



# DID HARD SUBSTRATE TAXA DIVERSIFY PRIOR TO THE GREAT ORDOVICIAN BIODIVERSIFICATION EVENT?

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Typescript received 14 October 2019; accepted in revised form 20 March 2020

**Abstract:** The Great Ordovician Biodiversification Event (GOBE) refers to one of the greatest increases in biodiversity during the Phanerozoic. Recent studies have shown that this taxonomic increase can be attributed to elevated origination rates around the Dapingian–Darriwilian boundary in the Middle Ordovician, while extinction rates stayed relatively constant throughout the Ordovician. Even though this global pattern of origination and extinction appears similar across diverse groups and geographical areas, earlier studies suggested that hard substrate taxa may have diversified prior to the GOBE, during the Early Ordovician. Here, we quantify Ordovician diversification dynamics of hard substrate taxa

while simultaneously accounting for temporally varying sampling probabilities. Diversification rates of hard substrate taxa, both as a whole and when analysed as separate groups, appear to be very similar to those of free-living benthic taxa. The observation that the diversification dynamics of many different taxonomic and ecological groups show the same temporal pattern, suggests a common cause of Ordovician diversification dynamics.

**Key words:** capture–recapture, hard substrate, echinoderm, bryozoan, Great Ordovician Biodiversification, diversification dynamics.

THE Great Ordovician Biodiversification (GOBE) was one of the greatest increases in biodiversity through the Earth's history (Sepkoski *et al.* 1981; Webby *et al.* 2004; Harper 2006; Servais & Harper 2018). Many previous studies have shown an increase in family, genus and species richness for many different taxonomic groups or regions during the Darriwilian (for an overview see Stigall *et al.* 2019). However, such increases can happen through either low extinction rates or high origination rates, since taxonomic richness is the result of the balance between extinctions and originations. A first attempt at estimating origination and extinction probabilities for the most commonly preserved Ordovician taxonomic groups was carried out by Connolly & Miller (2001a, 2002). Here, probabilities were estimated for equal-length time intervals that do not conform to current standard geological stages and are hence difficult to compare to much of the published literature. A recent study using more data and standard geological stages showed that the greatest increase in genus richness happened at the Dapingian–Darriwilian boundary, due to increased origination rates rather than lowered extinction rates (Franeck & Liow 2019a). Taxonomic groups for which there are large volumes of fossil occurrence data,

including trilobites, brachiopods and molluscs (Zhan & Harper 2006; Rasmussen *et al.* 2007; Harper *et al.* 2015; Trubovitz & Stigall 2016; Colmenar & Rasmussen 2018), separately show the same Dapingian–Darriwilian origination peak (see Franeck & Liow 2019b, figs S12, S13, S15). However, while taxonomic counts have been tabulated for other taxonomic groups, such as echinoderms (Smith 1988; Wright & Toom 2017) and bryozoans (Ernst 2018; Hageman & Ernst 2019) over the Ordovician, diversification dynamics have rarely been estimated for them. Some studies suggest a gradual increase in taxonomic richness from the Early or Middle Ordovician towards the Late Ordovician for crinoids and bryozoans (Wright & Toom 2017; Ernst 2018), but others find evidence for an Early Ordovician increase in taxonomic richness for echinoderms and bryozoans (Smith 1988; Hageman & Ernst 2019).

A natural question to ask is whether the previously under-investigated taxa show the same temporal patterns of diversification that are documented on a global scale. Given the generality of the Dapingian–Darriwilian peak in origination rates across vastly different taxonomic groups (e.g. trilobites, brachiopods and molluscs (see Franeck & Liow 2019a, SI), and also disparate geographical regions

(Baltica and Laurentia; see Franeck & Liow 2019a), a naïve expectation is that other groups should have the same temporal origination peak.

There are indications that the diversification of some benthic taxa, including certain groups of echinoderms and bryozoans may be controlled by the availability of hard substrates (Guensburg & Sprinkle 1992; Wilson & Palmer 1992; Wilson *et al.* 1992; Taylor & Wilson 2003; Ernst 2018). Hard substrate abundance increased dramatically, starting from the Cambrian, and this increase did not cease until at least the Middle Ordovician (Wilson & Palmer 1992; Taylor & Wilson 2003; Wright & Cherns 2016a). While Taylor & Wilson (2003) called the Ordovician the ‘golden age for epizoans on hard substrates’, it is currently unclear when such epizoans diversified and if the abundance of hard substrates may have influenced their diversification.

To remedy this gap in our knowledge, we investigate diversification rates of Ordovician epizoans (animals living on surfaces; Taylor & Wilson 2003) on hard substrates and ask when they experienced their greatest origination rates. Might it have been around the Dapingian–Darriwilian boundary, in the course of the GOBE (*sensu* Stigall *et al.* 2019)? Do their temporal diversification patterns give any support to the idea that the availability of hard substrates controlled their evolutionary rates?

To examine these questions, we estimate and contrast the diversification dynamics, whilst simultaneously modelling sampling probabilities, of taxonomically diverse groups of benthic epizoans with two contrasting life habits, namely those likely to be attached to hard substrates and those that are interpreted as free-living. Epizoans likely to be attached to hard substrates include crinoids (Brett & Liddell 1978; Palmer 1982), bryozoans (Palmer & Palmer 1977; Brett & Liddell 1978; Palmer 1982; Wilson & Palmer 1992; Webby 2002; Taylor 2016), tabulate corals (Wilson & Palmer 1992; Taylor & Wilson 2003), edrioasteroids (Taylor & Wilson 2003), some sponges (Webby 2002) and a limited number of brachiopods (Palmer 1982; Taylor 2016). Free-living benthos of the Ordovician include echinoids, asteroids, gastropods and trilobites. To understand how these taxonomic groups contributed separately to Ordovician dynamics, we also estimate diversification rates individually for those clades within these two groupings for which there are enough occurrence data for robust inference.

