

## Research



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# The Palaeozoic colonization of the water column and the rise of global nekton

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The colonization of the water column is among the most important transformations in the evolution of animal life and global ecosystems. The Devonian nekton revolution has been identified as a major macroevolutionary event signifying the rapid occupation of the water column by independent radiations of swimming animals. Using new data, an expanded taxonomic coverage, sample standardization and increased ecological resolution, we analysed patterns of nektonization during the Palaeozoic. We find that nekton and eunekton were well established prior to the Devonian and did not diversify dramatically during any Palaeozoic interval. Relative nektonic diversity and occurrences decreased rather than increased during the Devonian. Eunektonic diversity and occurrences increased throughout the Palaeozoic, but this rise was protracted and cannot be attributed to any single interval. Our new data indicate that the metazoan colonization of the water column was considerably more complex and gradual than previously understood.

## 1. Introduction

The Cambrian Explosion, the Great Ordovician Biodiversification Event and the Mesozoic Marine Revolution established marine diversity and ecology relatively rapidly. The exact timing, duration and magnitude of these events are debated, but their existence has proved robust to reanalysis (e.g. [1–4]). In a seminal study, Klug *et al.* [5] documented a previously unrecognized major radiation of actively swimming animals (nekton) during the Devonian ‘Age of Fishes’. This Devonian nekton revolution (DNR) was a transition so comprehensive that nekton accounted for more than 85% of non-benthic marine diversity by the Carboniferous, compared to less than 15% at the end-Silurian [5].

The DNR [5] coincides with an increase in benthic predation-resistant morphologies dubbed the mid-Palaeozoic precursor to the Mesozoic Marine Revolution [6]. The first forests [7] and the vertebrate colonization of land [8] also occurred during the Devonian. Furthermore, there were three mass extinction events (end-Givetian, end-Frasnian and end-Famennian) [9], which resulted in the collapse of the most extensive reef systems of the Palaeozoic [10,11]. Nekton are an important component of the global biosphere, greatly contributing to trophic complexity [12] and nutrient cycling [13]; thus, a consideration of these and other mid-Palaeozoic ecosystem dynamics requires an understanding of the timing, duration and magnitude of Palaeozoic nektonization.

New discoveries have blurred the distinction between the Cambrian Explosion and the Great Ordovician Biodiversification Event, suggesting that they are elements of a continuous diversification [14–16]. This prompted us to reassess the DNR and determine how it is impacted by the addition of new data, an expanded taxonomic coverage, sample standardization and increased ecological resolution. A ‘revolution’ is not a formal palaeontological term with clearly falsifiable precepts. We use it *sensu* Klug *et al.* [5] to imply a rapid evolutionary event that is ecologically, rather than taxonomically, driven and resulted in fundamental changes to global aquatic ecosystems.

## 2. Palaeoecology

Most studies of macroecological patterns through the fossil record emphasized benthic organisms and either assumed uniform ecologies for higher taxa or listed the range of ecologies exhibited by higher taxa without regard for their relative frequency (e.g. [17–20]). Here, we assess palaeoecology at the highest taxonomic rank within which all constituent genera represent the same strategy. Where species within a genus display different ecologies, the genus was assigned to the category representing most of its species. All assignments are justified, referenced and associated with a relative confidence score (electronic supplementary data). Following Klug *et al.* [5], we assigned each taxon to either the planktic, demersal or nektic megaguild, but we subdivided these into ecomorphological life modes (euplanktic, nektoplanktic, eudemersal, nektobenthic, planktonektic and eunektic) using terminology adapted from Aleyev [21]. This allowed us to more readily assign taxa that fall on the boundaries between megaguilds. The result is the most comprehensive palaeoecological survey yet attempted for fossil organisms in the water column.

As the behaviour of a fossil organism cannot be observed, we categorize taxa based on ecomorphology rather than ecology. Although ecomorphological categories may not correlate exactly with behavioural ecologies, this abstraction is necessary to allow consistent interpretation. Planktic taxa (euplankton and nektoplankton) usually have unstreamlined or parachuting morphologies, demersal taxa (eudemersus and nektobenthos) tend to be dorsoventrally depressed and nektic taxa (planktonekton and eunekton) are characterized by laterally compressed and tapering morphologies. Euplankton are true passive drifters (e.g. graptoloids), while nektoplankton are planktic animals with some swimming capability (e.g. euphausiids). Eudemersus (i.e. eudemersal taxa) are obligate swimmers restricted to near-benthic settings (e.g. holocephalans); nektobenthos are suprabenthic organisms capable of temporary swimming (e.g. xiphosurans). Planktonekton are small, poorer swimmers with nektic as opposed to planktic morphologies (e.g. conodonts). Eunekton are well-streamlined strong swimmers not confined to the near-benthos (e.g. palaeonisciformes); this is essentially equivalent to the conceptualization of nekton used by Klug *et al.* [5]. The electronic supplementary material (pp. 13–16) provides a full explanation of the ecomorphological categories we employed, with definitions, examples and a summary decision tree. Although there is a risk of artificial delimitation, such a framework is necessary to ensure repeatable, consistent results.

## 3. Material and methods

We analysed data from the Paleobiology Database (PBDB) and Sepkoski's 'Compendium of fossil marine animal genera' [22]. The PBDB is more comprehensive and up-to-date than Sepkoski's Compendium [22] (although it under-reports Palaeozoic biodiversity among non-tetrapod vertebrates and soft-bodied invertebrates). Since the analysis of Klug *et al.* [5], 10 528 Palaeozoic non-benthic aquatic metazoan occurrences of the higher taxa that they considered have been added to the PBDB (an 82% increase). Unlike Klug *et al.* [5], we considered all non-benthic, aquatic metazoans in both of these datasets; this increases generic diversity in the PBDB by an additional 29 395 occurrences (a 56% increase) and in Sepkoski's Compendium [22] by 1064 genera (a 31% increase). We further supplemented Sepkoski's

Compendium [22] with 724 additional genera of vertebrates, ammonoids and panarthropods (an additional 20% increase in Palaeozoic non-benthic diversity) to generate a database we refer to as the supplemented Sepkoski's Compendium of Genera or SSCG (electronic supplementary data). The electronic supplementary material (pp. 2–5) provides a detailed comparison of the SSCG and Sepkoski [22] datasets.

