DATA ARTICLE



BioDeepTime: A database of biodiversity time series for modern and fossil assemblages

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Abstract

Motivation: We have little understanding of how communities respond to varying magnitudes and rates of environmental perturbations across temporal scales. BioDeepTime harmonizes assemblage time series of presence and abundance data to help facilitate investigations of community dynamics across timescales and the response of communities to natural and anthropogenic stressors. BioDeepTime includes time series of terrestrial and aquatic assemblages of varying spatial and temporal grain and extent from the present-day to millions of years ago.

Main Types of Variables Included: BioDeepTime currently contains 7,437,847 taxon records from 10,062 assemblage time series, each with a minimum of 10 time steps. Age constraints, sampling method, environment and taxonomic scope are provided for each time series.

Spatial Location and Grain: The database includes 8752 unique sampling locations from freshwater, marine and terrestrial ecosystems. Spatial grain represented by individual samples varies from quadrats on the order of several cm^2 to grid cells of ~100 km².

Time Period and Grain: BioDeepTime in aggregate currently spans the last 451 million years, with the 10,062 modern and fossil assemblage time series ranging in extent from years to millions of years. The median extent of modern time series is 18.7 years and for fossil series is 54,872 years. Temporal grain, the time encompassed by individual samples, ranges from days to tens of thousands of years.

Major Taxa and Level of Measurement: The database contains information on 28,777 unique taxa with 4,769,789 records at the species level and another 271,218 records known to the genus level, including time series of benthic and planktonic foraminifera, coccolithophores,

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diatoms, ostracods, plants (pollen), radiolarians and other invertebrates and vertebrates. There are to date 7012 modern and 3050 fossil time series in BioDeepTime.

Software Format: SQLite, Comma-separated values.

KEYWORDS

deep-time, global, palaeobiology, species richness, temporal, timescale, turnover

BACKGROUND

One of the greatest challenges of our time is disentangling the multiple dimensions of biodiversity change and their drivers (McGill et al., 2015) across a broad range of timescales and charting a bestcourse forward in a biosphere strongly impacted by human activity (IPBES, 2019). To begin addressing this challenge, the neontological BioTIME database was published in 2018 after nearly a decade of data compilation efforts (Dornelas et al., 2018). BioTIME includes more than 12 million records of species presence and/or abundance from time series of at least 2 years in extent (duration) and has transformed our understanding of the impacts of humanity on biodiversity (e.g. Blowes et al., 2019; Dornelas et al., 2014; Gotelli et al., 2017). Although the temporal scope of BioTIME is exceptional, its records typically span only the last several decades, and only occasionally reach centennial extents. However, humans have been altering ecosystems for centuries and millennia (Ellis et al., 2013; Jackson et al., 2001; Koch & Barnosky, 2006; Lotze et al., 2006; Yasuhara et al., 2012), and ecological change has occurred for as long as life itself. Without data spanning longer timescales, it is difficult to disentangle anthropogenic drivers of biodiversity change from processes inherent to communities in the absence of human influence (Barnosky et al., 2017; Dietl et al., 2019; Dillon et al., 2022; Kiessling et al., 2023; Lewandowska et al., 2020; Smith et al., 2020; Yasuhara et al., 2020).

A long temporal perspective is necessary to understand the full extent of humanity's impact on the biosphere (Barnosky et al., 2017; Blowes et al., 2019; Dietl et al., 2015; Dornelas et al., 2014; Kiessling et al., 2023). Widespread changes in the range and abundance of species in marine and terrestrial environments are well documented (e.g. Antão et al., 2020; Dirzo et al., 2014; McCauley et al., 2015; Pauly et al., 1998), and projected rates of future extinction are high (IPBES, 2019; Pimm et al., 2014). Yet, the number of confirmed recent extinctions is relatively low (IPBES, 2019) and the observed species richness of local assemblages is surprisingly constant through time (Dornelas et al., 2014; Vellend et al., 2013, 2017, but see Gonzalez et al., 2016; Primack et al., 2018), despite high rates of community turnover (Blowes et al., 2019; Dornelas et al., 2014). The fossil record provides temporal context for contemporary biodiversity trends (Barnosky et al., 2017; Dietl et al., 2015; Dillon et al., 2022; Wolkovich et al., 2014; Yasuhara & Deutsch, 2022). Moreover, modern assemblage time series spanning only several decades are insufficient to capture the full extent of climatic impacts on biodiversity (Antão et al., 2020; Chavez et al., 2003; Kuwae et al., 2017; Valdés et al., 2008), which can operate on timescales

from a single year to millions of years (MacDonald et al., 2008; Mottl et al., 2021; Westerhold et al., 2020; Yasuhara et al., 2014; Yasuhara & Deutsch, 2023).