## DATA AND METHOD

### *Data*

We downloaded a dataset of occurrence data with accepted genus names from The Paleobiology Database

(PBDB, <https://paleobiodb.org/>) on 15 May 2019 (details in Franeck & Liow 2020). Cambrian and Silurian data were also included to provide extra time bins before and after the Ordovician to eliminate edge effects (see details below). The dataset thus consists of one to multiple observations of any given genus, regardless of whether it is associated with a specific epithet, in one to multiple time intervals (see next section). We manually inspected and corrected genus names for errors before analysing the data.

### *Binning of time intervals*

Each occurrence in the PBDB dataset is associated with a time interval, based on the stratum from which that data point was collected. This time interval is commonly either a regional or a global Ordovician stage or series. Durations of time intervals in the downloaded dataset range from 0.4 to 66 myr, with 75% of the occurrences associated with time intervals of up to 11.4 myr. Temporal resolution of the occurrences provided in the PBDB were improved using two extra sources of information, namely the Macrostrat database (<https://macrostrat.org/>) and the Rasmussen *et al.* (2019) compilation. Macrostrat provides age ranges for mainly North American formations that are more finely resolved than those provided in the PBDB. The Rasmussen compilation assigned formation names from the PBDB, using information from the published literature, to their respective Ordovician stage slices *sensu* Bergström *et al.* (2009). Each occurrence in our downloaded dataset is hence associated with one or more age ranges (i.e. the original from the PBDB, from Macrostrat and/or the Rasmussen compilation). We picked the finest temporal resolution for each occurrence for downstream analyses. After the incorporation of the more finely resolved age data, 75% of the occurrences are in time intervals of 7.8 myr or less (Franeck & Liow 2020, fig. S1). All occurrences in reported time intervals larger than 12 myr were excluded to reduce uncertainty of the age estimates in the analysed dataset. Using this filtered dataset, we simply assigned occurrences to the global stage in which the retained age interval falls. Occurrences in regional stages or series that cross one or more global stage boundaries (57% of the retained 150 530 occurrences) were randomly assigned to one of the global stages that they cross, assuming a uniform probability.

### *Hard substrate or free-living benthic taxa*

Encrusting or attaching hard substrate taxa (henceforth hard substrate taxa) in our study include representatives

of brachiopods, bryozoans, corals, sponges and echinoderms (Wilson & Palmer 1992; Sprinkle & Guensburg 1995; Taylor & Wilson 2003; Kröger *et al.* 2017a; Reich *et al.* 2017). Free-living benthic taxa in the comparison group include benthic trilobites, molluscs (except cephalopods) and free-living echinoderms. While we have tried to be as transparent and accurate as possible in our life habit assignments (Table 1; see also Franeck & Liow 2020), there are remaining ambiguities (see below for details).

Some inarticulate Ordovician brachiopods, namely craniids and discinids, attached themselves to hard substrates (Emig 1997) so they are in our hard substrate grouping (8 genera with 363 occurrences). All other brachiopods were excluded from our study (see Discussion, below).

Bryozoans were common as encrusters and are frequently observed in Ordovician reef assemblages (Webby 2002; Taylor 2016), all Ordovician bryozoans were therefore included as hard substrate taxa (196 genera with 4676 occurrences).

Tabulate corals have been found encrusting Palaeozoic hard substrates (e.g. Johnson & Baarli 1987; Johnson *et al.* 1998; Elias & Young 2000) and they are also common in Ordovician reef communities (Webby 2002; see Kröger *et al.* 2017b for examples from Baltoscandia). Hence, tabulate corals were included (1766 occurrences among 88 genera) as hard substrate taxa.

Demosponges (Molineux 1994; Bromley & Heinberg 2006), stromatoporids (Wood *et al.* 1992; Taylor & Wilson 2003) and hexactinellids (Bromley & Heinberg 2006) were common reef-builders in the Ordovician and hence were included as hard substrate taxa (198 genera with 1650 occurrences).

Echinoderms have a variety of life habits (Lefebvre *et al.* 2013). We used the presence of a preserved attaching mechanism as evidence for a capacity for hard substrate attachment. Attaching echinoderms include

edrioasteroids (Brett & Liddell 1978; Palmer 1982; Taylor & Wilson 2003; Taylor 2016), crinoids (Palmer & Palmer 1977; Brett & Liddell 1978; Palmer 1982; Sprinkle & Guensburg 1995; Holterhoff 1997), eocrinoids (Sprinkle 1973; Palmer 1982; Parsley & Prokop 2004), diploporids (Bockelie 1984) and paracrinoids (Brett & Liddell 1978; Guensburg 1991), totalling 212 genera with 1904 occurrences. Note that there are exceptions from these general assignments and assignment uncertainties (for details see Table 1 and Franeck & Liow 2020, assignments).

The free-living benthic taxa in our analyses consist of trilobites (1415 genera with 22 079 occurrences), molluscs (except cephalopods, 506 genera with 10 885 occurrences) and echinoderm classes that did not use skeletonized attachment strategies to hard substrates (85 genera with 788 occurrences), specifically: Stylophora (Lefebvre *et al.* 2013), Ctenocystoidea, Cincta (Parsley & Prokop 2004), Soluta (except *Coleicarpus*; see Daley 1996), Echinoidea, Rhombifera, Asteroidea, Ophiuroidea, Stenuroidea, Ophiocystioidea and Somasteroidea. Genera from other generally attaching echinoderm groups were also included if there was independent evidence reported in the literature that they were free-living (see Franeck & Liow 2020). Note that pelagic trilobites (see Fortey 1985), were completely excluded from the analysis. For a complete overview of which taxa were assigned to hard substrate or free-living taxa, which taxa were excluded, and the references on which these assignments were based, see Franeck & Liow 2020, assignments).