The SSCG provides more complete coverage than the PBDB, particularly among vertebrates, but it is a ranged-through (RT) count, biasing it to variation in sampling intensity [23]. The PBDB, in contrast, records occurrences within collections, which can serve as a proxy for abundance and facilitate sampled-in-bin (SIB) counts. SIB counts necessarily yield poorer coverage than RT counts, because they exclude inferred lineages (ranges in-between occurrences that lack observations), but they allow the application of standardization techniques to mitigate the effects of biases in the observed record when calculating diversity through time [23].

PBDB SIB counts were sample standardized by ecomorphological life mode using Alroy's [23] Shareholder Quorum Subsampling (SQS) routine as implemented by Holland's port of Alroy's script included in the R package VELOCIRAPTR [24]. This was done to mitigate biases introduced by uneven sampling intensity across stratigraphic units. Coverage-based rarefaction, such as SQS, was preferred over classical rarefaction and extrapolators, because classical rarefaction artificially flattens diversity curves and extrapolators perform poorly with small sample sizes [25]. Owing to limited coverage, we retained singletons and dominants, combined Cambrian stages into series and used a quorum of 0.3 (1000 trials). Although somewhat low, this quorum should not bias the results [26]. If any bin still contained too few genera to sample standardize (fewer than 5), we recorded 10% of the raw SIB generic diversity as the count for that bin (electronic supplementary data). Owing to their very low diversity, we excluded semi-aquatic taxa and included semi-terrestrial taxa with the eunekton. It has been demonstrated that diversity can be biased by palaeogeographical spread as a result of the species-area effect—we tested for this using the methods of Alroy [26] and Close *et al.* [27] (detailed in the electronic supplementary material, pp. 20–21). Raw SIB generic diversity appears to be impacted by palaeogeographical spread for all life modes, except the nektobenthos and perhaps the nektoplankton (electronic supplementary material, figure S10); however, SQS standardized generic diversity does not appear to be biased (electronic supplementary material, figure S11). Considering these results and the small sample sizes for several stratigraphic-ecological bins, we did not standardize for space prior to SQS standardization. Neither PBDB generic occurrences, raw SIB diversity nor SQS standardized SIB diversity appears to be biased by uneven chronostratigraphic bin length (electronic supplementary material, figures S12–S14).

All Palaeozoic metazoans from Sepkoski's *Compendium* [22] were downloaded from <http://strata.geology.wisc.edu/jack/> in January 2016. When incorporating new data into the SSCG, we retained Sepkoski's [22] data conventions (i.e. taxonomy and stratigraphy) to facilitate comparison with previous analyses. Several sources of our new data determined genera to be poly-/paraphyletic without recommending new assignments; we identify these genera using species names, inverted commas and informal designations as appropriate (electronic supplementary data). Stratigraphic ranges not resolved to at least stage were excluded, except when Sepkoski [22] used series instead of stages. Taxa spanning a boundary but without specific stage/series assignments were assigned to the shortest possible stratigraphic range (e.g. genera listed as Devonian–Carboniferous are counted as Famennian–Tournaisian). Although this artificially concentrates taxa at period/series boundaries, only 1% of genera were impacted, so the effect is minimal. The lower, middle and upper

Middle Cambrians were combined as International Commission on Stratigraphy (ICS) Stage 5, and the Llanvirnian and Llandeilian were combined as ICS Darriwilian [28].

All Palaeozoic taxa from the PBDB were downloaded from <https://paleobiodb.org/#/> on 6 March 2017 at 21:13. Non-metazoans and fully terrestrial taxa were excluded (electronic supplementary material, pp. 6–9). All taxa not identified to genus were excluded, as were those with ranges not refined to at least stage-level, except in the Silurian where series were accepted. All regional stages were converted to their ICS equivalent. If a regional-stage overlaps more than one ICS stage or Silurian series, biostratigraphic data were employed to refine the assignment; otherwise, the taxa were excluded (electronic supplementary material, p. 10). No attempt was made to correlate biostratigraphic ranges not listed in Gradstein *et al.* [28]; occurrences that could not be correlated were omitted. Given its importance, the Burgess Shale fauna was included, despite not being ICS constrained or sufficiently biostratigraphically refined in the PBDB. Correlations were based on *The Geologic Time Scale 2012* [28], *A Geologic Timescale 2004* [29] and *A Geologic Timescale 1989* [30], supplemented by additional publications as necessary (electronic supplementary material, pp. 11–12).

We scored our confidence in each ecological assignment (electronic supplementary data). Complete confidence equals 1.00, 0.25 was subtracted for every plausible alternative and an additional 0.25 was subtracted for assumptions based on related taxa. Assumptions were only employed when material was poorly figured, fragmentary or ambiguous.

Palaeoecology was assessed quantitatively for planispiral-coiled cephalopods (Ammonoidea, Nautilida and Tarphycerida) using coordinates in Westermann Morphospace or WM [31,32]. Each axis in WM corresponds to a shell coiling parameter: umbilical exposure (U), overall inflation (Th) and whorl expansion (w) [32]. U is maximized in serpenticones, Th in sphericones and w in oxycones; various other shell shapes are intermediary [32]. Although some criticize this ternary morphospace as an oversimplification of ammonoid disparity [33], we consider it sufficient for our purposes. The position of a specimen in WM corresponds to its hypothetical palaeoecology: highly streamlined (high w) oxyconic shells are considered eunektic; poorly streamlined (low w, and either high Th or high U) serpenticonic, cadiconic and sphericonic shells are considered nektoplanktic; intermediate planorbiconic, scaphitoconic and platyconic shells are considered eudemersal (electronic supplementary material, figures S6, S7 and S9) [31,32]. To calculate the coordinates, we measured whorl width, larger conch diameter, final whorl height, 180° whorl height and umbilical width (electronic supplementary material, figure S8) [32] in all adult ammonoid, nautilid and tarphycerid species (subadults were measured if the adults cease coiling) figured in *Ammonoidea Devonica* [34] and the *Treatise on Invertebrate Paleontology: Parts K, L, and L Revised, Vol. 2* [35–37], supplemented with specimens from the Yale Peabody Museum (electronic supplementary data). See the electronic supplementary material (pp. 17–19) for a more detailed explanation of Westermann Morphospace, equations for calculating U, Th and w, and a plot for all measured cephalopods in WM (electronic supplementary material, figure S9).

