood of particular types of elements being preserved when compared to others, such as ‘minimum number of elements’ (MNE) (Badgley, 1986; Brinkman, 1990) or various single-taxon correction factors (Brinkman, 1990; Milligan and Bamforth, 2021), may provide some mitigation of preservational biases, but also cause subjective observer-introduced biases. For an extended discussion of these considerations and their associated trade-offs, see supplemental file 5, which also contains additional numerical comparisons concerning related to these preservational biases (also tabulated in supplemental file 3). Ideally, attempts to remove or mitigate biases in these data should endeavour to be as universal/consistent in their application as possible, rather than trading one form of subjective bias for another.

Consequently, the most frequently used approaches to addressing this issue are to transform the raw count data to presence-absence occurrence data, or to examine them in a ranked or relative abundance context (Fig. 3). The former approach reduces potential bias by removing differences in abundance entirely, which greatly restricts the level of ecological resolution and hypothesis-testing possible (He and Gaston, 2000a, 2000b), but has the advantage of facilitating comparisons at coarser spatiotemporal scales and emphasizing diversity changes in rare taxa. A ranked or relative abundance approach, in contrast, emphasize a comparative approach based on isotaphonomy across sites. Ranked abundance, as the name suggests, ranks the taxa in a sample by their raw or corrected abundances (e.g. MNI, MNE, etc.), and facilitates comparisons between sites while also reducing the likelihood of the signal of rare-taxa being swamped out by highly abundant taxa (Brinkman, 1990; Tomašových and Kidwell, 2009). Relative abundance converts the raw abundances into their proportional abundances at a given site. These can then be used in inter-site comparisons to examine biotic changes within and between communities without the loss of ecological resolution associated with occurrence approaches. However, rigorous relative abundance comparisons depend on sites having both similar taphonomic profiles and robust sampling efforts (Blob and Fiorillo, 1996; Moore et al., 2007; Moore and Norman, 2009). While those two issues also exist for occurrence-based samples, their impacts are more pronounced in abundance-based samples given the higher resolution nature of the data. Thankfully, taphonomic consistency is generally expected based on current models of VMB formation (Rogers and Brady, 2010; Rogers et al., 2017) and can be tested for via specimen/grain size profiles (Blob and Fiorillo, 1996; Brinkman et al., 2004; Cullen et al., 2016), with robust sampling also easily satisfied in most cases due to the densely fossiliferous nature of most VMBs (Rogers et al., 2017). As a result of this, however, the relative abundances of sites forming under substantially different conditions (i.e. those that are not isotaphonomic) should not be considered directly comparable, nor should the relative abundance pattern of a single VMB in isolation be considered as directly representative of the original biotic community in anything but a very general sense.

To provide an illustration of the differences in interpretive power possible between occurrence and relative abundance approaches, even in a comparatively ‘best-case’ scenario for fossil vertebrates where sampling is spatiotemporally-constrained and sample sizes are robust, we perform UPGMA cluster analyses of site-taxon associations on a modified and updated version of the VMB dataset from Cullen and Evans (2016). This dataset (supplemental file 4) contains 48 VMB sites, with 55 identified taxa, and ~ 75,000 specimens, sampled throughout the roughly 3 million year span of the Belly River Group of Alberta, with

sites concentrated in two geographic sampling regions along a roughly 100–200 km north-south transect (Dinosaur Provincial Park and around the Milk River near the Montana border). See supplemental file 5 for additional information on the geological setting and paleoenvironments of the Belly River Group. Occurrence data were transformed using the Jaccard index, and abundance data with the Morisita-Horn index. The latter dissimilarity index (alongside other indices such as percentage-difference [i.e. Bray-Curtis]) is well-suited for examining community size, structure, and composition in sites of potentially uneven or imperfect sampling (Chao et al., 2006; De Cáceres et al., 2013; Schroeder and Jenkins, 2018). Conceivably, both sets of analyses would recover identical patterns if the additional information provided by the relative abundances of taxa are uninformative of general ecological patterns. However, disagreement between the metrics in a situation where sampling effort is robust and biases are minimal or constrained would reveal underlying inadequacies with a presence/absence approach, and suggest it is providing a resolution that is unsuitably coarse for testing many types of ecological hypotheses.

Results of the case-study cluster analyses are plotted in Fig. 4. In addition to the primary results of the cluster analyses (i.e. site clustering based on occurrence or abundance compositions), paleoenvironmental data and stratigraphic positions are provided to examine the resulting clusters and their correspondence to other data from the localities. Relative abundance-based clustering results in sites groupings based on major community differences (largely based on taxonomic abundance associations related to environmental conditions) and tracks these distinctions both temporally and geographically across the sampled interval. As these VMB assemblages primarily record gradational changes in community structure and often share a majority of taxa, occurrence-based cluster analyses can only recover the most discrete and binary differences (e.g. near total faunal turnovers in fully marine vs fully terrestrial conditions), and broadly mismatches all intermediate sites. Indeed, the occurrence results even lead to mismatches in which VMBs from nearly fully marine/estuarine communities (C1 & C5) are clustered as more similar to VMBs from fully inland/terrestrial ‘endmember’ communities (C3) than they are to VMBs from the same communities (C1 & C5). In contrast, only minor-mismatches occur in the relative abundance clusters, relating to transitional community/environmental intervals before and after the ‘end-member’ inland community present during the middle interval of the Belly River Group, and otherwise are able to discern changes in community structure across the sampled environmental shifts and temporal interval.

