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Comparisons between Cambrian Lagerstätten assemblages using multivariate, parsimony and Bayesian methods

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Abstract

Exceptional fossil deposits exhibiting soft-part preservation, or *Konservat-Lagerstätten*, are particularly prevalent in Cambrian rocks and provide detailed information on fossil assemblages not available from conventional deposits. It has long been recognised that many of these assemblages exhibit certain taxonomic similarities, with many elements seemingly having cosmopolitan distributions. These types of assemblages, particularly those of Cambrian age, have become known as Burgess Shale-type (BST) biotas, named for the famous deposit in the Canadian Rocky Mountains where fossils preserved in this way were first discovered. This study provides the first broad-scale analysis of the taxonomic relationships between

all major BST biotas. We compiled a database of the presences and absences of over 600 genera within 12 Lagerstätten from Laurentia, Siberia, South China and East Gondwana, ranging in age from Cambrian Series 2 through Series 3 (late-early to middle Cambrian; c. 518 – 502 Ma), and analysed this using a variety of quantitative methods in order to investigate the relationships between these sites. Non-metric multidimensional scaling (NMDS) ordination, cluster analysis and Parsimony Analysis of Endemicity (PAE) were used to group localities and examine relationships. We also used Bayesian inference and illustrate the benefits of this approach to biogeographic studies. Results suggest that both space and time have important effects on the taxonomic constitution of BST biotas, and that the similarity of these assemblages appears to increase from Series 2 through Series 3, largely driven by increases in cosmopolitanism of biomineralised taxa such as trilobites and brachiopods. There is also evidence of higher-level taxonomic turnover across this period. Endemic taxa help amplify these patterns, despite their frequent exclusion from biogeographic analyses.

Keywords: Chengjiang, Burgess Shale, Emu Bay Shale, BST, palaeobiogeography

1. Introduction

1.1 Background

Cambrian *Konservat-Lagerstätten* – fossil deposits exhibiting exceptional preservation of soft parts – offer great insight into the diversity and ecology of early communities following the ‘Cambrian explosion’ (Conway Morris, 1985). As well as providing enhanced biological information about individual organisms, they also provide a more faithful representation of the full diversity and relative abundances of taxa present within these communities. This information should allow us to undertake not only more informative and unbiased ecological analysis of these early communities, but also to examine their biogeographic relationships based on shared taxa. The former has been undertaken for several Cambrian Lagerstätten (e.g. Conway Morris, 1986; Ivantsov et al., 2005; Caron and Jackson, 2008; Dornbos and Chen, 2008; Zhao et al., 2010; 2014); the latter has also been pursued (e.g. Hendricks and Lieberman, 2007; Hendricks et al., 2008; Hendricks, 2013) and is the focus of the present contribution.

It is well known that many Cambrian Lagerstätten share common faunal elements. A substantial number of genera found within these assemblages exhibit largely cosmopolitan distributions, e.g. the sponges *Choia*, *Hazelia*, *Leptomitus* and *Protospongia*, sponge-like *Chancelloria*, cnidarian *Byronia*, brachiopods *Lingulella* and *Nisusia*, anomalocaridid *Anomalocaris*, lobopodian *Hallucigenia*, the euarthropods *Canadaspis*, *Isoxys*, *Leanchoilia*, *Liangshanella*, *Naraoia* and *Tuzoia*, annelid *Selkirkia*, and the enigmatic taxa *Haplophrentis*, *Wiwaxia*, *Eldonia* and *Dinomischus*. It is likely that at least some of these had larval stages capable of long

distance dispersal via ocean currents (García-Bellido et al., 2007; Han et al., 2008; Zhao et al., 2011). These taxa are not particularly informative in a biogeographic sense, as their broad distributions provide little evidence when attempting to draw conclusions about relationships between localities; however, their shared presences suggest that we are looking at similar types of communities. These have been termed Burgess Shale-type (BST) biotas, named for the famous Cambrian Series 3 deposit in the Canadian Rocky Mountains.