To understand why our results differ from Klug *et al.* [5], we calculated nektic, demersal and planktic diversity using the SSCG and their ecological assignments; unassigned taxa were not included. We then applied our ecological classifications to those taxa from Sepkoski's *Compendium* [22] that were considered by Klug *et al.* [5]. To determine the impact of our additions to Sepkoski's *Compendium* [22] (i.e. the SSCG), we also calculated diversity by ecomorphological life mode using Sepkoski's unmodified dataset [22]. Finally, to understand the impact of SIB counting and SQS, we calculated PBDB RT and raw SIB diversity by life mode.

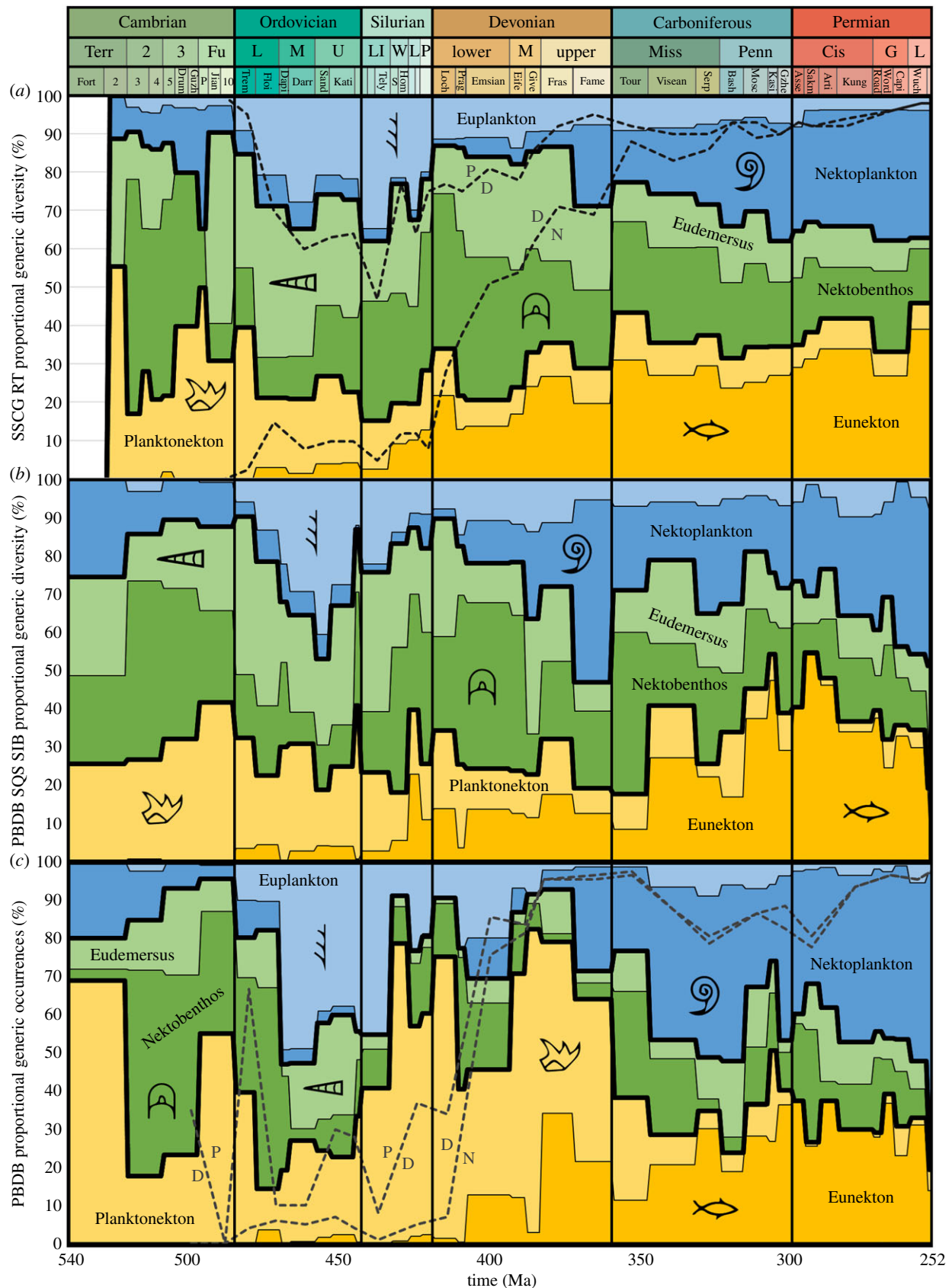
## 4. Results

In the Cambrian, metazoan euplankton were rare; most plankton were nektoplanktic cnidarians and arthropods (electronic supplementary material, figure S18). Demersal taxa accounted for the greatest proportion of diversity and occurrences with nektobenthos dominant (figure 1). From the Terreneuvian through Epoch 3, the demersus primarily consisted of panarthropods, such as eudemersal radiodonts (e.g. *Anomalocaris*) and megacheirans (great-appendage arthropods), and nektobenthic bradoriids and ostracods; these were largely replaced in the Furongian by nautiloid cephalopods (electronic supplementary material, figure S19). Nekton were important in Cambrian ecosystems, comprising 17–56% of non-benthic diversity and 18–69% of non-benthic occurrences, depending on the interval (figure 1). Planktonectic protoconodont chaetognaths (arrow worms), conodonts, trilobites, stem pancrustaceans and other taxa proliferated, while eunekton were rare. The only Cambrian eunekton in these data are the bivalved arthropods *Pseudoarctolepis* and *Dicerocaris*, and the chordate *Mylokunmingia* (electronic supplementary data).