4. Discussion

4.1. Data collection, vetting and taphonomic considerations

As demonstrated by our case studies above, even seemingly minor decisions made at all stages of a paleoecological project have the potential to significantly impact the results and subsequent interpretation of biological processes. The first, and arguably most crucial, stage is the data acquisition itself. A recent study (Whitaker and Kimmig, 2020) used the Kansas University Spence Shale collection to demonstrate the myriad ways in which anthropogenic biases can affect the collection efforts. Most critically, the authors point out that we can logically expect rare species to make up a disproportionately large amount of collections based on both research and exhibit interests. For this reason, among others, trying to census museum collections from even well sampled localities without understanding the details of the sampling regime the collectors used is problematic. These authors further noted that these issues made a comparison of the Spence Shale collection to an idealized, holistic sampling regime that better reflects the “true” original community impossible. We were able to accommodate for this with our Marble Canyon dataset by keeping comprehensive stratigraphically controlled records of all non-collected specimens.

We found that this simulation altered the observed pattern of

temporal diversity change in the Marble Canyon fauna. These differences, while seemingly minor, would lead to a significantly different interpretation of the temporal community dynamics of the Marble Canyon ecosystems. First, the F1 community type, dominated by epibenthic suspension feeders, appeared more temporally long lasting than in the true dataset. This change was partially driven by the removal of large amounts of small, predatory or scavenging arthropods such as *Liangshanella* that mostly found their way into the ROM collections by being co-preserved with species of more focal interest. Second, the sampling biased analyses also suggest a patchier temporal pattern of faunal change than the true dataset. Based on these two relatively minor seeming changes, one could conclude that the Marble Canyon biota was typified by similar temporal community dynamics as the original Walcott Quarry (Caron and Jackson, 2008): patchy re-occurrence of the same faunal types in temporally disjointed stratigraphic subunits. One might also infer that Marble Canyon was largely dominated by an epibenthic suspension feeding fauna, with predatory arthropods and nekto-benthic scavengers dominating relatively few strata, as opposed to the more even distribution of three faunal types revealed by the true dataset. These changes in broad scale interpretation based solely on the exclusion of commonly discarded taxa highlights how decisions on what specimens to collect and record made in the field have downstream consequences for the recognition of biological signals in the resultant dataset. This is doubly true in situations where collections-biases cannot be quantitatively assessed, as was the case in the Whitaker and Kimmig (2020) case study, and as is often true when using metadatabases without consulting locality experts. A clear, but not necessarily easy, recommendation is to collect data on all non-collected specimens with the same rigour as those that are eventually brought back to the lab, and include them in analysis with equal consideration.

Taphonomic bias is a more likely form of error to be reported than anthropogenic bias. However, being aware of the omnipresence of preservational biases on your dataset and having adequate methods to account for them are different issues. The distortion of original biotic information can come in many forms through the preservation process, with the idiosyncracies of the taxa being sampled resulting in heterogeneous capture: animals with escape capabilities and those that live above the sediment water interface are less likely to be captured and fossilized in marine settings. Differences in the recalcitrance of individual tissues are complex and reliant on many factors (such as ambient chemistry at the site of preservation) but broadly speaking, animals with “tougher” tissues (i.e. biomineralizing elements, collagenous tissues, sclerotized skeletons, etc.) are more likely to fossilize (Nanglu et al., 2015; Parry et al., 2018), regardless of their prevalence in the biosphere. It is also worth noting that these factors are not mutually exclusive and can, therefore, produce additive biases (Alroy, 1998; Brown et al., 2013b, a; Evans et al., 2013; Nanglu et al., 2015; Benson, 2018; Saleh et al., 2020; Shaw et al., 2020). Our data (Fig. 1) reinforce the importance of lagerstätte like the Burgess Shale for reconstructing ancient communities holistically, as they can preserve a much more comprehensive picture of the original fauna. However, even sites as exceptional as the Burgess Shale cannot be taken for granted as perfect representations of the original community composition. Saleh et al. (2021) have provided data suggesting that the Walcott Quarry has an overriding bias towards preserving endobenthic taxa, and Bath Enright et al. (2021) provide data from flume experiments suggesting that the body plans represented at Walcott Quarry may have been able to endure significant transport from their original environment. The implication is that the taxa found co-preserved at Walcott Quarry may not represent a single animal community, but rather an assemblage of communities across an original spatial gradient which have been averaged together.

Vertebrate microfossil bonebeds (VMBs) provide a strong example of the above phenomenon. By having original taxon counts distorted by the heterogeneous taphonomic effects specific to each animals’ anatomy, reconstructing the original paleocommunity becomes problematic. In the case studies we described several common methods for

accommodating these biases, and caution the importance of comparing relative differences between sites of equivalent taphonomic bias to track genuine patterns in community dynamics, while avoiding descriptions of any individual VMB assemblage as being a true representation of original community composition (and restricting broad community descriptions of isolated sites to general patterns/occurrences). However, despite these issues, VMBs remain among the highest resolution sources of ecological data (decades to centuries) that are abundantly available in

the terrestrial vertebrate fossil record. They provide a critical data source for testing a range of paleoecological hypotheses that are difficult to address when assemblages have coarser temporal resolution and more complex taphonomic biases. We recommend that future studies make broader use of data from VMBs (or similar assemblages) and ideally integrate those data with high-resolution sampling of isolated skeletons and macrofossil bonebeds in order to form temporally- and spatially-constrained baseline reconstructions of biodiversity and community