1.2 Previous work

Comparisons between BST biotas have been made by many authors; however, these have not always employed quantitative analysis. One exception is the work of Hendricks et al. (2008), who used species occurrence data and continental reconstructions to examine the geographic and temporal distribution of Cambrian arthropods, and showed that soft-bodied species had wider geographic and stratigraphic ranges than contemporaneous trilobites. Hendricks (2013) conducted a similar analysis of a wider range of Cambrian metazoan phyla, as well as algae and cyanobacteria, and showed that patterns varied across different clades, and that geographic range of species (and genera) was positively correlated with temporal persistence. However, these studies focused on distributions of individual taxa rather than on assemblage similarity as a whole. One of the few dedicated studies to focus on broad-scale assemblage similarity between Cambrian Lagerstätten was that undertaken by Han et al. (2008), who listed shared genera for a number of site comparisons as part of their analysis, in particular focusing on associations between sites in Laurentia and South China. They suggested that the

Chengjiang (Series 2) and Burgess Shale (Series 3) assemblages were closely related based on qualitative analysis of shared genera, and that the development of pelagic larvae may have resulted in the worldwide distribution of BST biotas. Similarities between the Chengjiang and Burgess Shale assemblages have also been mentioned by other authors (e.g. Conway Morris, 1989, 1998; Babcock et al., 2001). Common generic occurrences between the Kaili Biota (Series 3), and the Burgess Shale and Chengjiang Lagerstätten were discussed by Zhao et al. (2005), who presented figures of 38 and 30 shared genera respectively, and suggested that the greater similarity with the Laurentian site was possibly due to elements of middle-to-outer shelf faunas becoming more stable and widespread by this time. It was suggested by Zhao et al. (2011) that the similarity in age (as well as environment) between Kaili and the Laurentian Burgess Shale and Spence Shale (Utah, USA), may partially account for the similarity seen between these assemblages, and that perhaps age was a greater determinant of assemblage than geography during the late-early to middle Cambrian. Similar features between the Sinsk Biota of Siberia and the Burgess Shale assemblage (the Phyllopod Bed in particular) were noted by Ivantsov et al. (2005), including co-occurrence of a small number of genera. Numerous studies have acknowledged the existence of shared taxa (mostly at genus level) between the Emu Bay Shale (EBS) from South Australia, and other Cambrian Series 2 Lagerstätten in South China; this association has been strengthened in recent years with the discovery of new taxa from the EBS with Chinese representatives (Paterson and Jago, 2006; Paterson et al., 2010; 2012; 2015; 2016). Similarities between Laurentian Series 3 Lagerstätten, such as between those in Utah and the Burgess Shale, are well known (e.g. Hagadorn, 2002; Briggs et al., 2008).

Previous palaeoecological analyses have compared the ecological attributes of BST biotas, e.g. patterns in species abundances, species diversity, phylum-level abundance, and so on (e.g. Ivantsov et al., 2005; Caron and Jackson, 2008; Dornbos and Chen, 2008; Zhao et al., 2014). Ecological comparison of different assemblages has also been undertaken between subsets of individual Lagerstätten, both temporally (e.g. the 'bedding assemblages' from the Burgess Shale's Phyllopod Bed: Caron and Jackson, 2008), or spatially (e.g. the comparison of individual localities of the Chengjiang Biota: Zhao et al., 2012).

The majority of comments relating to taxonomic and biogeographic similarity between BST biotas have been made within studies mostly dedicated to other fields, e.g. palaeobiology and palaeoecology. The literature on the biogeography of these deposits is sparse, simply due to the fact that the spread of sites through space and time might make them seem poor candidates for biogeographic study – at least when considered in isolation. It is important to note that within the biotas there are many different groups that may show completely different biogeographic patterns due to factors such as the history of individual lineages and their dispersal abilities. It has been shown, for example, that early Cambrian trilobite distributions are possibly a vicariant result of the breakup of the short-lived supercontinent Pannotia during the late Neoproterozoic (Lieberman, 2003; Meert and Lieberman, 2004), whereas the distribution of non-trilobite arachnomorph arthropods is more likely a result of other factors such as dispersal ability and sea level change (Hendricks and Lieberman, 2007). For traditional biogeographic purposes it is more sensible to focus on mineralised groups that have wide collective distributions across space and time, such as trilobites (Álvarez et al., 2013; Hally and Paterson, 2014) and/or on clades with robust phylogenetic hypotheses (Lieberman, 2003; Hendricks and Lieberman,

2007). Unfortunately, many groups present within BST biotas do not display these characteristics. Despite this, Cambrian Lagerstätten still contain important biogeographic information that should be considered. The resolution with which we can view these exceptionally preserved assemblages, i.e. the fact that they provide a more faithful representation of taxa present than conventional fossil deposits, means that we can analyse taxonomic associations in greater detail, and then suggest what factors may be responsible for the relationships we see based on the characteristics of the sites in question.

Here we undertake the first quantitative analysis of the taxonomic relationships between all major BST biotas. The importance of these deposits to our understanding of early animal life and evolution has resulted in considerable scholarly attention, and the resulting literature has allowed for the compilation of a substantial database of generic occurrence to be constructed. We analyse this database using a variety of statistical methods to provide insights into how and why BST biotas are related. Our analyses are based on a 'whole of assemblage' perspective (i.e. all genera present at a site were considered, regardless of their biomineralisation), which provides the most informed comparison of biotas and thus a more complete view of the overall diversity of Lagerstätten assemblages compared to conventional deposits.