During the Great Ordovician Biodiversification Event, the diversity of each life mode increased, especially the euplankton, eudemersus and planktonekton, which all exhibited peak diversity in the Ordovician (electronic supplementary material, figure S15). Plankton expanded to 30–40% of global aquatic diversity and up to 53% of occurrences (figure 1). This Ordovician Plankton Revolution [16] can be attributed almost entirely to euplanktic graptolites and orthocerid nautiloids (electronic supplementary material, figure S18). Cnidarians, trilobites and tarphycerid nautiloids filled the lower-diversity nektoplankton (electronic supplementary material, figure S18). Despite increased planktic diversity, demersal diversity (though not occurrences) remained dominant, with eudemersal nautiloids the largest contributor (figure 1; electronic supplementary material, figure S19). The less diverse nektobenthos were primarily represented by trilobites, eurypterids (sea scorpions) and polychaete worms (electronic supplementary material, figure S19). The nekton constituted 19–41% of diversity and 15–40% of occurrences through the Ordovician (figure 1). Conodonts and trilobites continued to dominate the planktonekton, which constituted most of the nekton. However, coiled tarphycerids, early chondrichthyans (cartilaginous fishes) and 'acanthodians' (spiny sharks) comprised an expanding, low-diversity (less than 5%) eunekton (figures 1 and 2; electronic supplementary material, figure S20).

The Late Ordovician mass extinctions severely diminished euplanktic, eudemersal and planktonekton diversity; none regained Middle Ordovician levels during the Palaeozoic (electronic supplementary material, figure S15). Euplankton continued to be important, increasing generic diversity, but proportional diversity and occurrences declined through the Silurian following graptoloid extinctions (figure 1; electronic supplementary material, figures S15 and S18). The nektoplankton maintained relatively low diversity and occurrences (figure 1). The euplankton gained dacryoconarids (small conical fossils) and myodocopid ostracods, while the nektoplankton lost trilobites (electronic supplementary material, figure S18). The demersus accounted for more than 47% of diversity but less than 20% of occurrences through the Silurian (figure 1). Eudemersal diversity was somewhat turbulent in the Silurian, but nektobenthic diversity increased (electronic