Longer time series are needed to answer pressing questions including whether the rate, magnitude and direction of modern change are anomalously high relative to natural variability in the fossil record (Lewandowska et al., 2020; Williams et al., 2021). Such time series are also needed to address issues of scaling effects. Comparisons of biodiversity patterns between relatively short historical timescales and longer geological timescales are complicated by the fact that rates appear inherently slower when viewed through a coarser temporal lens (i.e. larger temporal grain) or when viewed across larger time steps, a phenomenon that is known to affect the perception of Earth system change (Sadler, 1981), climate change (Kemp et al., 2015), species diversification (Henao Diaz et al., 2019; Louca et al., 2022) and extinction (Foote, 1994; Spalding & Hull, 2021). Although the greatest strength of the fossil record is arguably the fact that it documents changes in species, communities and ecosystems through time—which can be used as temporal context for modern biodiversity change—there has yet to be a community-driven effort to compile fossil assemblage records and combine them with neontological time series in a single database that spans clades, environments and, critically, temporal scales across many orders of magnitude. Combining data on these various aspects, as in BioDeepTime, will enable progress in addressing these priority questions and associated challenges.

The BioDeepTime database combines taxonomically well-resolved assemblage time series of at least 10 time steps from existing modern and fossil databases and from the primary literature. BioDeepTime builds on efforts to synthesize and curate modern and fossil assemblage time series with a high degree of taxonomic resolution and temporal certainty. This version of the new database is focused primarily on taxonomic groups well represented in existing databases like BioTIME (Dornelas et al., 2018), Neotoma (Williams et al., 2018), Neptune Sandbox Berlin (Renaudie et al., 2020) and Triton (Fenton et al., 2021). The BioDeepTime database was created from available data filtered according to criteria for inclusion that enabled the integration and comparison of modern and fossil biodiversity dynamics.

METHODS

BioDeepTime is a relational database (Smith et al., 2023b) created through a working group of the Paleosynthesis Project. Taxon records of presence and abundance are linked to additional tables providing

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context for each record (see Appendix S1, Figure S1.1). There are three nested levels of organization: record, assemblage sample and assemblage time series (Figure 1). Records are the finest resolution and indicate the observed presence, abundance (e.g. biomass, counts, percent cover) or relative abundance of a single taxon in a single sample of a time series. An assemblage sample (i.e. the observation of an assemblage) is composed of records that belong to the same sampling event with a constrained temporal duration such that all taxon records in a sample are considered to be of the same age. The amount of time contained in a single sample (i.e. temporal grain; Figure 1) may be on the scale of days or hours for some modern time series and up to tens of thousands of years in fossil time series (Table 1). The spatial grain of a sample is consistent within time series, ranging from cm² to ~100 km², but varies among time series due to factors including life history, underlying sampling processes and taphonomy.

Time series are internally consistent in sampling methodology, location (at time of sampling, rather than deposition) and taxonomy, but there is considerable variation across time series as sampling methods vary among practitioners working on different environments, timescales and taxonomic groups. At each organizational level, contextual variables are provided to facilitate the use of these data for community analyses (Figure S1). These additional variables include extended taxonomic information, references to original data sources, types of abundance units and uncertainties in age, among others. A congruence table is included in Appendix S1 to describe differences in variable names and content originating from the source databases (see 'Synonymy of sources' in Smith et al., 2023b).

2.1 Data acquisition

Data were compiled from BioTIME (Dornelas et al., 2018, queried June 2021), Neptune Sandbox Berlin (Renaudie et al., 2020, queried

October 2022), Neotoma (Williams et al., 2018, queried May 2022) and Triton (Fenton et al., 2021, queried December 2022; see Appendix S2 for information on database-specific queries). A single example time series each from the Paleobiology Database (PBDB, http://paleobiodb.org) and the Geobiodiversity Database (GBDB, http://www.geobiodiversity.com) were included to demonstrate future potential for database expansion. Additional data were aggregated from the literature, including modern planktonic foraminifera time series (from sediment traps-SedTraps, see Appendix S1: Appendix S2.2) and a new database called MARBEN (Tomasovych et al., 2022)-a compilation of marine benthic fossil assemblages collected in sediment cores containing ostracods, molluscs and foraminifera, mostly from the Pleistocene and Holocene (see Appendix S1: Appendix S2.3 for more information on MARBEN). Finally, two time series are included as 'Direct uploads' (see Appendix S1: Appendix S3.1), representing a pathway for inclusion of data that are not already tied to an existing database (e.g. from researchers in the scientific community). A list of the data sources is found in Appendix \$5.