1.3 Locations and relative ages

In this study we consider 12 BST biotas from East Gondwana (Emu Bay Shale), South China (Chengjiang, Kaili, Guanshan, Balang), Laurentia (Burgess, Wheeler, Marjum, Spence and Kinzers Shales, and Sirius Passet) and Siberia

(Sinsk) (Fig. 1), and ranging in age from Series 2 through Series 3 (formerly late-early through middle Cambrian; Tab. 1). Absolute ages are estimated below and are based on correlation with the Cambrian timescale presented in Peng et al. (2012, Fig. 19.3), unless otherwise stated.

The Chengjiang Biota occurs within the Maotianshan Shale – the middle member of the Yu'an-shan Formation based on the organisation of MacKenzie et al. (2015; as per Hu, 2005; Zhao et al., 2012), overlying the 'Black Shale' and underlying the 'Upper Siltstone' members. Fossils of the Chengjiang Biota occur primarily in the middle-to-upper part of the Maotianshan Shale member, essentially in the middle of the Yu'an-shan Formation (MacKenzie et al., 2015). This is consistent with a mid-late Atdabanian age (e.g. Steiner et al., 2007), or c. 518 Ma based on correlation with Fig. 19.11 of Peng et al. (2012). The Sirius Passet Lagerstätte (lower Buen Formation) is stratigraphically poorly constrained and its position based mainly on the nevadiid affinities of the trilobite *Buenellus* and subsequent correlation with the *Nevadella* trilobite zone of Laurentia (Babcock and Peel, 2007), the middle of which is dated to around 517 Ma. Incidentally, this is the same age tentatively assigned to Sirius Passet by Budd (2011). Based on the presence of the Sinsk Biota within the *Bergeroniellus gurarii* zone (Astashkin et al., 1990) we estimate an age of 515 Ma. The age of the Balang Formation is approximately 514 Ma based on placement within the *Arthrocoephalus chaveau* zone (Yan et al., 2014). The Guanshan Biota (Wulongqing Formation) falls within the *Palaeolenus/Megapalaeolenus* zone and is therefore approximately coeval with the Balang Formation (see Tab. 1 of Peng, 2009), as is the Emu Bay Shale based on correlation with the *Pararaia janeae* zone of mainland South Australia (e.g. Paterson and Brock, 2007; Paterson et al., 2008). The Kinzers Lagerstätte is confined to the

basal Emigsville Member of the Kinzers Formation, Olenellid trilobites from which suggest a Dyeran age; however, trilobites from higher levels suggest that the Series 2/3 boundary lies higher in the formation (Skinner, 2005) and, as such, we assign a late Dyeran age of 512 Ma (see Fig. 19.11 of Peng et al., 2012). The Kaili Biota is found within the *Oryctocephalus indicus* zone and the lower part of *Peronopsis taijiangensis* zone within the Kaili Formation (Zhao et al., 2011), and is thus given an age of 508 Ma. The Spence Shale Member of the Langston Formation is found within the *Glossopleura* zone of Laurentia (Robison and Babcock, 2011) and dated at 506 Ma. The boundary between the *Glossopleura* and *Bathyriscus-Elrathina* zones, which is equivalent to the base of the *Ehmaniella* zone (Peng et al., 2012), is found in the lower part of the Burgess Shale Formation between the Yoho River Limestone and Campsite Cliff Shale Members (Collom et al., 2009). Soft-bodied preservation within the Burgess Shale occurs at various stratigraphic levels above this and is therefore approximately 505 Ma. The lower part of the Wheeler Shale is within the *Ptychagnostus gibbus* zone and the upper within the *P. atavus* zone (Robison and Babcock, 2011), and is thus given an age of 504 Ma. The centre of the Marjum Formation is within the *P. punctuosus* zone (Robison and Babcock, 2011) and dated at 502 Ma. A point to note from the above is that the majority of Series 3 sites are Laurentian and the Series 2 sites Gondwanan, although there are exceptions.