### Model

We used a capture–recapture model that is now commonly applied to palaeontological datasets (e.g. Connolly & Miller 2001b; Liow & Nichols 2010; Sibert *et al.* 2018) to estimate extinction, origination and sampling probabilities simultaneously. The data manipulation and

**TABLE 1.** Overview of the data.

Clade	Hard substrate taxa			Free-living benthos			Excluded		
	Occurrences	Presences	Genera	Occurrences	Presences	Genera	Occurrences	Presences	Genera
Bryozoans	4676	486	196	0	0	0	0	0	0
Brachiopods	363	35	8	0	0	0	30 069	2317	950
Corals	1766	215	88	0	0	0	1472	231	116
Echinoderms	1904	355	212	698	208	131	854	151	91
Poriferans	1650	342	198	0	0	0	91	26	23
Trilobites	0	0	0	22 079	2590	1415	3344	313	181
Molluscs	0	0	0	10 885	1180	506	4422	754	395

The table shows the number of PBDB occurrences, presences and genera that were considered in our analysis as either hard substrate or free-living benthic taxa.

modelling are only briefly described here as they have been detailed several times elsewhere (e.g. Connolly & Miller 2001*b*; Liow *et al.* 2015; Franeck & Liow 2019*a*).

We converted the downloaded, filtered and time binned occurrence data into an observation/non-observation matrix. In this matrix, each row represents one genus, and each column represents one time bin, that is, a global Ordovician stage. If a genus was recorded in a time bin, it is marked with a 1 in the matrix. When a genus is not observed in a given time bin, it is marked with a 0. This 0 indicates that the genus was either extant but not sampled, or truly not extant in that time bin. Note that also the two last Cambrian (series) and first two Silurian (stage) time bins were included, to eliminate boundary effects (Pradel 1996; Connolly & Miller 2001*b*). Using this matrix as our input data, we used the Pradel seniority model (Pradel 1996), a type of capture–recapture model, to estimate survival, seniority, sampling probabilities and population growth rate. This model was originally developed to describe population dynamics for single-populations of extant organisms. Since we are using fossil data, focusing on genus instead of population dynamics, the complement of survival is interpreted as extinction, the complement of seniority as origination, and net population growth as net diversification rate (see e.g. Connolly & Miller 2001*b*; Liow & Nichols 2010; Franeck & Liow 2019*a*). Given that Ordovician stages differ in duration, estimated probabilities were converted into rates using a Poisson model (for details see Liow *et al.* 2015; Franeck & Liow 2019*a*). Estimated probabilities of 1 and 0, and confidence intervals that are 0 or 1 (i.e. those that encompass the full range of possible estimates) indicate convergence issues and were thus removed, as in Liow *et al.* (2015). Net diversification rates greater than 15 (arbitrarily selected as a cut-off after inspection of preliminary results) were also not presented in our plots for the same reason.

We built individual models for each of the life modes (combined hard substrate taxa and combined free-living benthic taxa) and also for the taxonomic groups within the hard substrate taxa (including attaching echinoderms, bryozoans and reef-building poriferans). Models in which life habit was incorporated as a covariate were compared with those without the covariate, using all data combined. For these model comparisons, we ran analyses assuming no difference between the life habit groupings (hard substrate or free-living, see below) for any of the parameters, but also those assuming differences between them (see Table 1 for the specific models we ran). These models were ranked based on the corrected Akaike information criterion (AICc; see Burnham & Anderson 2002). Higher model weights signify a better relative fit. As both AICc and model weights differ among runs, due to the assignment of occurrences in regional stages or series to global

stages, we present the mean and median model weights after 100 runs (Table 2). The analysis, including the model comparison, was performed using the program MARK (White 2016) using the R package RMARK v. 2.2.7 (Laake 2019).

## RESULTS

Origination rates of combined hard substrate taxa estimated separately from free-living benthic taxa, show a peak at the Dapingian–Darriwilian boundary (Fig. 1; Franeck & Liow 2020, fig. S2). Thereafter, they are relatively low and decrease slightly until the end of the Ordovician. Origination rates of free-living benthic taxa are elevated at the Cambrian–Ordovician boundary, drop thereafter until the Floian–Dapingian boundary, and show a peak at the Dapingian–Darriwilian boundary. For the remaining Ordovician, they are low and decrease toward the Silurian boundary, similar to the origination rates of the hard substrate taxa.

Extinction rates for hard substrate taxa increased slightly from the Cambrian–Ordovician boundary towards the Floian–Dapingian boundary. Thereafter, they are relatively low, but increase progressively again until the end of the Ordovician. Extinction rates for free-living benthic taxa are relatively stable from the Tremadocian to the Floian–Dapingian boundary, drop at the Dapingian–Darriwilian boundary, and increase thereafter on average until the end of the Ordovician.

Net diversification rates for hard substrate taxa are positive at the Cambrian–Ordovician and Tremadocian–Floian boundaries (but note the relatively large 95% confidence levels), drop to zero at the Floian–Dapingian boundary and peak at the Dapingian–Darriwilian boundary. Thereafter, they are close to zero, and become negative at the Katian–Hirnantian boundary. Net diversification rates for free-living benthic taxa are high at the Cambrian–Ordovician boundary, drop slightly below zero between the Tremadocian and the Dapingian, and show a peak at the Dapingian–Darriwilian boundary. Thereafter, they are close to zero again, and become negative at the Katian–Hirnantian boundary.