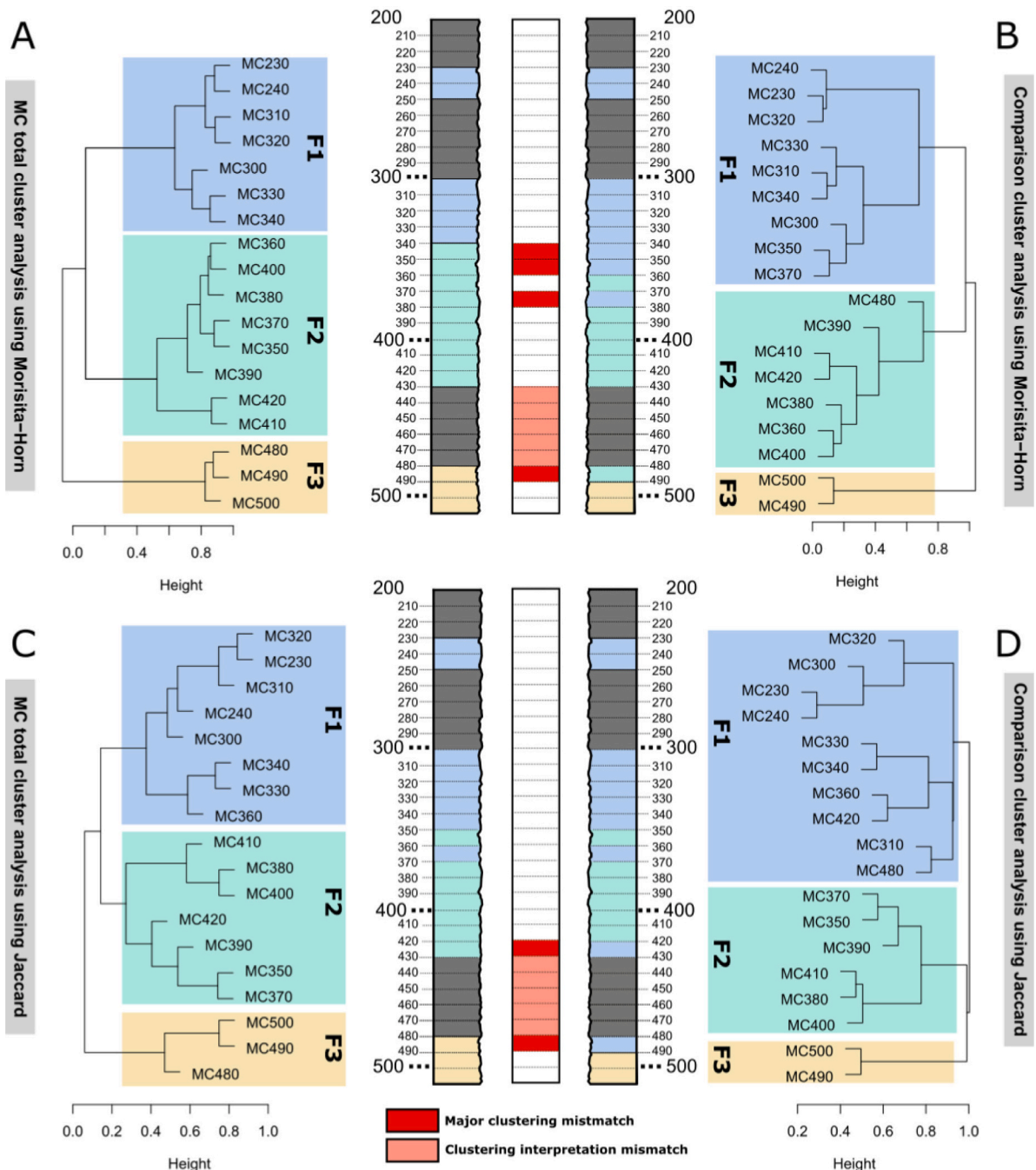


Fig. 2. Cluster analyses comparing how relative abundance (A,B) and presence/absence (C,D) metrics perform on the Burgess Shale dataset from Nanglu et al., 2020 (A,C) compared to the induced sampling biased dataset developed herein (B,D). Stratigraphic columns next to the cluster analyses indicate which bedding assemblages belong to which faunal cluster. Nanglu et al. (2020) identified three major faunal types based on cluster analysis and correspondence analysis, F1, F2 and F3. These clusters are defined by the predominance of suspension feeding, predatory, and deposit feeding species, respectively. The central column highlights in red the differences in clustering that occur when the simulated dataset is used, which introduce both artificial temporal patchiness as well as a greater degree of stratigraphic homogenization. Pink bedding assemblages represent strata that were not analyzed directly but which may have different temporal dynamics inferred when using the sampling biased dataset. Principally, much of the lower strata of the quarry would be interpreted as belonging to faunal type 1 rather than 3 when analyzed using the induced sampling bias dataset. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

structure (Pearson et al., 2002; Badgley et al., 2008; Eberth et al., 2013 as potential examples of this approach). Where these baselines exist, further patterns can be quantified and more complex hypotheses tested, building further through the integration of community ordinations, isotopes, disparity studies of the ecomorphology, etc.