The localities considered in this study are interpreted to have been deposited under a range of different environmental settings. Most were deposited in mixed siliciclastic-carbonate low-angle ramp settings seaward of carbonate platforms, such as those that surrounded Laurentia during the Cambrian (Gaines, 2014). The Utah Lagerstätten (the Spence, Wheeler and Marjum Shales), the Kinzers Shale, as well

as the Kaili, Balang and Sinsk Formations, are examples of this (Ivantsov et al., 2005; Peng et al., 2005; Skinner, 2005; Brett et al., 2009; Gaines et al., 2011; Garson et al., 2012). The Burgess Shale Formation, while occupying a similar setting, was deposited directly adjacent to the (older) platformal carbonates of the Cathedral Formation, which provided a steep, local escarpment at the time of deposition (Fletcher and Collins, 1998; Collom et al., 2009). The Sirius Passet Lagerstätte is thought to have been deposited in a somewhat comparable environment (Ineson and Peel, 2011). The depositional setting of the Chengjiang Biota is quite different to that discussed above, and is interpreted as a shallow, gently sloping, siliciclastic shelf (Hu, 2005). The Guanshan Biota occupied a similar environment (Hu et al., 2010). Perhaps the most unique setting of any BST biota is that of the Emu Bay Shale, in that it was deposited in an inner-shelf, fan-delta setting adjacent to an active tectonic margin (Gehling et al., 2011; Gaines et al., 2016). Despite the evident differences in local environmental settings, BST biotas do have some similar characteristics, e.g. all are interpreted to involve rapid burial in fine sediment, at or below storm wave base.

1.4 Considerations in comparing assemblages

Comparisons between BST biotas are complicated by the fact that these deposits are distributed somewhat unevenly through space and time, with potential local environmental and depositional conditions, as well as taphonomic and collection biases, also having an effect on assemblage compositions. As discussed above, the localities considered in this study are aged between c. 518-502 Ma (Cambrian Series 2 through Series 3); however, the earlier Series 2 sites are mostly

confined to Gondwana, and the later Series 3 sites concentrated in Laurentia. The fact that these sites are spread across a substantial time period also makes it difficult to infer biogeographic relationships due to the fact that multiple dispersal events are likely to have occurred between areas during this period. Not only that, the Cambrian is considered to be a time of considerable tectonic change (e.g. Meert and Lieberman, 2004; 2008), and geographic relationships between areas themselves were not static. It is generally accepted, however, that at this time the supercontinent Gondwana occupied a position stretching from the south pole to the equator, and was separated from Laurentia to the west by the palaeocontinents of Siberia and Baltica, as well as various microcontinents (McKerrow et al., 1992; Álvaro et al., 2013; Torsvik and Cocks, 2013). The Iapetus Ocean separated Laurentia (comprising the majority of modern day North America and Greenland rotated approximately 90 degrees clockwise) from Gondwana to the west and south (Fig. 1). This general pattern is not considered to have changed substantially during the period in question.

The deposits themselves also show considerable variation. Quality and type of preservation, effects of weathering, density of specimens, stratigraphic continuity and geographic range all vary greatly between localities (e.g. Briggs et al., 1994; Hou et al., 2004; Peel and Ineson, 2011; Zhao et al., 2011; Gaines, 2014; Robison et al., 2015; Paterson et al., 2016). A three-tiered ranking system of Burgess Shale-type deposits was proposed by Gaines (2014) based on the number of soft-bodied taxa known (taxonomic richness) at each locality (>100 = Category 1; 10-100 = Category 2; <10 = Category 3), and the fact that fidelity of preservation is generally correlated with taxon counts; however, he noted that this system does not take into account differences in collection effort between sites, and that further developments

could alter the current rating of a deposit. Our dataset contains representatives from each of these classes. Category 1 assemblages such as Chengjiang (232 total, 74 shared, 158 singleton taxa identified to generic level) and the Burgess Shale (165, 90, 75) have been particularly well studied, with multiple sub-localities and long histories of collection. Category 2 assemblages are less diverse, e.g. the Guanshan Biota (57, 34, 23) and the Wheeler Shale (86, 59, 27). The Kinzers Lagerstätte (27, 14, 13) represents a Category 3 biota (see Tab. 1 for a full list of BST biotas considered here, including total, shared and singleton genera counts).

It should be noted that Gaines (2014) defined Burgess Shale-type *deposits* based on the standard mode of preservation for BST assemblages, which involves the preservation of primary carbonaceous films. Our analysis therefore includes two deposits specifically excluded from the list of Burgess Shale-type deposits based on their anomalous preservation styles (Sirius Passet and the Emu Bay Shale). While these localities do not appear to be typical Burgess Shale-type deposits in a preservational sense, they do seem to house relatively typical Burgess Shale-type biotas, and were therefore retained in our analysis. As discussed above, Cambrian Lagerstätten are also represented by a variety of different environmental and depositional settings (Gaines, 2014). This is difficult to account for in a quantitative sense and we have not attempted to introduce this variable into our quantitative analysis at this stage, but we acknowledge this as a potential factor affecting assemblage composition.