Sampling rates for both hard substrate and free-living benthic taxa increase on average from the Tremadocian towards the Hirnantian.

The best model (1 in Table 2, model weight 98%) among those investigated using all the data combined, is one with independent temporal changes of extinction and sampling but with the same relative changes in origination rates, where hard substrate taxa have higher origination rates than free-living benthic groups (see Table 2; Franeck & Liow 2020, fig. S6). Although our data support uncorrelated changes for extinction and sampling for the

**TABLE 2.** Model weights for the combined dataset.

No.	Model name	AIC.mean	AIC.median
1	Extinction(~t * c)Sampling(~t * c)Origination(~t + c)	0.905	0.977
2	Extinction(~t * c)Sampling(~t + c)Origination(~t + c)	0.075	0.009
3	Extinction(~t * c)Sampling(~t * c)Origination(~t * c)	0.015	0.005
4	Extinction(~t * c)Sampling(~t)Origination(~t * c)	0.005	0
5	Extinction(~t + c)Sampling(~t * c)Origination(~t * c)	0	0
6	Extinction(~t)Sampling(~t * c)Origination(~t * c)	0	0
7	Extinction(~t + c)Sampling(~t + c)Origination(~t * c)	0	0
8	Extinction(~t)Sampling(~t)Origination(~t + c)	0	0
9	Extinction(~t)Sampling(~t + c)Origination(~t + c)	0	0
10	Extinction(~t + c)Sampling(~t + c)Origination(~t + c)	0	0
11	Extinction(~t * c)Sampling(~t + c)Origination(~t * c)	0	0
12	Extinction(~t + c)Sampling(~t)Origination(~t + c)	0	0
13	Extinction(~t)Sampling(~t)Origination(~t * c)	0	0
14	Extinction(~t * c)Sampling(~t * c)Origination(~t)	0	0
15	Extinction(~t * c)Sampling(~t)Origination(~t)	0	0
16	Extinction(~t + c)Sampling(~t + c)Origination(~t)	0	0
17	Extinction(~t)Sampling(~t * c)Origination(~t)	0	0
18	Extinction(~t + c)Sampling(~t)Origination(~t)	0	0
19	Extinction(~t)Sampling(~t + c)Origination(~t)	0	0
20	Extinction(~t)Sampling(~t)Origination(~t)	0	0
21	Extinction(~c)Sampling(~c)Origination(~c)	0	0
22	Extinction(~1)Sampling(~1)Origination(~1)	0	0

Mean and median model weights after 100 replicate runs of parameter estimation and model comparison using all the data in combination (in contrast with Fig. 1 but as in Franeck & Liow 2020, fig. S6). ~t, time-dependence; ~c, covariate (i.e. life habit) dependence; ~1, constant parameters through time by; +, additive combinations by (i.e. varying in concert); \*, multiplicative combinations (i.e. independently varying).

two life habit groups, their extinction dynamics are similar, at least post-Floian (see Fig. 1 for individual estimates of the two groups).

Just like the dynamics of hard substrate and free-living benthic taxa, the individually estimated dynamics of different taxonomic groups among hard substrate taxa (attaching echinoderms, bryozoans and reef-building poriferans) show a Dapingian–Darriwilian peak of origination and net diversification rates (Fig. 2).