Both of our case studies and the pertinent literature cited underscore a relatively simple point that cannot be overstated in importance: in the absence of a time machine, we may never recover the full picture of the paleocommunities of interest. Taphonomic bias will always seep in, whether through time averaging, the mixture of original spatial gradient signals, or the breakdown and loss of specimens. It is therefore important when generalizing the spatiotemporal diversity patterns found in exceptional fossil assemblages to macroecological trends that these inferences are tempered by a thorough consideration of taphonomy. It is also important to keep in mind that just because the record is not perfect does not mean that we can learn nothing from studies of the fossil record, and indeed it is quite the opposite. Taphonomic phenomena, despite complicating our attempts to understand ancient ecosystems, also inform us about differences in the original environments of different sites and their relation to biodiversity (Brett and Baird, 1986; Peters and Foote, 2001). But because various different preservational filters are acting (and interacting) in the fossil record, we must remain vigilant for their impacts on our interpretations and diligent in our selection of

datasets and analytical approaches when testing paleoecological hypotheses.

4.2. The right metric for the right question

As demonstrated in our case study comparative re-analyses (Figs. 2 & 4), even well-sampled data from sites of high temporal and spatial resolution produce less-informative ecological results if differences in the relative proportions of taxa are ignored and only their presence vs. absence is evaluated. The use of exclusively presence-absence data will highlight changes in the diversity of rare taxa and larger-scale ecological shifts, but will not detect the nuances of changes in relative proportions or gradual ecological changes. It therefore bears emphasizing that the exclusive use of presence-absence data when analyzing spatiotemporal trends in biodiversity (as is the case with many global-scale database-driven approaches) may lead to the interpretation of patchier, more fluctuating dynamics than actually occurred.

More broadly, it can be said that analyses dependent on datasets without strong temporal, spatial, or taxonomic resolution are more likely to suffer from serious issues impacting the interpretability and utility of their results, which in the worst cases can lead to situations described as ‘garbage in, garbage out’ (see Price, 2018; also echoed almost verbatim in an open peer-review document (Condamine et al.,