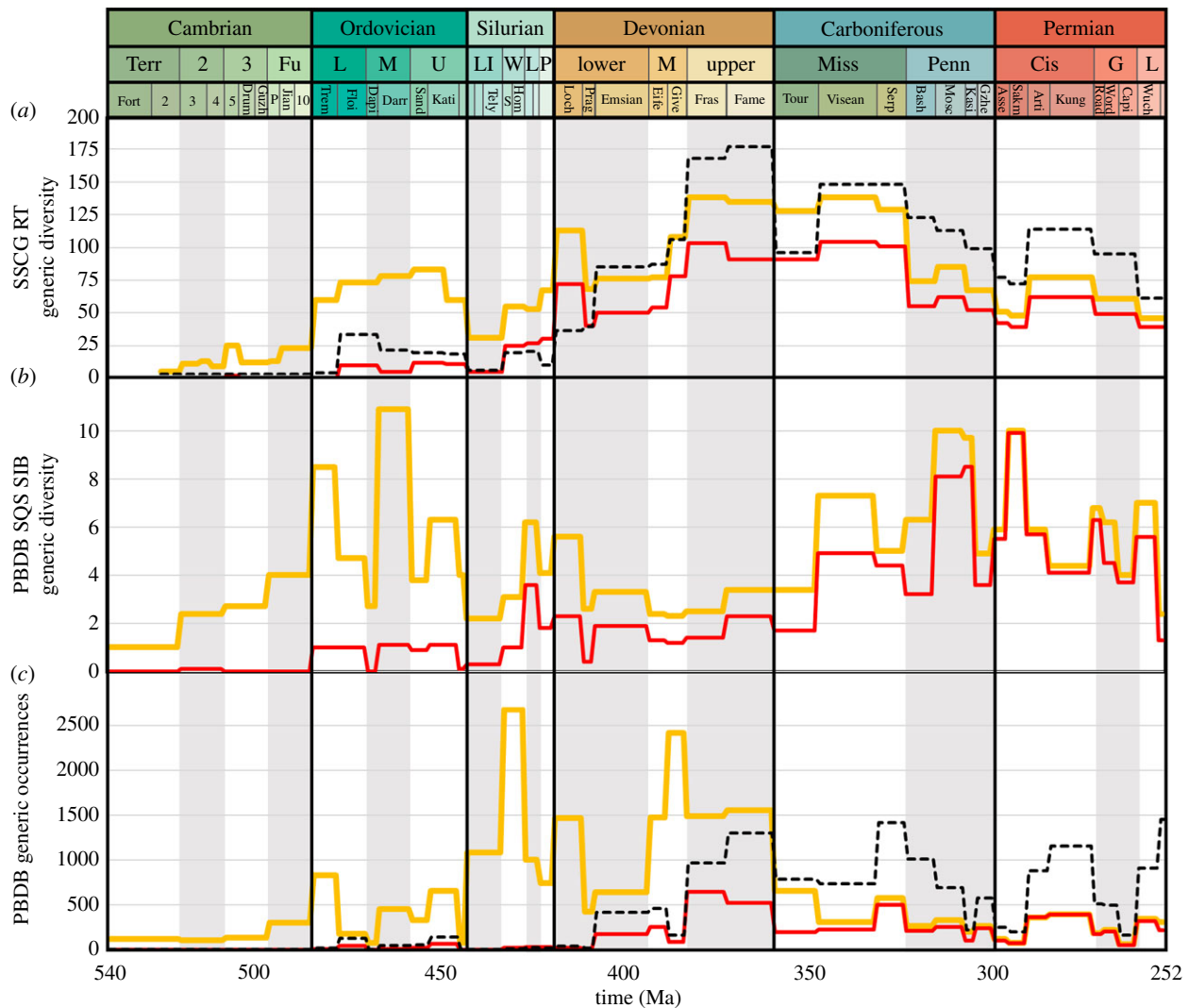




**Figure 1.** Proportional Palaeozoic water-column generic diversity and occurrences by ecomorphological life mode. Blue denotes plankton, green demersus, yellow nekton. Dashed lines indicate Klug *et al.* [5] DNR results for comparison, P, plankton; D, demersus; N, nekton. United States Geological Survey symbols here denote life mode not taxonomy; they do not necessarily indicate that all or most of the genera from the symbolized taxon exhibit the relevant life mode. (a) SSCG (supplemented Sepkoski's compendium of genera) RT (ranged-through) diversity. (b) PBDB (Paleobiology Database) SQS (shareholder quorum subsampling) standardized SIB (sampled-in-bin) diversity. (c) PBDB generic occurrences. See electronic supplementary material, figure S17 for an alternative version of this figure without dashed lines and with demarked semi-terrestrial taxa.

supplementary material, figure S15) as tentaculitids, 'ostracoderms' (jawless armoured fishes) and especially eurypterids diversified (electronic supplementary material, figure S19).

Overall, proportional nektonic diversity was less than in the Ordovician, primarily because of Late Ordovician planktonic losses (figure 1; electronic supplementary material, figure S16).



**Figure 2.** Palaeozoic nektic generic diversity and occurrences through time. Yellow denotes all nekton, red eunehton, dashed-line indicates Klug *et al.* [5] reported nektic diversity/abundance. (a) SSCG (supplemented Sepkoski's compendium of genera) ranged-through (RT) diversity. (b) PBDB (Paleobiology Database) SQS (shareholder quorum subsampling) standardized sampled-in-bin (SIB) diversity. (c) PBDB occurrences.

Although Silurian planktonic diversity was at approximately 50% of its pre-extinction level (figure 2) and comprised only 10–20% of total Silurian diversity (figure 1*a,b*), the plankton alone accounts for 41–78% of the occurrences in any given series (figure 1*c*). Throughout the Palaeozoic, no other life mode ever reached similarly high-occurrence counts (electronic supplementary material, figure S16*c*). Planktonic trilobites disappeared at the end-Ordovician (electronic supplementary material, figure S20). Phyllocarid and thylacocephalan arthropods and cyathaspidid heterostracan 'ostracoderms' diversified, but the increased occurrences are almost entirely attributable to conodonts (electronic supplementary data). The Silurian marks the initial rise of eunehton as an important contributor to global aquatic diversity (figure 1). The Ordovician eunehton taxa were joined by osteichthyans (boney fishes) and heterostracan, anaspid and thelodont 'ostracoderms' (electronic supplementary material, figure S20). As a result, eunehton comprised 7.5% (SSCG) to 23.1% (PBDB) of diversity by the Ludlow, compared to just 1.6% (SSCG) and 3.2% (PBDB) in the Llandovery (figure 1).

Early–Middle Devonian euplanktic diversity was broadly similar to the Pridoli (electronic supplementary material, figure S15), but euplankton declined in proportional diversity and occurrences in the Late Devonian (figure 1). Graptoloids went extinct in the Early Devonian followed by the

dacryoconarids and homotenids in the Frasnian and Famennian mass extinctions (electronic supplementary material, figure S18). Nektoplanktic diversity, however, increased by 17.6 (SSCG) and 45.0 (PBDB) percentage points from the Lochkovian to the Famennian (figure 1). This sudden diversification is a result of the origin and radiation of ammonoids and bactritids (electronic supplementary material, figure S18), especially the Famennian Clymeniida and Goniattitida. Thus, our data suggest that plankton, rather than nekton, exhibit the most dramatic diversification of the Devonian; proportional planktic occurrences remained similar to the Silurian (figure 1*c*). Demersal genera account for the largest share (41–65%) of Devonian diversity in each stage, except the Famennian in the sample standardized PBDB diversity results (figure 1*b*). The SSCG shows increasing eudemersal diversity throughout the Devonian, except for minor decreases in the Givetian and Famennian (figure 1*a*; electronic supplementary material, figure S15*b*), whereas the sample standardized PBDB displays a pronounced decline between the Lochkovian and the Pragian with sustained low diversity through the remaining Devonian, except for a temporary increase in the Givetian (figure 1*b*; electronic supplementary material, figure S15*e*). The Devonian eudemersal primarily consisted of arthrodire 'placoderms' (jawed armoured fishes), nautiloids and ammonoids (electronic supplementary material, figure S19). The strikingly

lower PBDB diversity (electronic supplementary material, figure S15e) is a consequence of sample standardization (compare to RT PBDB diversity: electronic supplementary material, figures S26–S28) and poor vertebrate, especially ‘placoderm’, coverage. ‘Placoderms’ were the most diverse vertebrates of the Devonian, with 238 genera recorded in the SSCG; by contrast, the PBDB only registers 27 ‘placoderm’ genera resolved to ICS stages. Both the SSCG and PBDB show increasing nekto-benthic diversity in the Early Devonian, followed by decreasing diversity from the Eifelian to the Frasnian, and an increase in the Famennian (figure 1*a,b*; electronic supplementary material, figure S15). Trilobites, eurypterids, tentaculitids and sarcopterygian (lobe-finned fish), ‘placoderm’ and ‘ostracoderm’ vertebrates constituted most Devonian nekto-benthic diversity (electronic supplementary material, figure S19). The jawless ‘ostracoderms’ largely disappeared in the Middle Devonian which, coupled with the trilobite crises [38] and Late Devonian tentaculitid extinctions, produced the observed nekto-benthic diversity decline, despite sarcopterygian increases (electronic supplementary material, figures S15 and S19).