The primary criteria for inclusion of data in BioDeepTime were established to create a database of high-quality assemblage-level records for time-series analysis, including accurate age estimates that will enable future analyses that could incorporate environmental data. The criteria were: (i) internally consistent taxonomy within a time series, (ii) original sampling conducive to assemblage analysis and internally consistent, (iii) minimum of 10 samples with unique ages and (iv) age estimates for samples at each time step were reported, or could be inferred from age controls provided, for example, samples in a fossil time series (see Appendix S3 for more detail on criteria). The first criterion of internally consistent taxonomy was imposed to mitigate the effects of variable taxonomic resolution across groups. As the intended biodiversity analyses of BioDeepTime are specific to individual time series (and not comparisons of taxa across

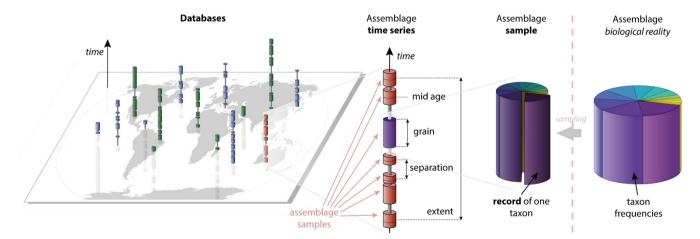


FIGURE 1 The BioDeepTime database includes assemblage time series from existing databases and the literature. Each assemblage time series is composed of multiple samples from biological assemblages, which are distorted by preservational, sampling and other processes. Within a sample, records (e.g. relative abundance, presence) for multiple taxa are included. Assemblage samples are characterized by an age and temporal grain (i.e. total time represented by the sample), with variable temporal separation between samples of different ages. Time series are characterized by their temporal extent (i.e. total duration) and other data including geographic location, taxonomic composition and environment.

TABLE 1 Approximate temporal grain (the amount of time represented in a sample) for time series, number of time series and number of samples from source databases included in BioDeepTime.

| Database | Approximate temporal grain | Comments | Number of time series | Number of samples |
|------------------------|--|--|-----------------------|-------------------|
| BioTIME | Minutes to days | Most records were collected in real time, with little temporal averaging | 6982 | 797,425 |
| Direct Upload | - | This group of time series will have variable temporal grain, as they are not derived from a single source (e.g. an existing database) | 2 | 239 |
| GBDB | 10 ³ -10 ⁴ years | Fossil records are based on section data and provide quality control at the level of bed-by-bed rock units | 1 | 33 |
| MARBEN | 1–10 ⁴ years | Some marine records are reworked more than others, resulting in a large amount of variation in the temporal grain in samples from this depositional environment | 257 | 13,812 |
| Neotoma | 1-10 ³ years | Most pollen records used here are from lake and mire sediments from the Quaternary, which tend to have sediment deposition times on the order of 0.1–50 years per cm, and a mode of 10 years per cm (Goring et al., 2012). Typical sediment sample size is 1 cm ³ | 1358 | 96,164 |
| Neptune Sandbox Berlin | 10 ³ -10 ⁴ years | Marine records are often reworked and low sedimentation rates in the deeper ocean can result in relatively large temporal grain in this depositional environment | 609 | 31,634 |
| Paleobiology Database | 10 ³ -10 ⁴ years | Records are from deeper in the fossil record where there are greatest uncertainties in temporal grain | 1 | 19 |
| SedTraps | Days to months | Time series are from moored sediment traps, which record export flux integrated over precisely controlled intervals | 30 | 1295 |
| Triton | 10 ² -10 ⁴ years | Marine records are often reworked and low sedimentation rates in the deeper ocean can result in relatively large temporal grain in this depositional environment | 822 | 44,685 |

time series), internal consistency in nomenclature within a time series was considered sufficient for inclusion—taxonomic nomenclature of the same group might differ among time series. Time series from most databases have ongoing updates and synonymizations of their taxonomy (e.g. BioTIME, Neotoma, Triton), and future versions of BioDeepTime will incorporate these as they become available.