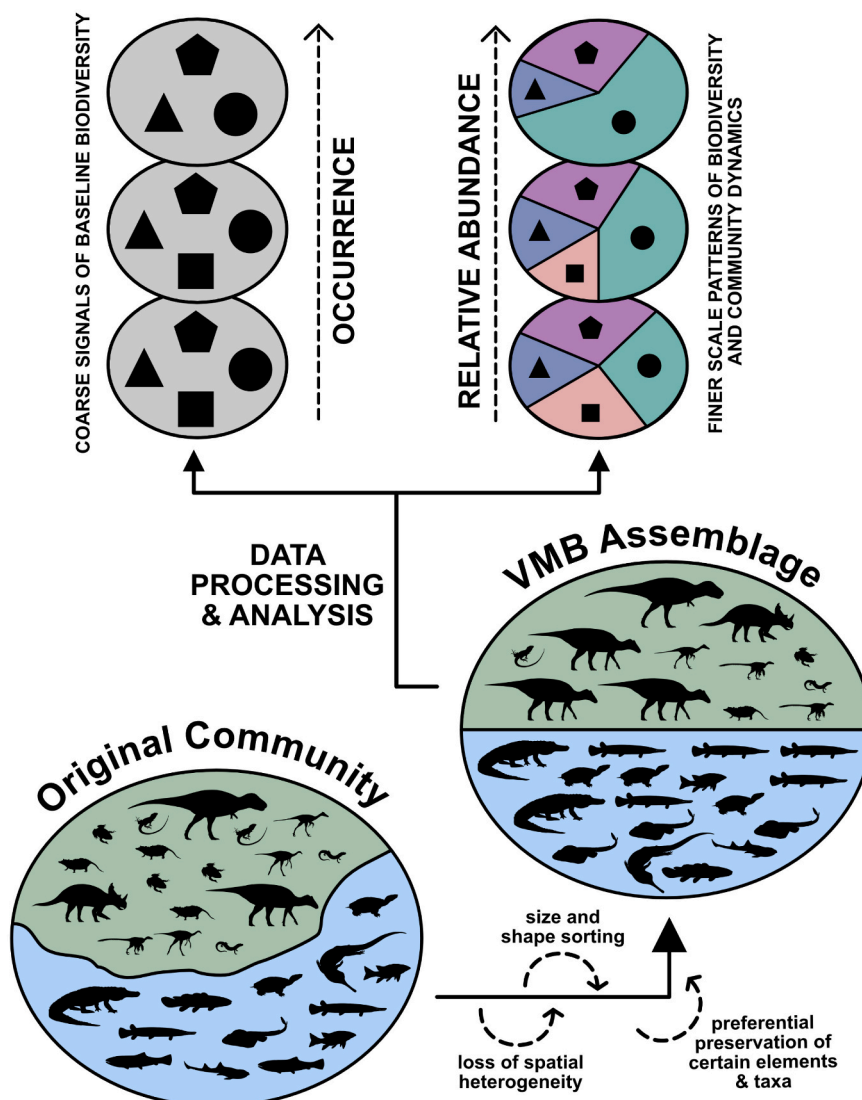


Fig. 3. Depiction of taphonomic filtering of vertebrate microfossil bonebed (VMB) localities, compared to original paleocommunity, and description of primary data processing methods to account for these preservational biases when performing community analyses using these assemblages. The transition from original community to preserved VMB assemblage results in a mixing of materials and loss of the original spatial heterogeneity of the taxa in the community. Similarly, various skeletal elements which are easily preserved (e.g. formed from enamel or enameloid/ganoine), within a particular size/shape range, and/or numerous within a single specimen (e.g. teeth of polyphyodont vertebrates, fish scales, turtle shell fragments, etc.) will likely be preserved preferentially and in greater abundance than delicate or rare materials. Consequently, the ‘raw’ abundances preserved in a VMB assemblage will be biased towards certain taxa when compared to their ‘original’ abundances in the biotic community from which the assemblage was derived. This is displayed in the figure in the proportional shift in proportion of silhouetted taxa. Two major forms of data processing for analysis are then shown. The first of which is the transformation of abundance data into occurrence data, which removes many biases related to differences in preservation potential at the cost of reducing the data resolution such that analyses are restricted to examining when taxa appear or disappear across multiple assemblages. The other major alternative is to transform the ‘raw’ abundance data into relative abundance data, which allows changes in community structure to be quantified between sites, but limits some of the interpretations possible at the scale of an individual assemblage. In both cases, a degree of taphonomic equivalency must be assumed (or tested for), as both the occurrence and relative abundance patterns can be impacted by major taphonomic differences between sites.