As discussed above, our dataset contains sites with greatly differing taxon counts, largely due to the peculiarities of the individual sites (e.g. differing levels of collection effort, single site vs. multiple sub-sites, local biodiversity differences, etc.); this 'poor sampling' is essentially unavoidable in this instance. Due to this, we chose

to conduct analyses including (as well as excluding) singleton taxa, as this retains the proportionality of shared/singleton taxa between site pairings, and should therefore give more meaningful results. Palaeobiogeographic studies that utilise presence/absence data often exclude singletons and focus only on taxa shared between localities. This may be appropriate in certain cases (e.g. when taxon counts and proportions of shared/singleton taxa are similar across sites), but we argue that this is not always the case. Removing singletons increases the similarities between assemblages, and changes the ratios of shared/singleton taxa utilised in similarity and distance coefficients, which can result in assemblages being classified as very similar to each other despite large differences in their endemic taxa.

The choice of an appropriate distance coefficient is also extremely important when conducting multivariate analyses in palaeobiogeography. Shi (1993) compared 39 different binary similarity and distance coefficients based on a number of different criteria and concluded that Jaccard's coefficient of community (Jaccard, 1908) was the most informative (but see also Archer and Maples, 1987; Maples and Archer, 1988). The Jaccard coefficient, in a biogeographic sense, is the ratio of taxa shared between two localities, over the combined pool of taxa present in both localities; as such, it ignores shared absences of taxa, an important characteristic given the problem of 'double zeroes' in palaeobiogeography (i.e. the problem of distinguishing between true absence compared to non-discovery). The Jaccard coefficient, however, is not particularly suited to situations where there are large variations in sample size (i.e. taxon diversity). When comparing sites with disparate sample sizes, the Jaccard coefficient will always be relatively small (Hammer and Harper, 2006). Despite this, the Jaccard coefficient is considered a standard and is commonly used in palaeobiogeographic studies, and as such we have used both this and another of

the coefficients recommended by Shi (1993) – Ochiai's coefficient of closeness (Ochiai, 1957). The Ochiai coefficient was chosen due to the fact that, like the Jaccard coefficient, it discounts instances of shared absence, but is defined as the ratio of shared taxa over the geometric mean of the two sample sizes, thus somewhat reducing the effect of disparate samples.

2. Data and Methodology

The database constructed for this study contains presence/absence information for 607 genera (in 15 animal phyla, as well as algae and cyanobacteria) within the 12 deposits under consideration. All relevant literature was examined in the compilation of this database, and is up-to-date as of February, 2017. Given the broad nature of this study, both in space and time, data from Lagerstätten with multiple localities were pooled. Questionably assigned genera (?, cf., aff.) were conservatively coded as '?'. We realise that certain assignments contained within our dataset may be in need of review, and that certain genera may be considered 'wastebucket' taxa; however, we have used the published data currently available, and given we are looking at broad comparisons across whole assemblages this should have little effect. The complete data matrix and references pertaining to the generic presence/absence data are provided in Supplementary Tables S1 and S2 respectively.

We analysed the presence/absence data using ordinations to help visualise the relationships between localities and cluster analysis to group sites based on assemblage composition. Using both the Ochiai and Jaccard coefficients, Non-Metric

Multidimensional Scaling (NMDS) ordination plots were produced, and cluster analysis was used to produce 'Q-mode' dendrograms based on the unweighted arithmetic average (UPGMA) algorithm.

Analyses were carried out through the 'R' statistical software environment (R Core Team, 2015) using the RStudio® interface (RStudio Team, 2015). Ordination and cluster analysis were carried out using the 'vegan' package for R (Oksanen et al., 2015). Dendrograms were exported from R and edited in FigTree v.1.4.2 (Rambaut, 2014). Assemblage distance matrices using the Ochiai and Jaccard coefficients were produced in PAST Version 3.10 (PALaeotological STasistics; Hammer et al., 2001) before importing to R in order to easily allow for pair-wise deletion of missing values. R-script and CSV files for all analyses are included in the supplementary content (Supp. Files S3–8).

Parsimony analysis of endemicy (PAE; Rosen and Smith, 1988) was conducted based on the presence/absence data. PAE essentially constructs a cladogram of relationships between areas, using taxon occurrences as 'characters', and therefore clusters areas according to inferred individual histories of taxa rather than overall faunal similarity. This method has been criticised in the past, particularly for its inability to distinguish between episodes of vicariance and geodispersal, the fact that lower diversity sites will tend to map as basal (although this may also be true of other methods), and because PAE does not consider the phylogenetic relationships of taxa under investigation (for a review see Morrone, 2014); however, PAE does provide an alternative way to assess biogeographic relationships from multivariate ordination and clustering methods when phylogenetic information is lacking, as is the case for many of the groups included in our dataset. All PAE analysis used PAUP* (Swofford, 2001), with all characters in the matrix (i.e.

presence/absence of genera) equally weighted, and branch-and-bound searches which guarantee to find all most-parsimonious trees. An “all zero” root (i.e. a hypothetical area with all taxa absent) was used to root the analysis. Support for groupings of areas was ascertained using bootstrapping (each replicate using branch-and-bound searches).