The sampling standards used to ensure high-quality data for assemblage analyses likewise varied by taxonomic group, environment and timescale, leading us to use a broad criterion for inclusion conducive to assemblage analysis (i.e. individuals in a sample counted and identified)—to allow for this heterogeneity. For example, with planktonic foraminifera from Triton, a random sample of ~300 individuals from a larger sample are counted and identified to the species level. However, in fish trawls from BioTIME, for example, all individuals in a trawl are counted and identified to the lowest possible taxonomic level (e.g. genus level). Time series were required to have at least 10 samples with unique ages. Some sediment core samples had different depth values but identical age estimates; in these cases, we allowed for 10 samples with unique depths (instead of ages). There was no constraint on the temporal extent of a time series, which ranged from years to millions of years (Figure 3a,c). For modern samples extracted from BioTIME, date of observation is recorded. For fossil samples, ages were inferred using a variety of age constraints and age-depth modelling approaches (see below and Appendix \$4).

Version 1.0 of BioDeepTime (Smith et al., 2023b) represents the first milestone of the data gathering process. Data acquisition is ongoing and future versions of the database with significant additions will periodically be released. In addition to new queries of the databases drawn from here, future data integration efforts will (1) aim to expand the taxonomic coverage of the database and (2) incorporate data from more ancient periods beyond the Cenozoic, with a particular emphasis on quantifying the uncertainty of age-depth models in these times (Figure 2).

2.2 Data curation and quality control

Field names (i.e. data table columns) from existing databases were synonymized for inclusion in BioDeepTime (see Appendix S1, Tables S1.1–S1.17 and 'Synonymy of sources' in Smith et al. (2023b)). To include as many time series as possible, we allowed the methods and types of data used to infer sample ages to vary among data sets, as long as the methods were consistent within each time series. For several databases (BioTIME, Neptune Sandbox Berlin, Triton, SedTraps), the ages assigned to samples in the original database or publication are the ages used in BioDeepTime, as are the uncertainties around those estimates, when available. For Neotoma samples, we generated updated age-depth models for most time series (1281 of 1362) using Bchron (Haslett & Parnell, 2008) based

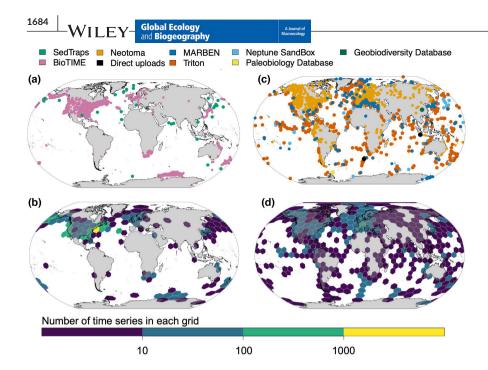


FIGURE 2 Distribution of assemblage time series from modern, neontological (a, b) and fossil, palaeontological (c, d) sources. Specific time-series locations are indicated in (a, c), with spatially binned data shown in (b, d) to visualize the density of time series. The distribution of time series also corresponds to the coverage of environments (e.g. Marine, Terrestrial) in BioDeepTime. Landmass polygons from NaturalEarth (Robinson projection; https://www.naturalearthdata.com/) and grid cells were created using icosa (Kocsis, 2017).

on chronological controls stored in Neotoma for each site, which were commonly uncalibrated radiocarbon ages but included biostratigraphic markers (e.g. European settlement in North America), calibrated radiocarbon ages and laminated varves. *Bchron* generates an ensemble of possible age models (n=1000) in a Bayesian framework considering the uncertainty in age-depth constraints, including differences in radiocarbon calibration curves (see Appendix S4), with the median age estimate for each sample used as the sample age in BioDeepTime version 1.0 (see 'neotoma_bchron' in Smith et al., 2023b). Although not currently implemented for all time series, this Bayesian approach provides an example of how age models might be improved and standardized across BioDeepTime in future releases and highlights the importance of storing fossil data with the original age controls used for age-depth modelling. Details for age estimates and models used are in Appendix S4.

For a compact data format in BioDeepTime, each entry is a presence (or abundance/biomass, indicating presence) record. However, these can be converted to 'presence-absence' format for those taxa that are not observed in a particular sample but are otherwise observed in at least one other sample in the same time series. That is, observed zeros can be restored by converting from long to wide format (i.e. assuming zeros where data are otherwise lacking).