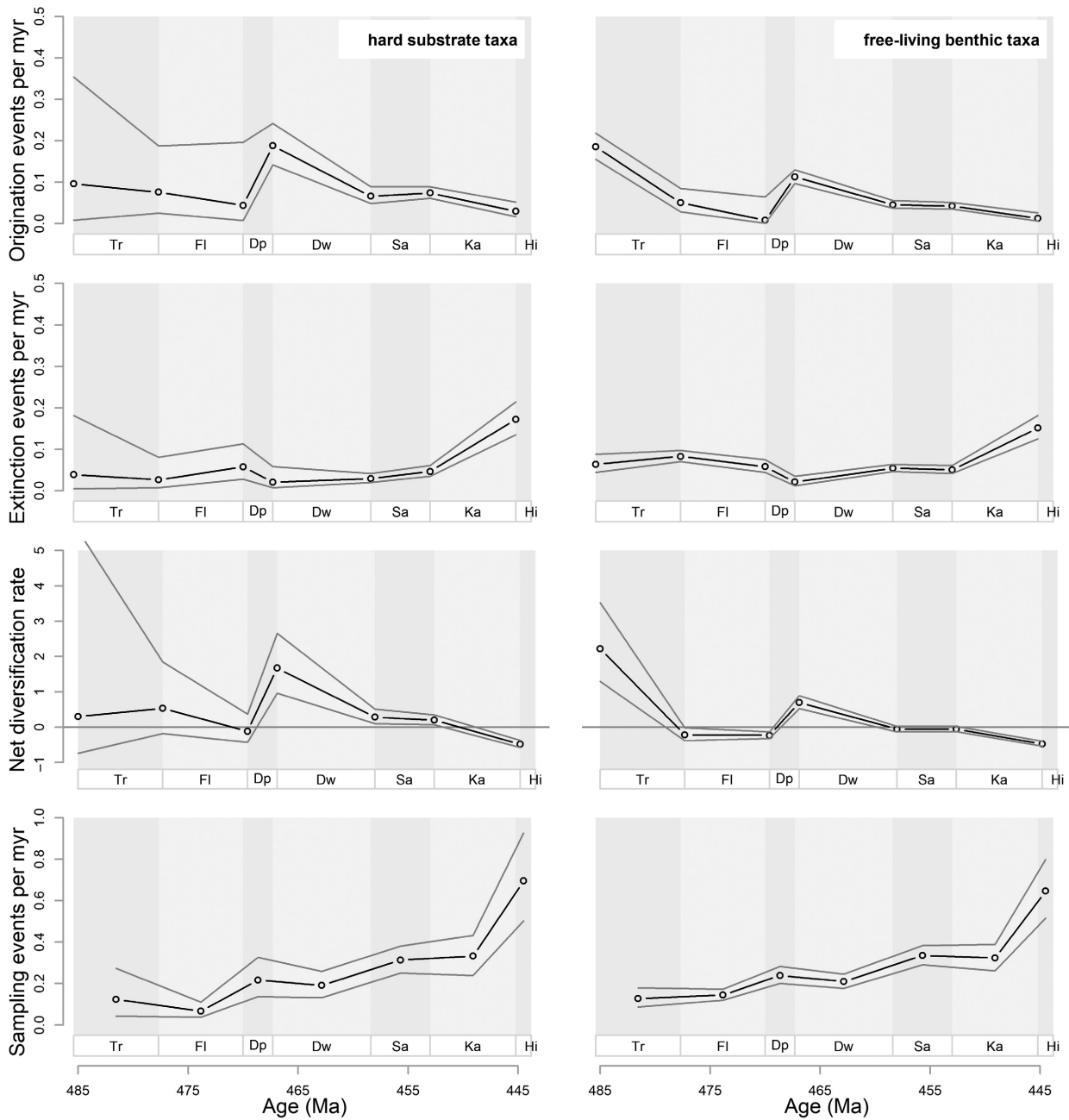
Origination rates for attaching echinoderms and bryozoans are relatively high at the Tremadocian–Floian boundary (Fig. 2, left and middle column), drop thereafter slightly, show a peak at the Dapingian–Darriwilian boundary and decrease thereafter until the end of the Ordovician. Poriferan origination rates (Fig. 2, right column) are relatively low until the Dapingian, show a Dapingian–Darriwilian peak, decline thereafter, and are slightly elevated again at the Sandbian–Katian boundary, before they drop again towards the Hirnantian.

Extinction rates of attaching echinoderms are elevated at the Floian–Dapingian and Dapingian–Darriwilian boundaries, decrease thereafter, and increase again towards the Katian–Hirnantian boundary. Extinction rates of bryozoans are slightly elevated at the Tremadocian–Floian boundary, drop thereafter, stay relatively low until

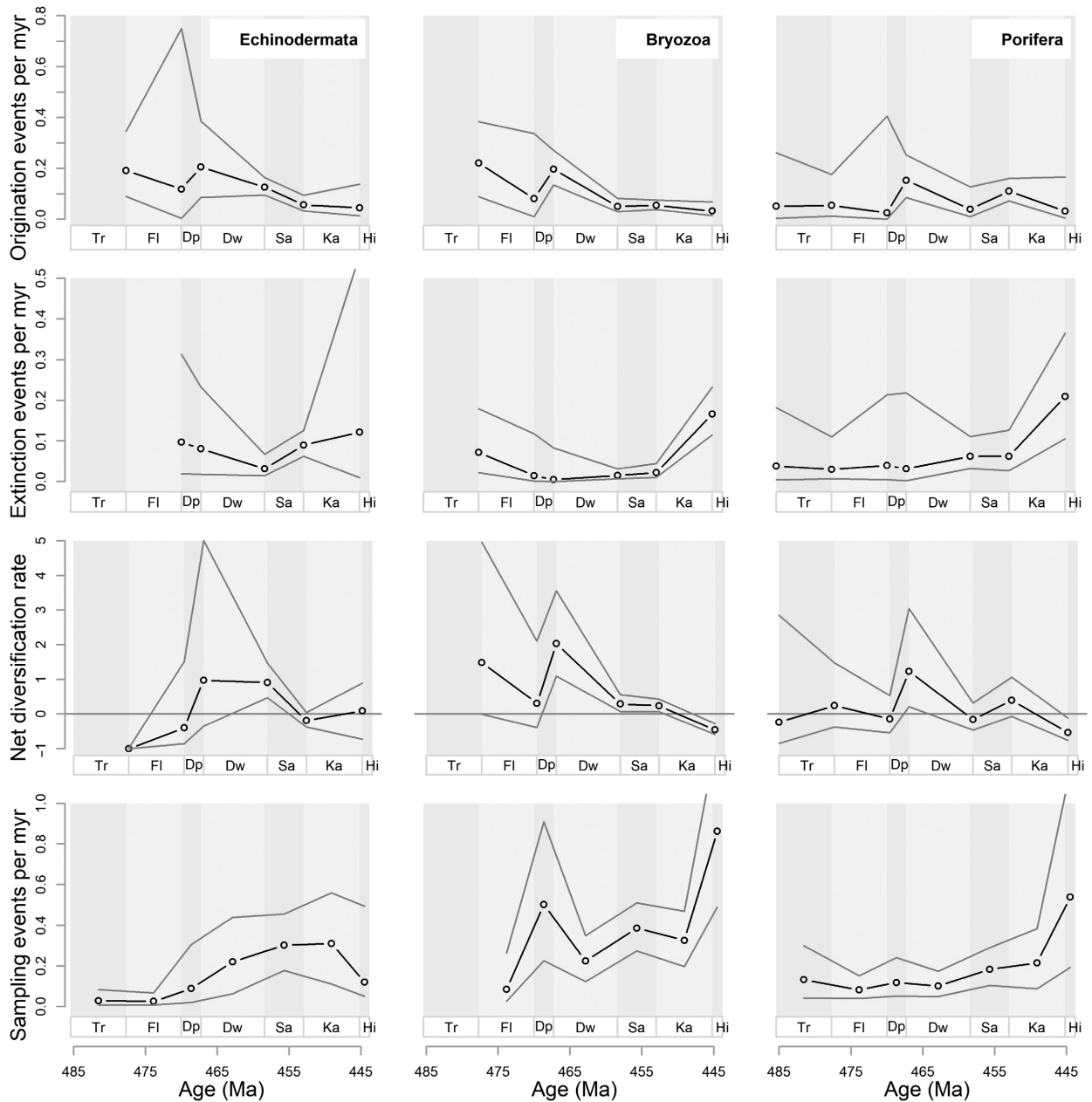
the Sandbian–Katian boundary, and increase towards the Katian–Hirnantian boundary.