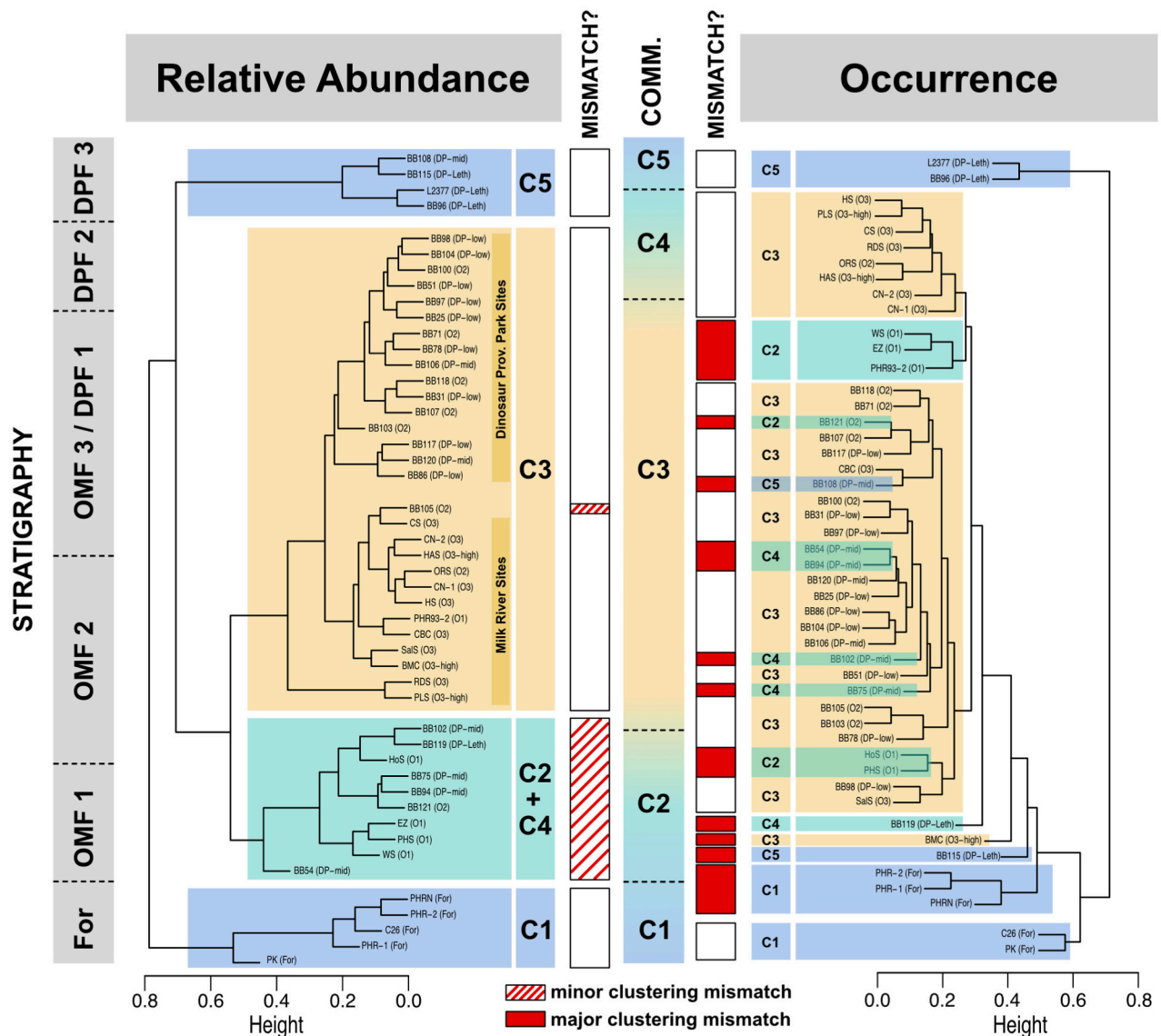


Fig. 4. Cluster analyses comparing levels of analytical resolution possible from abundance and occurrence treatments of original vertebrate microfossil bonebed (VMB) data. Relative abundance cluster results are listed on the left, and occurrence on the right, with central columns displaying the previously-identified community assemblages ('COMM' column in the figure, and C1-C5 for the specific community assemblages), as well as locations of mismatch between these community assemblages and the results of the individual cluster analyses. Community assemblages are: C1 and C5, strongly marine-influenced community assemblages, characterized by large abundances of chondrichthyans and limited numbers of amphibians, and distinguished from one another partially by taxonomic differences related to species which either disappear after the Foremost Formation or first appear within the Dinosaur Park Formation; C3, inland terrestrial communities, characterized by large abundances of amphibians and other terrestrial taxa and limited abundances of chondrichthyans, with some occurrence and abundance differences based on geographic sampling area; C2 and C4 are community assemblages which are transitional between the aforementioned 'end-member' communities of C1/C5 and C3, and typically are characterized by a mixture of amphibian and chondrichthyan taxa and a large abundance of aquatic taxa generally (see Cullen and Evans, 2016 for further information). Stratigraphic zonation within the Belly River Group, which is broadly consistent with, but not identical to, the community assemblage patterns, is noted on the far left of the figure. In the relative abundance cluster analysis, discrete differences in the marine-influenced intervals at the bottom and top of the Belly River Group are recovered as distinct clusters. Similarly, the transitional assemblages in the environmentally-transitional intervals of the lower Oldman Formation and upper Dinosaur Park Formation are recovered as a discrete cluster, with a minor mismatch in that the clustering algorithm cannot easily distinguish the transitional intervals before and after the fully-terrestrial communities of the middle interval of the Belly River Group. The fully-terrestrial community assemblages of the Belly River Group also cluster both as a single cluster, and contain two sub-clusters which relate to the geographic-sampling area from which they were collected (sites from Dinosaur Provincial Park in the north vs. Milk River area in the south). There is a single minor clustering mismatch here as well, with one site grouped in the Milk River sub-cluster when it was in fact sampled from the Dinosaur Provincial Park area (but is otherwise correctly clustered by community assemblage and paleoenvironmental associations). In contrast, the occurrence data provide a coarse approach to removing sources of preservational bias, resulting in near total loss of finer-scale environmental, community, or biogeographic signal (aside from fully marine vs fully terrestrial), and featuring multiple mismatches of sites when compared against known community associations and related paleoenvironmental, stratigraphic, and sampling location data. Specifically, in the occurrence analysis the marine-influenced sites do not form discrete, inclusive, clusters (as in the relative abundance analyses), but rather a grade of small clusters outside of the largest cluster (containing primarily the purely terrestrial sites). The central cluster in the occurrence analysis is primarily the terrestrial sites, but also contains multiple small clusters of transitional sites from the lower Oldman Formation and upper Dinosaur Park Formation, as well as individual sites from those intervals interspersed among the sites from the middle and upper Oldman Formation communities, and one of the 'end-member' marine-influenced community sites, while generally lacking the notable sub-clustering related to geographic sampling area.

2021 supplementary materials)). Indeed, data science studies concerned with 'Big Data' applications have cautioned about recognizing the limits of data 'repair' techniques and when additional primary data are required to avoid a 'garbage in, garbage out' situation (Baesens, 2014; Batareseh et al., 2020). While broad-scale database studies of the fossil record have been instrumental in building our understanding of major macroevolutionary patterns, biodiversity changes, and perhaps most significantly the 'Big 5' mass extinctions of the Phanerozoic (Raup and Sepkoski, 1982; Foote and Sepkoski, 1999; Alroy et al., 2008; Foote, 2016; Crampton et al., 2018), the quality of the data available, its applicability to particular questions, and the issues of sampling biases, resolution, and taphonomic effects must be carefully weighed when addressing hypotheses relating to finer-scale patterns and processes. This is particularly critical because issues of primary data insufficiency often cannot be truly fixed by post-hoc data processing, merely obscured or simulated, despite noteworthy attempts to deal with some of these issues (Lloyd et al., 2008; Foote, 2016). As our case studies (and other similarly high-resolution studies) demonstrate, there can be substantial impacts on results and to their interpretative value when one or more of these sampling, analytical, or data quality issues exists, even for otherwise high-resolution and well-constrained assemblages. If that is true in these comparatively 'best-case' scenarios, then the effects of similar biases will be even greater for less-constrained samples or when comparing broadly across the entire fossil record. In such cases it is doubly important to ensure dataset biases and data quality issues are effectively understood and mitigated when performing paleocological analyses. That being said, large-scale databases are undoubtedly useful, particularly when paired with modern data (Jones et al., 2019; Saupe,

2019), although their utility will vary considerably depending on the system (ie. groups of taxa, time period, consistency of comparison) in question. As noted earlier, while a very simple remedy conceptually, additional primary data collection remains an important step in situations where data quality issues are a problem, with a suite of other actions and recommendations also existing for situations of more intermediate data quality, as outlined in Box 1.