Proportional nektic diversity and occurrences increased across the Silurian–Devonian boundary, but both decreased overall from the Lochkovian to the Famennian and precipitously declined in the Pragian (figures 1 and 2; electronic supplementary material, figure S16). As in the Silurian, the majority of Devonian occurrences are of planktonekton, especially conodonts (figures 1*c* and 2*c*; electronic supplementary material, table S3). Planktonektic diversity increased in the Lochkovian, decreased from the Pragian to the Eifelian, and either increased (SSCG, electronic supplementary material, figure S15*a*) or stagnated (PBDB, electronic supplementary material, figure S15*f*) from the Givetian to the Famennian. During the Devonian, the planktonekton lost the cyathaspidid heterostracan ‘ostracoderms’ and gained the boletzkyid cephalopods (electronic supplementary material, figure S20). Eunektic diversity increased in the Lochkovian and sharply decreased in the Pragian (figures 1 and 2). The eunekton did not recover Lochkovian diversity until either the Givetian (figures 1*a* and 2*a*) or Late Devonian (figures 1*b* and 2*b*); however, proportional occurrences already surpassed all preceding intervals by the Emsian (figure 1*c*). Following the Pragian, proportional eunektic diversity and occurrences increased to the Frasnian, although occurrences decreased in the Middle Devonian (figure 1). Proportional eunektic diversity and occurrences decreased following the Late Frasnian biodiversity crisis (figure 1; electronic supplementary material, figure S16). Sample standardization and the discrepancy in ‘placoderm’ coverage between the SSCG and PBDB datasets likely explain the higher diversity recorded by the SSCG (figures 1*a,b* and 2*a,b*; electronic supplementary material, figures S26–S28). In the Early Devonian, the eunekton primarily consisted of heterostracan ‘ostracoderms’, thelodont ‘ostracoderms’, ‘acanthodians’ and emergent ammonoids—after the Emsian, the jawless fishes were supplanted by arthrodire ‘placoderms’, chondrichthyans, actinopterygians (ray-finned fishes) and coelacanthiform sarcopterygians (electronic supplementary material, figure S20). The Devonian also featured the emergence of nautilids in the eunekton.

The end-Famennian mass extinction was devastating for nekto-planktic, eudemersal and planktonektic taxa—the eunekton saw modest decreases (electronic supplementary material, figure S16). Conversely, euplanktic diversity, occurrences and taxonomic composition were little impacted

(figure 1); homocutenids went extinct, but their diversity was already reduced by the Late Frasnian crisis (electronic supplementary material, figure S18). The extinction of the clymeniids and other ammonoids accounts for most of the Famennian–Tournaisian nekto-plankton losses, but radiating goniatite and prolecanitid ammonoids, nautilids and malacostracans provided a prompt recovery (electronic supplementary material, figure S18). Despite a further perturbation in the Moscovian, nekto-planktic diversity and occurrences gradually increased through the Carboniferous (figure 1). The end-Devonian heralded the end of demersal diversity dominance. Although relative occurrences surpassed Silurian and Devonian levels, after the Tournaisian the demersus never again constituted the major proportion of water-column diversity (figure 1). The end-Devonian mass extinction may have reduced eudemersal generic diversity to approximately one-fifth of its Famennian level (electronic supplementary material, figure S15*b*), but this pattern is not evident in the PBDB, perhaps as a result of under-reported pre-extinction ‘placoderm’ diversity and occurrences. The eudemersus suffered the extinction of the ‘placoderms’, clymeniids and other ammonoids (electronic supplementary material, figure S19); many nautiloid taxa either went extinct or survived as dead-clades-walking, disappearing before the Pennsylvanian (electronic supplementary material, figure S19). The radiations of nautilids, prolecanitid ammonoids and subterbranchialian chondrichthyans account for a recovery (electronic supplementary material, figure S19), but eudemersal diversity gradually declined to the end-Permian (figure 1*a,b*; electronic supplementary material, figure S15). The nekto-benthos benefited from the end-Devonian catastrophe, increasing diversity and occurrences (figure 1; electronic supplementary material, figures S15 and S16), but was hard hit by the Serpukhovian mass extinction and overall decreased through the Carboniferous (figure 1; electronic supplementary material, figure S15). The nekto-benthos lost ‘placoderms’ and many sarcopterygians, but malacostracans, annelid worms, elasipodid holothurians (sea cucumbers) and tetrapodomorph sarcopterygians diversified (electronic supplementary material, figure S19). Nektic occurrences ceased to dominate after the end-Devonian (figure 1*c*), despite the Carboniferous being the first period when nekton consistently represented the largest share of diversity (figure 1*a,b*). Planktonektic taxa largely declined throughout the period, but the pattern is complex in the PBDB diversity results (figures 1 and 2). Eunekton displayed a nearly 40 percentage point increase in proportional diversity in the PBDB through the Carboniferous (figure 1*b*). These increases accord with occurrence data (figure 1*c*), but not with SSCG diversity data, which nonetheless show sustained high proportional diversity throughout the Carboniferous (approx. 25–31%, figure 1*a*). The SSCG and PBDB both portray the end-Devonian mass extinction as a relatively minor event for eunektic diversity—the clymeniids and ‘placoderms’ went extinct, but these losses were offset in the Tournaisian and Visean by actinopterygians, chondrichthyans, prolecanitid ammonoids and nautilids (electronic supplementary material, figure S20). Eunektic occurrences were relatively unaffected (figure 1*c*). Eunektic diversity declined during the Serpukhovian mass extinction (figure 2)—the greater severity apparent in the SSCG data (when compared with the SQS standardized SIB PBDB results) in part reflects the upper stratigraphic limit of the incorporated Sallan and Coates [39] dataset (electronic supplementary



material, figure S3*d,e*). The proportion of eunekton continued to increase during the Pennsylvanian (figure 1*a,b*), as generic diversity either slightly declined (figure 2*a*) or greatly increased (figure 2*b*).