Net diversification rates of attaching echinoderms increase towards the Dapingian–Darriwilian boundary, stay at a similar level at the Darriwilian–Sandbian boundary and drop thereafter to values close to zero. Bryozoan net diversification is elevated at the Tremadocian–Floian boundary (however, note the relatively large 95% confidence intervals), and thereafter shows a peak at the Dapingian–Darriwilian boundary. After this peak, bryozoan net diversification drops to values just above zero, and becomes negative at the Katian–Hirnantian boundary. Poriferan net diversification is around zero at the Darriwilian–Sandbian boundary and is slightly elevated again at the Sandbian–Katian boundary, before it drops towards the Katian–Hirnantian boundary.

Sampling rates of attaching echinoderms increase on average from the Tremadocian until the Katian and drop towards the Hirnantian. Sampling rates of bryozoans increase from the Floian to the Dapingian, decrease thereafter again, stay relatively stable until the Katian and are relatively high at the Hirnantian. Sampling rates for poriferans are relatively low, but stable from the Tremadocian until the Darriwilian, where they start to increase slightly until the Katian, and are relatively high in the Hirnantian.



**FIG. 1.** Diversification and sampling dynamics of hard substrate taxa and free-living benthic taxa. We present the medians of origination, extinction, net diversification and sampling estimates after 100 runs for 702 hard-substrate genera (10 359 occurrences) and 2052 free-living benthic genera (33 662 occurrences). With each grouping, these are estimated simultaneously. Circles indicate parameter estimates and grey lines the median of 95% upper and lower confidence levels, respectively. Grey, horizontal lines in the net diversification plots mark zero net diversification. *Abbreviations:* Tr, Tremadocian; Fl, Floian; Dp, Dapingian; Dw, Darriwilian; Sa, Sandbian; Ka, Katian; Hi, Hirnantian.



**FIG. 2.** Diversification and sampling dynamics of selected hard substrate taxa. Circles indicate median parameter estimates of attaching echinoderms (left column), bryozoans (middle column) and reef-building poriferans (right column) after 100 replicate runs and grey lines the median of 95% upper and lower confidence intervals, respectively. *Abbreviations* as in Fig. 1.

## DISCUSSION

### *Dissecting components of diversification dynamics*

A recent review of Ordovician evolutionary and ecological dynamics suggested that the Darriwilian was the critical time-interval over which Earth-system and ecological restructuring occurred, even if general increases in

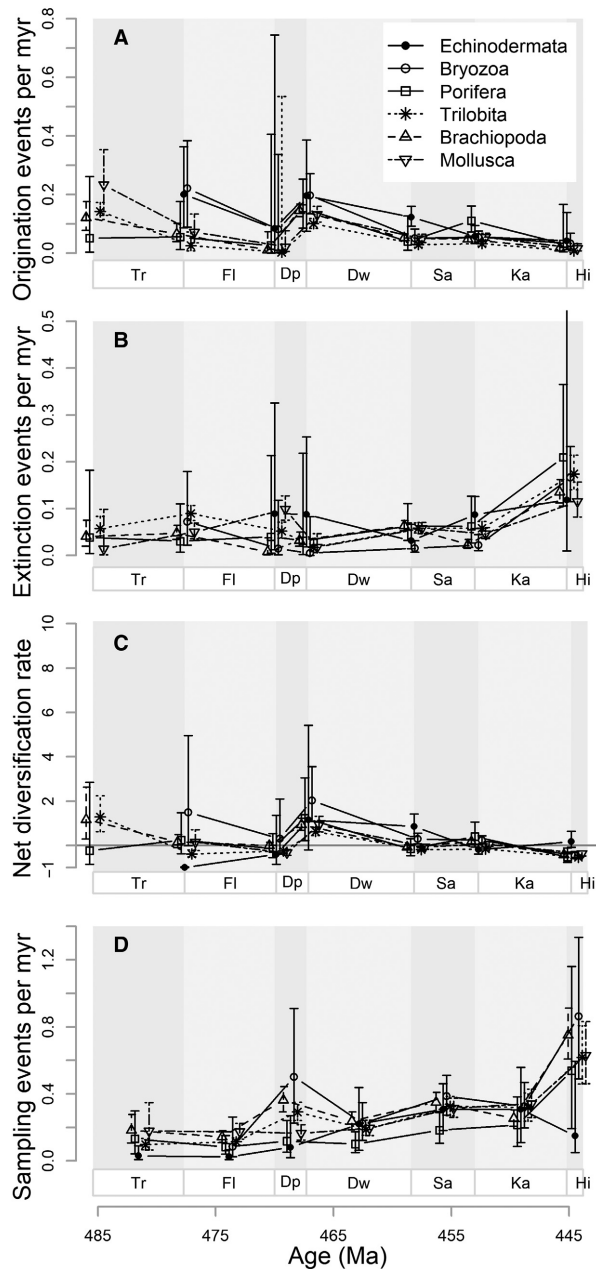
taxonomic and ecological richness are apparent throughout the ‘Ordovician Radiation’ (Stigall *et al.* 2019). Stigall and coauthors suggested associating the term GOBE with only the Darriwilian, as net diversification rates are exceptionally high in this global stage. Clear Dapingian–Darriwilian sampling-corrected origination peaks have already been demonstrated in commonly preserved Ordovician taxa including trilobites, brachiopods and molluscs (see