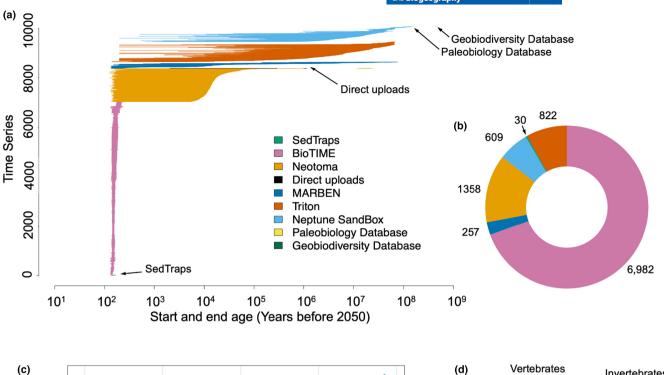
3 | DESCRIPTION OF DATA

BioDeepTime currently includes 7,437,847 taxon records distributed in 985,306 samples from 10,062 time series collectively spanning 451 million years (Figure 3). These records are from terrestrial, freshwater and marine environments globally (Figure 2), although there is limited coverage in the global south (Figure 2b,d). These geographical gaps reflect documented biases in global data distribution in ecology and palaeontology, which are underlain by

inequities that include funding, research infrastructure and geopolitical histories (e.g. Dornelas et al., 2018; Nuñez et al., 2021; Raja et al., 2022). Addressing these geographical biases in the data distribution is a critical and ongoing research goal that is essential for gaining a comprehensive understanding of biodiversity change.

The mean duration of a time series in BioDeepTime is 1.63 million years, with a median duration of 29 years. As BioTIME contributed the largest number of time series (n = 6982, 69%) and samples (n=797,425, 81%), the difference in mean and median duration is primarily due to the distribution of samples and ages across the BioTIME data (mean duration=22.6 years; mean age of modern samples = 25 years old) as compared to the fossil time series (mean duration = 5.38 million years; mean age of samples = 5.09 million years; Figure 3a). The fossil data can be further divided into 'neartime' paleontological data (here defined as having their oldest samples since the start of the Quaternary, 2.58 million years ago) and 'deep-time' data (with oldest samples >2.58 million years). Of the fossil data, 60.1% are near-time, with 649 (21.3%) of the 3050 fossil time series having a maximum age that falls in the Holocene (last 12,000 years) and another 1184 (38.8%) having their oldest records further back in the Quaternary. The remaining 1217 (39.9%) extend into the 'deep time' palaeontological record (>2.58 million years). All but 67 (2.2%) of the fossil time series have a maximum age within the Cenozoic (<66 million years). The paucity of time series from the older fossil record reflects the propensity for increased uncertainty in age estimates and taxonomic assignments in deeper time, which resulted in exclusion from BioDeepTime based on our current criteria.

BioDeepTime includes more than 28,700 taxon entries. When possible, taxa are included at the level of species (n=4,769,789; 64.1%) or genus (n=271,218; 3.6%). These taxa were subsequently grouped into 16 taxonomic categories and a 'Mixed' category, when a time series includes taxa from multiple groups (Figure 3d), to



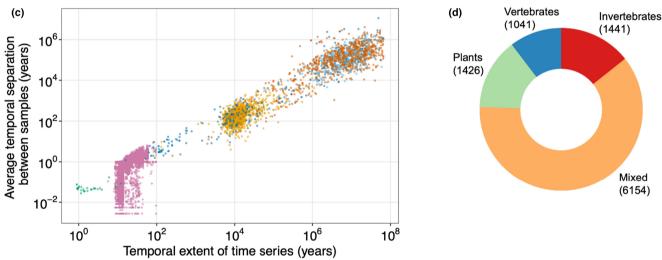


FIGURE 3 (a) Temporal distribution of assemblage time series in geological time, by database. (b) Number of assemblage time series in BioDeepTime drawn from each database, using the same legend as panel (a). (c) Average temporal separation between samples of a time-series plotted against its temporal extent (total duration). (d) Distribution of taxonomic groups in BioDeepTime in broad categories: mixed, invertebrates (e.g. foraminifera, ostracods), plants (e.g. pollen, bryophytes), and vertebrates (e.g. amphibians, mammals). To avoid negative age values in panels (a, c), 100 years were added to the age of each sample so that all dates represent years before 2050 (instead of years before 1950 and negative values from 1950 onwards). Assemblage time series from direct uploads (n=2), Paleobiology Database (n=1) and Geobiodiversity Database (n=1) are present in panels (a-c) but hard to visualize. Note: the colour scheme used in panels (a-c) is consistent and refers to the database from which time series originated; panel d uses an independent colour scheme.

facilitate time-series analysis based on potential groups of interest. These categories are variable in specificity, with higher levels of detail retained when possible (e.g. 'Vertebrates' and 'Amphibians' are both used). Apart from the Mixed category, vascular plants (i.e. pollen) and foraminifera account for the majority of time series (62.8%; Figure 3c). This taxonomic composition reflects, in part, our choice to include the highest quality fossil time series available, as these groups and the method by which they are sampled (i.e. sediment cores) allow for the construction of the most reliable age models.