The taxa occupying each life mode in the Carboniferous largely continued to do so through the Permian with the exception of annelids and osteichthyans (electronic supplementary material, figure S19) in the demersus and ‘acanthodians’ in the nekton (electronic supplementary material, figure S20). Overall, euplanktic diversity was slightly less in the Permian than in the Carboniferous (figure 1*a,b*; electronic supplementary material, figure S15*a,d*). Nektoplankton largely decreased in diversity through the Permian (electronic supplementary material, figure S15*a,d*), but gradually increased their share of non-benthic diversity and occurrences (figure 1). The demersus decreased except for a temporary nektobenthic proliferation in the Guadalupian (figure 1; electronic supplementary material, figure S15*b,e*). Planktonekton were not a large component of Permian ecosystems, comprising less than 8.5% of diversity and less than 8% of occurrences throughout the period (figure 1). The SSCG shows increasing proportional eunektic diversity throughout the Permian (figure 1*a*), whereas the PBDB places the peak in the Sakmarian, decreasing thereafter (figure 1*b*), and depicts relatively steady proportional occurrences until the Changhsingian (figure 1*c*). The coarser stratigraphic bins of the SSCG likely account for much of this discrepancy.

The proportion of diversity and occurrences represented by each megaguild varied through the Palaeozoic. Overall, the plankton and nekton expanded intermittently, while the demersus decreased. Euplanktic, eudemersal and planktonektic taxa decreased from their Ordovician diversity maxima. Occurrences depict a similar trend for the euplankton and eudemersus, but planktonekton peaked in the Middle Palaeozoic and collapsed thereafter. Nektobenthic diversity decreased in the Furongian, increased up to and through the Middle Palaeozoic, and then decreased; occurrences largely decreased after the Cambrian and Early Ordovician. The eunekton and nektoplankton both display an overall positive trend—the eunekton outpaces the nektoplankton in diversity, with the converse pattern in occurrences.

The proportion of nekton fluctuated from 15 to 56% of diversity through the Palaeozoic, with an average of 32% in both datasets (figure 1*a,b*). There was no notable increase in proportional nektic diversity during the Devonian. In the SSCG data (figure 1*a*), total nekton at the beginning of the Devonian represent 34.1% of water-column diversity (21.8% eunekton), decreasing to 29.1% at the end-Devonian (19.6% eunekton); in the PBDB results (figure 1*b*), nekton represent 34.4% of Lochkovian diversity (14.1% eunekton) and only 19.2% of Famennian diversity (13.0% eunekton). Across the Devonian, the SSCG data show a decrease in proportional nektic diversity by 5 percentage points (eunekton: 5.5-points), and the PBDB results show a decrease of 15.2-points (eunekton: 1.1-points). Proportional nektic occurrences overall decreased throughout the Palaeozoic (figure 1*c*). During the Devonian, nektic occurrences decreased from 75.3% in the Lochkovian to 64.3% in the Famennian, while eunekton increased from 1.4% to 21.6% (figure 1*c*). Through the Palaeozoic, proportional eunektic diversity increased from 1 to 2% in the Cambrian to 36% (SSCG) and 54% (PBDB) in the Permian, while eunektic occurrences increased from less than 1 to 31% (figure 1). These values are much lower than those obtained by Klug *et al.* [5];

their data yielded an increase in diversity of approximately 40 percentage points, and in occurrences of approximately 90-points through the Devonian alone. Although our analyses document notable eunektic increases from the Pragian to the Frasnian, eunektic diversity did not surpass the Lochkovian level until the Givetian (figure 2*a*). Non-recovery eunektic diversifications were most pronounced during the Silurian–Lochkovian (SSCG) and Carboniferous–Sakmarian (PBDB), not during the Devonian.

## 5. Discussion

The databases analysed here indicate that global nekton were established in the Cambrian and continued to be an important component of the water column throughout the Palaeozoic. The 29–40% of total diversity and 79% of total occurrences in the Silurian (figure 1) emphasize the importance of nektic taxa prior to the Devonian. Our data show that relative nektic diversity and occurrences declined rather than increased through the Devonian. Nor do Silurian data support an earlier revolution—occurrences show a 38-point increase from the Llandovery to the Wenlock, but there is no similar diversity trend. Furthermore, these occurrences are almost entirely of conodonts, suggesting that this was primarily a taxonomic rather than ecological radiation.

Planktonekton initially dominated the nekton, but eunekton became increasingly prominent through the Palaeozoic, achieving greater diversity in the Silurian and greater occurrences in the Carboniferous. This does not, however, suggest replacement of the DNR with a eunekton revolution. Eunekton increased from less than 1% of diversity and occurrences in the Cambrian to 39% (SSCG) or 54% (PBDB) of diversity and 37% of occurrences in the Permian. By contrast, the DNR documented by Klug *et al.* [5] comprised a diversity increase from 28 to 69% and an occurrence increase from 7 to 96% from the Lochkovian to the Famennian alone. Neither the nekton, nor the eunekton alone, show increases of this rate or magnitude during any interval in our analysis. The most pronounced eunektic increases occurred during the Wenlock–Lochkovian and Carboniferous–Permian, but neither of these were substantive enough to represent a revolution.