Franeck & Liow 2019*b*, SI). Here, we further corroborate Stigall *et al.*'s idea, with the demonstration that the individual dynamics of attaching echinoderms, bryozoans, and reef-building poriferans individually but also as a group (namely hard substrate taxa), show increased origination rates at the Dapingian–Darriwilian boundary (Fig. 2).

A direct comparison of the inferred stage-level diversification dynamics of hard substrate taxa, with trilobites, brachiopods and molluscs, shows similar relative interval-to-interval changes in diversification dynamics for all groups investigated (Fig. 3). This supports the idea that one or more global/common drivers might have affected diversification dynamics, especially post-Darriwilian. However, the early Ordovician origination rates of attaching echinoderms and bryozoans are elevated, compared to the rates of the other taxonomic groups (note that median 95% confidence are also greater for these specific estimates, Fig. 3). Echinoderms had elevated origination rates both during the Early Ordovician and the GOBE, hence lending support to Sprinkle & Guensburg's (1995) idea that they already experienced rapid radiation early on (Fig. 3a). On the contrary, Wright & Toom (2017), found no Early Ordovician increase in the taxonomic richness of crinoids. A different conclusion, suggesting a pre-GOBE diversification was reached by Hageman & Ernst (2019) who found that taxonomic richness of bryozoans was elevated around the Floian–Dapingian boundary, using more highly resolved temporal data (with time bins that range from 1.35 to 2.97 myr). However, an explanation for the differing results may be that the Hageman & Ernst study used raw taxonomic counts as a proxy for taxonomic richness, rather than accounting for incomplete sampling and estimating diversification rates, as we have done here.

#### *The increasing availability of the hard substrate niche*

The idea that there is a positive association between the increase in the taxonomic richness of hard substrate taxa and the availability of hard substrates over the Palaeozoic, especially during the Ordovician, has previously been raised (e.g. Wilson & Palmer 1990, 1992; Guensburg & Sprinkle 1992; Rozhnov & Palmer 1996). This also includes the increased availability of skeletal material, which can act as a hard substrate (Pruss *et al.* 2010; Pruss & Clemente 2011). For a better handle on if and how the availability of hard substrates could have driven the evolution of taxa exploiting this niche (Palmer 1982; Wright & Cherns 2016*a*), there is a need to estimate the temporal dynamics of both the niche (hard substrates in this case) and the taxa involved. Our results provide estimates for the latter. Unfortunately, the current temporal resolution



**FIG. 3.** Diversification and sampling dynamics of attaching echinoderms, bryozoans, reef-building poriferans, superimposed on the three most represented taxonomic groups from the whole Ordovician data set (trilobites, brachiopods and molluscs). Note the similar origination, extinction and net diversification dynamics post Darriwilian for all groups plotted. Circles indicate median parameter estimates after 100 replicate runs, and vertical lines indicate the median of 95% upper and lower confidence intervals. *Abbreviations* as in Fig. 1.

of hard substrate occurrences and hence their temporal distributions (see e.g. Christ *et al.* 2015; Wright & Cherns 2016*b*) are not fine enough to be quantitatively or even



only qualitatively associated with the temporal dynamics we see in our taxonomic analyses. That said, the hypothesis that the increase in hard substrate availability and the increased origination of hard substrate taxa were connected may still be valid.

Although attaching epizoa are already observed in the Cambrian fossil record, this sessile niche was much less exploited than compared with the Ordovician (Taylor & Wilson 2003) in terms of the number of genera using it. Given that some taxa could already attach themselves to a substrate in Cambrian times, why do we first see an increase of such taxa only in the Ordovician? A valid question in this context is how and why the availability of hard substrates had been changing from the Cambrian to the Ordovician. Wilson & Palmer (1992) wrote that hardgrounds, which are synsedimentarily lithified carbonate sea-floors, 'became extraordinarily common in the Ordovician'. This Ordovician increase in hardground availability has been attributed to the increased intensity and depth of bioturbation compared to the Cambrian (Wright & Cherns 2016a, b). A continued increase in hardground availability may be due to positive feedback mechanisms. For instance, crinoid ossicles function as crystallization cores for calcite precipitation (Wilson *et al.* 1992) that often result in hardground formation (Christ *et al.* 2015), which in turn creates more available habitat to be exploited by crinoids and other hard substrate taxa.

Although hard substrate taxa included in our study were, in many cases, associated with reefs (Webby 2002), which are a special kind of hard substrate (Taylor & Wilson 2003; Kröger *et al.* 2017a), our inferred diversification dynamics should not be read as that of only reef complexes. This is not least because the evolution of hardground communities and reef expansion were probably decoupled (Webby 2002). In addition, our analyses go beyond those of hardground assemblages *sensu stricto*, as the taxa included in this study could also attach to hard substrate which might be lying on mud (e.g. skeletal debris). While the number of reef-associated hard substrate taxa would be interesting to quantify here, it is not possible with the data that was available.