We also analysed the presence/absence matrix using Bayesian inference. The potential advantages and shortcomings of Bayesian phylogenetic methods are widely discussed elsewhere (e.g. O'Reilly et al., 2016). The most relevant differences in this context are as follows. (1) PAE typically weights all taxa equally, but it might be expected that taxa with greater dispersal ability might exhibit less biogeographic signal (i.e. more 'area homoplasy'). Bayesian approaches typically employ a gamma parameter, allowing certain traits to change more rapidly, while parsimony approaches typically apply equal weighting to all changes. Bayesian methods can thus potentially identify and accommodate taxon-specific variability in rates of dispersal, by allowing some taxa to 'evolve' (i.e. change areas) rapidly and exhibit more expected homoplasy with the overall area cladogram. However, these rate assignments are not made *a priori* (e.g. based on biological characteristics), rather as part of the actual analysis, based on overall biogeographic congruence across all taxa. (2) Unlike parsimony, Bayesian inference doesn't attempt to find a single 'best' area cladogram. Rather, it integrates over all possible cladograms, weighted by their posterior probability (good topologies are weighted more highly). Thus, it might better estimate uncertainty in area relationships. We refer to this method as Bayesian Analysis of Endemicity (BAE) and use this term hereafter. BAE was undertaken using MrBayes 3.2.5 (Ronquist et al., 2012). Variation in rates across taxa was accommodated using the gamma parameter; inclusion of this

parameter was supported by Bayes Factors ($=20$), as calculated using stepping-stone sampling. Four replicate MCMC runs were performed to confirm convergence. Each run composed 4 incrementally heated (temperature 0.2) chains, run for 10 million generations with sampling every 10 thousand generations, with the first 20% discarded as burnin. The majority-rule consensus tree, with posterior probabilities of all groupings of areas, was obtained from the concatenated post-burnin samples of all 4 runs. Both parsimony and Bayesian methods essentially produce unrooted trees; for ease of topological comparison we arbitrarily rooted the trees based on the rooting identified in the UPGMA analyses. Executable files for the PAE and BAE analyses are included in the supplementary content (Supp. Files S9–10, 13).

The number of genera (including singletons) within each major taxonomic group considered (mostly phyla) at each site were summed and proportions calculated; this information was then presented as a stacked histogram chart. Changes in certain groups were then examined further using biplots and regression analysis (conducted in PAST Version 3.10; Hammer et al., 2001). Note that we have separated trilobites from non-trilobite arthropods for this analysis, in order to examine suspected changes in relative abundances within the Arthropoda over the period in question. While non-trilobites should ideally have been split further into cohesive clades, this would have resulted in very small sample sizes.

3. Results

3.1 Ordinations and cluster analysis

The NMDS ordinations and UPGMA cluster analyses were conducted on the presence/absence matrix using the Ochiai and Jaccard coefficients as distance measures, both with and without singleton taxa included. Stress levels are relatively high, but acceptable (0.12–0.14). The ordinations all show similar patterns (Fig. 2). The Series 3 ‘northern’ Laurentian sites (Wheeler, Marjum, Spence and Burgess Shale) and Kaili (South China) tend to group together; this is particularly evident in the Ochiai distance plot that includes singletons (our preferred combination: Fig. 2A) where these sites form a relatively tight cluster. The Series 2 South Chinese sites (Chengjiang, Guanshan and Balang) tend to form a looser association adjacent to the cluster mentioned above. While Kaili seems to group more consistently with the Laurentian sites, in particular with the Burgess Shale, it is usually more closely associated with the South Chinese sites (Chengjiang in particular) than other members of the cluster. The late Series 2 Kinzers Shale plots close to the Series 3 group, in general being more closely associated with Kaili and Spence, i.e. those sites closest in age. The other three sites (Sirius Passet, Sinsk and Emu Bay Shale – all Series 2) are positioned more distantly to both the clusters mentioned above, and to each other. Emu Bay appears to be more closely related to the Series 2 South Chinese sites (Balang in particular), while Sinsk appears to have some affinity with both these and the Laurentian cluster. Sirius Passet appears to be the most distinct locality, with no close associations. From a temporal perspective, the Series 3 sites (Burgess Shale, Kaili, Wheeler, Marjum and Spence) tend to be closely associated. The Series 2 sites by comparison are rather more scattered.