There have not been a significant number of newly described pre-Silurian nekton since Klug *et al.* [5] published the DNR hypothesis. Rather, the increased taxonomic resolution of our ecological assignments (genus-level as opposed to class- or order-level) accounts for many of the differences between our results and those of Klug *et al.* [5]. They considered all ammonoid, nautilid and tarphycerid cephalopods, and all jawed vertebrates (gnathostomes) nektic, whereas our reinterpretation assigns only 31.5% of ammonoid, 22.3% of nautilid, 54.6% of tarphycerid and 49.0% of gnathostome genera to this megaguild (SSCG, electronic supplementary data). We interpret most Palaeozoic ammonoids (55.2%) as planktic, and most nautilids (56.2%) and gnathostomes (51.0%) as demersal (SSCG, electronic supplementary data). This has the effect of reducing Devonian nektic diversity. Furthermore, our analysis places 38% of ‘ostracoderm’ grade vertebrates in the nekton (SSCG, electronic supplementary data), whereas Klug *et al.* [5] considered all these demersal—this greatly increases pre-Devonian nektic diversity. When the ecological classifications of Klug *et al.* [5] are applied to SSCG diversity data, the result is a slightly more extensive DNR than they depicted (electronic supplementary

material, figure S22*a*). Conversely, when our classifications are applied to the diversity data of Klug *et al.* [5], no DNR can be discerned (electronic supplementary material, figure S22*b*). Thus, ecological classifications control much of the resultant pattern (electronic supplementary material, figure S21). These re-coding scenarios (electronic supplementary material, figure S22) can be somewhat misleading though; higher taxa not discussed by Klug *et al.* [5] cannot be reassigned to any megaguild. Differences affecting the Cambrian, for example, reflect the addition of arthropod, chaetognath, chordate and cnidarian taxa (electronic supplementary material, figures S18*b*, S19*b*, S20*b* and S21). Similarly, our analyses include more Devonian–Permian demersus (electronic supplementary material, figure S19*b*) and Ordovician–Silurian nekton (electronic supplementary material, figure S20*b*), because many of the taxa filling those niches during those periods, such as conodonts, were not considered by Klug *et al.* [5] (electronic supplementary material, figure S21).

Conodonts comprise much of the Early Palaeozoic nektonic diversity and control the relative occurrence curves (figure 1; electronic supplementary material, figure S20). If conodonts are assigned to either the demersus or the plankton, then nekton are no longer as notable a presence prior to the Devonian. However, conodonts are so prevalent in the Devonian that the conodont-free nekton would be limited to at most 34% of occurrences—well below the 96% depicted by Klug *et al.* [5]. A DNR is impossible if conodonts are included in the analysis, regardless of how they are treated ecologically.

Klug *et al.* [5] assigned all ammonoids to nekton, whereas we distinguished planktic, demersal and nektonic morphologies. If all ammonoids are assigned to the nekton, there is a 21-point nektonic diversity increase (SSCG) through the Devonian, which, while notable, is well below the approximately 40-point nektonic increase depicted by Klug *et al.* [5]. Even with this more inclusive nekton, the Devonian increases are still surpassed by the Permian increases (22-points, SSCG).

## 6. Conclusion

Nekton were common throughout the Palaeozoic, and eunekton gradually increased diversity and occurrences. Thus, our analyses did not reveal evidence for a DNR; nor do we find that saturation of demersal niches was a trigger for nektonic diversifications (contra [5]). Increases in the rate of eunektonic diversification began in the Silurian (as in [5], albeit at a higher rate in our analysis), when demersal diversity and occurrences were reduced relative to the Ordovician (figure 1; electronic supplementary material, figures S15 and S16). Demersal occurrences were similarly reduced in the Devonian when eunektonic occurrences first proliferate (electronic supplementary material, figure S16*c*), and in the Carboniferous when occurrences in the eunekton overtook those in the planktonekton (figure 1*c*) and eunektonic diversity further increased (figure 1*b*).

Sea level has been proposed as a possible control on early vertebrate diversity [40], but global Palaeozoic sea-level changes do not appear to be correlated with eunektonic diversity and

occurrence patterns (electronic supplementary material, figure S32). Increases in the rate of eunektonic originations occur in the Silurian, and eunekton first represent the majority share of non-benthic aquatic diversity in the Carboniferous. This is broadly consistent with major developments in terrestrial plant evolution, i.e. the origin of tracheophytes (vascular plants) in the later Silurian and Early Devonian [41,42], and the exponential increase in plant diversity and biomass in the Carboniferous [42]. Increased terrestrial vegetation resulted in an increased nutrient flux, which in turn increased aquatic productivity [43,44]. This heightened productivity could have provided the resources necessary to sustain diverse and abundant nektonic communities.

Ocean O<sub>2</sub> concentrations were lower in the Early Palaeozoic than today, and there is an emerging consensus that a mid-Palaeozoic oxygenation event coincided with these developments in terrestrial plant evolution [45–47]. Eunekton are among the largest and most active marine organisms. Oxygen levels limit both metabolic rate and body size [48], so it is likely that O<sub>2</sub> concentrations could also limit eunektonic diversity and abundance. Most O<sub>2</sub> curves predict increasing atmospheric oxygen during the Late Ordovician–Silurian, a decrease in the Early–Middle Devonian and a further increase through the Late Devonian and Carboniferous [45–47]. This is broadly consistent with the timing of eunektonic increases and the planktonekton to eunekton transition, although the data are not sufficiently robust to justify a statistical correlation (electronic supplementary material, figure S33).

We did not observe a DNR. Nekton were already established by the Cambrian. The Early Palaeozoic was dominated by demersus, euplankton and planktonekton, which likely had lower O<sub>2</sub> requirements than larger, more active eunekton. Eunekton may have diversified in the Silurian in response to increasing global O<sub>2</sub> concentrations, but the Middle Palaeozoic was dominated by high-occurrence, low-diversity, planktonekton. Planktonektonic taxa were devastated by the end-Devonian mass extinction; the more diverse eunekton were also impacted, but recovered more readily. Eunekton increased in diversity and occurrences through the remainder of the Palaeozoic and remain prominent today.

**Data accessibility.** Electronic supplementary data are archived at <https://doi.org/10.5061/dryad.d69512q>.

**Authors' contributions.** C.D.W. and D.E.G.B. conceived the study. C.D.W. designed the research, assembled the data, performed analyses and created figures. C.D.W. and D.E.G.B. interpreted the results. C.D.W. prepared the manuscript with input from D.E.G.B. Both authors approved the final version.

**Competing interests.** We declare we have no competing interests.

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