4 | USAGE NOTES

BioDeepTime version 1.0 can be downloaded from Zenodo (Smith et al., 2023b). All users of BioDeepTime data should cite this present paper, original data sources and papers presenting the contributing databases. In all cases, data users should also follow the data use agreements set by contributing databases (see also Appendix S1: Appendix S3.2). The procedurally compiled relational database is available as an SQLite file, which was denormalized to the level

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of records (i.e. taxon presence or abundance) and is provided as a comma-separated values file so users familiar with other database products can readily explore and analyse the compiled data.

Users of BioDeepTime should note several features of the database that may affect their analyses. Most notably, the database was compiled for the purpose of examining biodiversity patterns (e.g. observed richness, turnover) within time series, and in such a way that future analyses can readily evaluate these patterns relative to environmental data. Variation across time series in the underlying data included in BioDeepTime—in time (age models), space (sampling area), taxonomic resolution, collection methods and other biases (e.g. preservational biases)—can be a strength of the database or can become a source of biases. In general, as the temporal extent of a time series increases, so does the distance between samples (Figure 3c) and the temporal grain of the sample. All ages use 1950 as a reference point, with positive values for samples collected before 1950 and negative values for those collected after 1950.

When a fossil assemblage has accumulated over an extended period of time, the sampled assemblage will be time-averaged and its observed richness and evenness often will be higher than found in a living assemblage observed at any given point during the same period of time (e.g. as observed in a 'snapshot' neontological survey; Adler et al., 2005; Olszewski & Kidwell, 2007; Tomašových & Kidwell, 2010). Increases in temporal grain and time averaging result in a prolonged sampling window. The effects of prolonging this sample window are multifarious and have well-known effects on diversity and turnover (e.g. Jarzyna & Jetz, 2018; Olszewski & Kidwell, 2007; Tomašových & Kidwell, 2010). Depending on the analysis, these effects can be accounted for as an uncertainty on diversity estimates (e.g. Smith et al., 2021) and a modifying term for rate-of-change analysis (e.g. Lotter et al., 1992). Temporal grain in fossil samples, approximated by the inverse of sedimentation rate (i.e. the amount of time represented in a sample; not accounting for bioturbation), ranges from days to tens of thousands of years (Table 1).

Some data sets included here have information on sampling effort, but many do not and this information is important for macroscale biodiversity analyses that correct for the effect of sampling effort on observed species richness by, for example, standardization of sampling using rarefaction methods (Chao & Jost, 2012; Roswell et al., 2021). We encourage authors to include data related to sampling effort in future published data sets to enable a broader range of cross-community analyses.

5 | MOVING FORWARD

The BioDeepTime database enables integrated biodiversity analyses across a far greater range of temporal scales than has previously been possible. It can be used to provide critical insights into how natural systems will respond to ongoing and future environmental changes as well as new opportunities for theoretical insights into the temporal scaling of biodiversity dynamics. The taxonomic and

environmental scope of BioDeepTime are broad but still encompass only a small fraction of the potentially suitable data. The database will continue to grow and we welcome data contributions from the broader scientific community to expand the utility of this community resource (see Appendix S3).

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The BioDeepTime database and the code to reproduce the data compilation are accessible from the Zenodo repository (Smith et al., 2023b). A second repository with code required to reproduce the figures and summary statistics in this paper is present at Smith et al. (2023a).

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BIOSKETCH

The BioDeepTime working group (funded by the Paleosynthesis Project) seeks to address one of the central challenges in biodiversity science by compiling and harmonizing ecological time series from modern and fossil sources to investigate the scaling and drivers of biodiversity and community dynamics across timescales ranging from months to millions of years. The working group formed in 2020 and continues to pursue questions related to temporal dynamics of biodiversity using neontological and palaeontological records in the BioDeepTime database and beyond.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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