4.3. The right spatiotemporal scale for your question

The issues we have discussed and the case studies we have chosen intentionally concern short spatiotemporal scales (from a geological perspective). Our initial goal was to demonstrate how even small choices can affect datasets that have been thoroughly vetted by taxon and locality experts, collected holistically, sampled beyond the level typical of most paleontological studies, and with high stratigraphic resolution. However, it is clear that an overarching trend in paleoecology at the moment is to move beyond the level of describing regional- or locality-specific faunas in favour of demonstrating generalizable trends at global or continental scope over geologic time scales (despite many studies illustrating the spatial heterogeneity of sampling in large databases (Jones et al., 2021; Vilhena and Smith, 2013)). This is a noble goal, but the way in which it is pursued is critical. For example, applying methods suitable for describing short temporal-scale faunal changes to a larger dataset is not all that is required for an expansion of scope. Processes operating at local scales may either not be the same or as important at larger scales, or may simply be intractable to substantiate in most macro-paleontological datasets. Many sampling biases may also exist from

Box 1

Guidelines for project design

1. Collaborate with experts on your chosen system. These can be experts on specific taxa of interest, localities, or time periods. While this seems obvious, it can be tempting to cut out the middleman and use published data or meta-databases without consulting the expertise of specialists. We argue that while this might be most expedient, it can lead to an un-nuanced understanding of the underlying data, and ultimately flawed pattern inference. As importantly, specialist expertise may help distinguish between genuine phenomena revealed by the data, and statistical results that have little true biological significance.
2. Define concepts taken for granted. For example, within the context of your study, what constitutes a "community"? While these definitions may not make it into the manuscript, a strong philosophical basis for your project is the cornerstone of well-selected data and methods.
3. Choose a dataset appropriate for the question. Consider a priori questions such as: do the ecological processes that you are interested in operate at the spatiotemporal scale you are investigating?; can you collect data adequate to answer your question?; if not, what questions can be answered with the data available?
4. Scale back your conclusions when the data are not appropriate to a sweeping statement. This may be the hardest guideline to follow, as we are all operating under the constraints of an academic system that often encourages hyperbole. However, there is a difference between informed speculation (which helps drive the field forwards) and unsupported generalizations which obfuscate more reasonable conclusions.

How to ameliorate data- and method-related issues

5. For experts in specific taxa, localities, and time periods: collaborate with methods and analysis experts and innovators. When you become hyper-familiar with your system of interest, it can be tempting to think that you can discriminate patterns accurately without the need for new methodologies. We argue that while this might be expedient, it can lead to missing significant phenomena that can only be discerned with a more quantitative eye. As importantly, methods experts may bring entirely new ideas for questions that could not be pursued without their specialized skillset.
6. Vet your data. It can be difficult to just visually assess whether or not the data available is satisfactory for answering your questions. Applying methods to quantify sampling effort, or even simply considering sample size qualitatively, can prevent you from inferring patterns in datasets that are fundamentally inadequate to answer detect your phenomena of interest.
7. Use methods appropriate to the question. Aside from the considerations discussed in this paper (ie. presence/absence vs. abundance metrics), consider what methods may ameliorate issues in your data. For example, uneven sampling efforts might be improved by sub-sampling methods; under-sampling may be addressed with extrapolation.
8. Draw from new methodologies as appropriate. There is an understandable lag between new method development and adoption. However, this disconnect might be shortened through closer collaborative networks between system experts and methods experts (items 1 and 5). The cross pollination of ideas is one of the best safeguards against the many methodological pitfalls described throughout this paper.

locality to locality, over time, or from institution to institution that can bias attempts to integrate local data together for broader-scale analyses (Benson et al., 2022; Brown et al., 2013b, a; Panchen et al., 2019).

As an example, consider the question of competitive exclusion, the process by which some sets of conspecifics are excluded from a community through competitive interactions. Neontological data provide both laboratory and field based observations that suggest that this phenomenon can occur under select regimes conducive to high competition, for example, limited nutrient resources (Hardin, 1960) or access to space (Paine, 1974). It should be noted, however, that even in neontological datasets, competitive interactions can be both difficult to identify, occurring slowly, be scale-dependent, and/or seasonal/temporary in nature (Du Toit, 1990; Davies et al., 2011; Débarre and Lenormand, 2011; De León et al., 2014; Mateo et al., 2017; Yackulic, 2017). With the long ranging time series data available in the fossil record, it is tempting to explore the macroecological effects of competitive structuring over geologic time scales. However, how many datasets would pass the minimum threshold for being able to answer this question concretely? To identify competitive exclusion confidently, you must at minimum be able to demonstrate: 1) that two species co-existed spatially, 2) that two species co-existed temporally, 3) that two species either interacted directly or had significant niche overlap leading to competition, and 4) that resources in this zone of niche overlap are sufficiently limited to not permit long-term coexistence. In the absence of these criteria, the best we can hope for is illustrating patterns that are consistent with competitive exclusion, but which may also be explained by other hypotheses. The concept of clade competition (of which the authors contend that competitive exclusion is a subset) was discussed in recent reviews of the effects of biotic interactions in shaping biodiversity over time (Fraser et al., 2021; Strotz and Lieberman, 2023). They accurately point out that temporally continuous evidence of species interactions over large time scales is exceedingly rare. We agree with their advocacy for approaches that can identify such patterns in spite of missing data, however, we take some umbrage at the suggestion that these models actually “go beyond” more direct methods of examination. Rather, they can accommodate sub-optimal data parameters (i.e. non-continuous stratigraphic occurrence data), but there can be no doubt that similar models would be even more useful on idealized or at least more thoroughly-sampled datasets.