#### *Caveat I: identifying hard substrate taxa*

Some of the taxonomic groups we included here have a great variety of probable attaching mechanisms to different kinds of substrates (Taylor & Wilson 2003; Lefebvre *et al.* 2013; Topper *et al.* 2018) hence, our assignment of taxa to substrate types and life-habits comes with a level of uncertainty. Although we are transparent about our assignments, attributing decisions to the published literature where possible (for specifics, see Data and Method, above, and Franeck & Liow 2020) our assignment of

brachiopods and echinoderms warrant extra discussion here. We only included eight attaching hardground brachiopod genera in our analyses, because it was not possible to assign one of the two life-habit covariates (hard substrate or free-living) to the remaining 600+ brachiopod genera without expert knowledge and/or further detailed research on the morphology and ecology in each of them. In addition, generalist species amongst brachiopods seem to be able to settle on and attach to diverse substrates (Richardson 1997). While there is uncertainty around our general inference because of the brachiopod 'problem', this does not change our inferences based on the specific dataset we have used here. Future work on brachiopod life-habits could shed light on whether hard substrate versus non-hard substrate genera among them conform to patterns we see among our largely non-brachiopod taxa (see Fig. 1).

The presence of a holdfast for an echinoderm is taken as positive evidence that it can attach itself to a hard substrate (Lefebvre *et al.* 2013; Zamora *et al.* 2017). Echinoderms may have had even more diverse life habits than brachiopods, and there are 91 genera (out of 434) for which no life-habit could be assigned (see Table 1). For instance, cyclocystoids were excluded from our analysis, as their attachment mode is debated (Sprinkle *et al.* 2015; Reich *et al.* 2017). Likewise, callocystids were excluded as their attaching mechanism is often not preserved or debated (see also descriptions and discussions in: Kesling & Mintz 1961; Brett 1978; Broadhead & Strimple 1978; Sumrall & Sprinkle 1999).

Those echinoderm taxa that are known to possess root structures (e.g. Brett 1981), or other attachment mechanisms to soft substrates (e.g. Dornbos 2006; Zamora *et al.* 2017), were excluded from our analysis (see Franeck & Liow 2020, assignments). While there may be a few remaining errors to our assignments to life-habits, the overall inferred Middle Ordovician diversification dynamics of all echinoderms does not differ much from the diversification dynamics of attaching echinoderms (Franeck & Liow 2020, fig. S5). Hence, we believe that our results are robust to remaining errors.

#### *Caveat II: issues of preservation and sampling*

We have dealt with the incompleteness of the fossil record by using a capture–recapture model, where sampling probabilities were estimated simultaneously with the diversification dynamics to account for biases introduced by incomplete sampling. However, all models come with assumptions, and capture–recapture models are no exception. The specific assumptions and the robustness of estimates to the violation thereof for the Pradel model have been discussed in detail elsewhere (Nichols & Pollock

1983; Pollock *et al.* 1990; Pradel 1996; Connolly & Miller 2001*b*). One assumption we want to emphasize here is that estimated parameters for any given grouping are assumed to be the same within the studied time intervals. In other words, we assume that all hard substrate taxa included in any set of analysis have the same sampling, origination and extinction probabilities within each Ordovician stage, and we might interpret our results as universal across all other unsampled, skeletonized hard substrate taxa. The same applies to the free-living benthic taxa we analysed. Note that we cannot account for groups that are completely absent from the data available, notably soft-bodied organisms which may otherwise belong to our hard substrate or free-living benthos groups.

## FUTURE PROSPECTS AND CONCLUSION

There is a lively debate on the potential global drivers of the GOBE. These include the cooling and oxygenation of the Ordovician oceans (Saltzman & Young 2005; Trotter *et al.* 2008; Rasmussen *et al.* 2016; Edwards *et al.* 2017), increased tectonic activity (Miller & Mao 1995; Miller & Connolly 2001), extraterrestrial input (Schmitz *et al.* 2008; discussed in Lindsog *et al.* 2017) and the appearance of plankton in the fossil record from the Late Cambrian (Servais *et al.* 2008, 2016). In order to put any of these hypotheses to test, we argue that the components of diversification dynamics (i.e. both origination and extinction) must first be estimated, in addition to changing taxon richness. However, reliable diversification estimates require not only good models but also data that are robust and plentiful. We hence emphasize the need for detailed morphological and ecological (life habit in our case) data and a continued effort in taxonomic work so that past evolutionary changes in our biosphere can be understood.

The Ordovician evolutionary dynamics clearly follow an overarching pattern, showing a Dapingian–Darriwilian peak of origination and net diversification rates. This study also provides evidence for a synchronization of diversification dynamics among diverse taxonomic, ecological and biogeographical groupings throughout the Ordovician. Increasingly nuanced analyses can contribute to the details and hence mechanistic underpinnings of broad radiations including the Ordovician Radiation and GOBE.

*Acknowledgements.* This work was funded by a graduate student fellowship of the Natural History Museum at the University of Oslo, Norway. FF is grateful to Mark Wilson, Paul D. Taylor, Melanie Hopkins, Seth Finnegan, Selina Cole, Sarah Sheffield, Lars Holmer, Christian Rasmussen, Andrej Ernst, Hans Arne Nakrem, Wolfgang Kiessling, James Saulsbury, Mike Reich, Josh

Zimmt, David Bapst and Bjørn Tore Kopperud for discussions. We thank Samuel Zamora and an anonymous reviewer for their constructive criticisms. This article is a contribution to IGCP Project 653: ‘The Onset of the Great Ordovician Biodiversification Event’. This is PBDB publication number 368.

## DATA ARCHIVING STATEMENT

Data and supplementary material for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1jwstqjrb>

*Editor.* Imran Rahman

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