In general, the results of the UPGMA cluster analyses (Fig. 3) are consistent with the NMDS ordinations. The Series 3 sites form a single cluster in all the dendrograms, within which the stratigraphically continuous Marjum and Wheeler

formations show close affinity, while the older Spence Shale groups with its closest contemporary, the Burgess Shale. Kaili is either a sister unit to the latter grouping (singletons included), or to the whole cluster (singletons excluded), with the late Series 2 Kinzers sitting outside this larger group. The Series 2 Gondwanan sites (Chengjiang, Guanshan, Balang and Emu Bay) form a separate cluster in all dendrograms except that using the Jaccard coefficient with singletons included (Fig. 3C), where Chengjiang swaps to sit basal to Kinzers in the mostly Laurentian cluster. Within the Gondwanan cluster, Emu Bay groups with Balang in all cases, while Chengjiang groups with Guanshan (except for the exception discussed above). The position of Sinsk is rather uncertain, with the Siberian site sitting outside the two larger groupings (singletons included: Fig. 3A, C), outside the Series 3/Kinzers group (Ochiai coefficient, singletons excluded: Fig. 3B), or forming a basal 'outgroup' with Sirius Passet (Jaccard coefficient, singletons excluded: Fig. 3D). Sirius Passet is the most basal site in all topologies (jointly with Sinsk in Fig. 3D). The cophenetic correlations of the dendrograms vary somewhat, and are higher for those that include endemic taxa (suggesting greater tree-like structure), which could explain some of the variation in topology observed.

Analysis (using the Ochiai coefficient) was also undertaken on a subset of the presence/absence dataset that excluded the biomineralised Trilobita and Brachiopoda, in order to examine whether these large groups were having a noteworthy influence on the results. Somewhat surprisingly, placement of assemblages both within the ordination plots and dendrograms was extremely similar to that produced by the full dataset (see Supp. File S11, compare with Figs. 2A, B and 3A, B).

3.2 PAE and BAE

PAE produced a single most parsimonious tree of 755 steps (Fig. 4A). Tree topology was very similar to the dendrograms produced by cluster analysis. In this instance we have presented the results as a phylogram, meaning that branch length reflects the number of steps; therefore, terminal branch length reflects the number of unique presences or absences (e.g. singleton taxa) within each of the assemblages considered. In these trees, all Series 3 sites group together, with Kinzers sitting immediately outside this grouping; the Series 2 Gondwanan sites form the other major clade. The relationships within the larger groups do, however, differ from the dendrograms. Kaili is more deeply nested within the Series 3 group, being most closely related to the Burgess Shale, with Spence outside of this. Within the Gondwanan Series 2 group, Chengjiang and Guanshan group together, with Balang sitting outside this group and Emu Bay further outside again. Sirius Passet and Sinsk form the most basal group inside the “all zero” root (similar to Fig. 3D). We have transposed bootstrap values for different groupings onto the tree from the 50% majority-rule bootstrap consensus tree (Supp. File S12). Inclusion of uninformative characters (in this case singleton genera) generally decreases bootstrap support (Carpenter, 1996), so we also produced a bootstrap consensus tree excluding singletons for comparison (Supp. File S12–13); in general, bootstrap values are slightly higher (though comparable) for this tree. Certain bootstrap values are relatively low and suggest that some of the groupings are weakly supported.

The topology of the majority-rule consensus tree produced by BAE was very similar to that produced by PAE, the only differences being that Kaili and Spence switched places within the Series 3 clade, and Sinsk moves to sit inside of Sirius

Passet (Fig. 4B). Branch lengths in this instance reflect percentage divergence in assemblage composition (0% = identical pattern of taxon presences and absences). In contrast to the bootstrap values of the PAE phylogram, groupings are generally well supported by posterior probabilities.

3.3 Higher-level taxonomic diversity

Examination of the composition of assemblages through time reveals a number of patterns at higher taxonomic levels. The stacked histogram chart in Figure 5 shows the percentage composition of major taxonomic groups; sites are listed from oldest (left) to youngest (right). In general, older sites are characterised by low ratios of trilobite to non-trilobite arthropods, low echinoderm and algal/cyanobacterial diversity, the presence of 'chordates' (including vetulicolians after García-Bellido et al., 2014), and higher proportions of *incertae sedis* taxa. Conversely, the younger sites are generally characterised by high ratios of trilobite to non-trilobite arthropods, higher echinoderm and algal/cyanobacterial diversity, and a general lack of chordate and *incertae sedis* taxa. There are some exceptions to this, e.g. the Burgess Shale exhibits a lower relative proportion of trilobites, and the Sinsk Biota having an unusually high level of algal/cyanobacterial diversity.