Many of the issues related to coarse temporal sampling that introduce bias into paleocommunity reconstructions are also present spatially. Continental to global scale meta-analyses must contend with non-uniform and non-random factors, potentially biasing both preservation as well as the evolutionary and ecological responses to biotic and abiotic influences (Upchurch et al., 2011; Brusatte et al., 2015; Butler et al., 2011; Benson et al., 2016; Close et al., 2017; Benson, 2018). These can be difficult to quantify when integrating a series of heterogeneous regional datasets to form a global data pool, and differing methodological decisions to mitigate these issues can variably help or hinder efforts to identify original biotic and abiotic patterns (Mannion et al., 2015; Dunhill et al., 2016; Benson, 2018; Maidment et al., 2021). These can lead to potentially contradictory conclusions from similar source data when differing mitigation/analytical approaches are used (Brusatte et al., 2012; Nórdén et al., 2018) or when data quality issues are unaddressed (Schroeder et al., 2021; Benson et al., 2022). The compounding nature of these varying preservational, sampling, and methodological issues further underscore the importance of additional analyses at regional spatial scales where these factors can be more directly accounted for and mitigated, prior to their inclusion into broader meta-analyses (Benson, 2018).

4.4. A fog of uncertainty, the human factor, and reasons for optimism

Doubtlessly, methodological advances and the development of meta-databases (Alroy et al., 2001; Fan et al., 2020) represent considerable promise for the future of macroecological studies. They constitute an

approach to understanding ecological processes over geologic time-scales and vast distances that can both reflect biological truth as well as increase the accessibility of large paleontological datasets for analysis and scrutiny. In addition, there are many simple, practical options for improving the quality of data analysis that require little more than forethought and care. We outline some of these in Box 1, which lists several approaches or guidelines for macroecological research from data collection to project design. Indeed, examples of research following these approaches, integrating multiple lines of evidence, and/or accounting for these various biases do exist (e.g. Benson and Upchurch, 2013; Chiarenza et al., 2019; Woolley et al., 2022, etc.) and demonstrate the value of investigations using robust fossil data. However, on a final note, we caution against any underlying assumption that our current, “basic” knowledge of the natural world is well understood enough that the next major advances must necessarily come from more sophisticated analyses or integration of already published data. That philosophy can easily lead to the dismissal of fundamental exploratory and descriptive paleontological work, including the detailed, stratigraphically and spatially constrained, studies that form the bedrock for understanding ecological dynamics over geologic time. To ground this argument in a more concrete example, the discovery of the Maotianshan Shale in China, arguably the most significant advance in our understanding of the Cambrian biosphere since the discovery of the Burgess Shale, could not have been easily presaged by a statistical or conceptual advance.

Equally importantly, what is known and published in the literature is a reflection of human history, not a perfect record of geologic history. Aside from the many taphonomic and collections biases we described above, it would be irresponsible to suggest that our best studied model systems are adequate for fashioning general rules about how species interactions and distributions have played out over the Phanerozoic. A recent study has demonstrated that roughly 97% of all the fossil occurrence data in the PBDB has been submitted by researchers from North America and Western Europe (Raja et al., 2022). Equally stark are the notably low numbers of fossil localities being published on outside of North America and Western Europe, with the exception of a few countries identified as “popular research destinations,” which requires other ethical and historical considerations in and of itself. In modern contexts, sampling regimes influenced by modern geopolitical boundaries (a natural consequence of performing field work) have been found to mischaracterize true diversity patterns (Murphy, 2021). It does not require a significant stretch of the imagination to extend this lesson to paleontological data, which is no less susceptible to sampling bias induced by political structures.

Further, a study on the “dark data” (accessioned but unpublished fossil data in collections) from nine institutions in California, Washington and Oregon found that there was a twenty three-fold difference in what has been collected versus what has been formally published and is available in the PBDB (Marshall et al., 2018). Combining this massive under-sampling of the world’s fossil record driven by socio-economic imbalance and exploitation with the sheer tonnage of rock already collected by museums that has yet to see the light of peer reviewed scientific study, one might ask: “What new analytical technique could possibly rival the insights of a comprehensive, collaborative, ethical, and direct accounting of the what has lived and died in multi-billion year history of eukaryotic life?” This is not an argument against new methods development or a dismissal of what they can provide. It is only advocacy for fundamental, first-principles-based observational and exploratory research not becoming extinct in an era of more sophisticated modelling. We should instead view these efforts as a golden opportunity for growth in our field. Encouraging funding for foundational, exploratory research and novel field collections need not detract from methodological advances. Rather, the two should move hand in hand, with new explorations leading to new theories to be validated with new methods, eventually leading us back to the natural systems that originally brought us to research. In this way, and if pursued in a manner that is equitable, observational and

exploratory science provides an exciting gateway for new researchers to indulge in their inherent love for the natural world.

Open research statement

Raw data for case study reviews were modified from Nanglu et al., 2020 and Cullen and Evans, 2016, and is provided for peer review, in the following repository: https://datadryad.org/stash/share/1_usQncHytrG-JjfJQdNdRacw2uT49cxcha4VDOn5qA. Data will be permanently archived in Dryad if the manuscript is accepted.

CRedit authorship contribution statement

Karma Nanglu: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Thomas M. Cullen:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.earscirev.2023.104537>.

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