4. Discussion

4.1 General patterns

In general, relationships between sites were concordant across all analyses undertaken. Results were also generally consistent within analyses regardless of the distance coefficient used (Ochiai or Jaccard) or whether singleton taxa were included or excluded. Overall results suggest two major groupings; a Series 3 cluster (Burgess Shale, Kaili, Spence, Wheeler and Marjum) and a somewhat less defined Series 2 Chinese cluster (Chengjiang, Guanshan, Balang). Kinzers is closely associated with the former, and Emu Bay with the latter. These two major clusters generally form sister groups in the tree-based methods, or are positioned adjacent to one another in the ordination plots. Sinsk appears distantly related to both major groupings while Sirius Passet appears to be the most unique site with no close associations. Despite the consistency in topology between the different tree-based methods, the ordinations suggest that there is no tight clustering in the data and that relationships are relatively continuous. This illustrates a potential shortcoming of the dendrogram-based methods in that the algorithms impose a hierarchical (groups within groups) and ultrametric (all tips of the tree aligned) pattern on the dataset even if there is no such arrangement (e.g. see the non-ultrametric PAE and BAE trees in Fig. 4).

In the NMDS ordination plots (Fig. 2), the Series 3 sites tend to group closely, whereas the Series 2 sites are much more disparate. This could potentially be due to environmental differences, although it seems unlikely that the greater variation observed between these older sites can be completely explained by this (see discussion below). This disparity between Series 2 assemblages (and particularly the oldest sites), in contrast with those from Series 3, suggests an increasing importance of age as a determinant of assemblage homogeneity through the period in question, and a decrease in provinciality (at least from a broad assemblage point of view). This

increase in similarity between Cambrian Lagerstätten assemblages through time has been noted before and has been linked to the advent of pelagic larvae and their dispersal (Zhao et al., 2005; 2011; Han et al., 2008).

Bayesian methods are of particular interest in this instance as they have characteristics that might make them particularly suitable for comparing assemblages. Usually in presence/absence studies, occurrence patterns of different taxa are equally weighted. This is not necessarily the best approach given that taxa could be expected to show a range of biogeographic signal given variations in dispersal ability. It might be desirable that occurrence patterns of cosmopolitan taxa should receive a lower weighting than taxa displaying stronger regional affiliations. Bayesian inference accommodates this by down-weighting 'characters' (in this case 'taxa') that display higher levels of 'area homoplasy', in a manner analogous to the treatments of homoplasious characters in a phylogenetic analysis.

It is also important to note that pairs of sites with higher sampled diversity (e.g. due to multiple sub-sites and/or greater levels of collection effort) are likely to show higher levels of similarity, and may therefore erroneously group closer together than is really the case. This may in part account for the greater similarity that the Burgess Shale exhibits with Kaili, compared to geographically closer sites of similar age (e.g. Spence, Wheeler), as well as the fact that these two sites often group quite closely to the exceptionally diverse Chengjiang biota. This potential bias is reduced when singletons are included, as these taxa increase the uniqueness of well-sampled sites and offset any extra overlap with other localities caused by increased sampling alone. This is one potential argument as to why it may be beneficial to retain singleton taxa in an analysis, particularly when sample sizes vary greatly; at any rate, analyses including and excluding them might be advisable. This is perhaps

the reason behind previous assertions of greater similarity between the Lagerstätten of Laurentia and South China (e.g. Han et al., 2008), i.e. these exhibit the highest sampled diversity and are therefore more likely to share taxa. These sites do tend to group together as a broader cluster within our various analyses, but only compared with the small number of other, much more singular sites, making it difficult to draw conclusions as to how closely related these two groups really are.

4.2 Individual comparisons

Unfortunately, the concentration of Series 2 sites in Gondwana and Series 3 sites in Laurentia makes it difficult to interpret the observed differences in assemblage compositions, however, there are exceptions from which some conclusions may be drawn. The Kaili Formation contains the only Series 3 biota from South China in our database; all other Chinese sites are of Series 2 age. If we assume that both space and time have (similar) significant effects on composition, then we could predict that such a site should be positioned somewhere between the Series 3 sites (the rest of which are all Laurentian) and the Series 2 South Chinese sites in terms of assemblage relationships. In fact, in the ordinations Kaili tends to group more closely with the Laurentian sites, and particularly its closest contemporaries, the Burgess and Spence Shales. This is reflected in a greater number of shared genera between Kaili and the Burgess Shale (42), than between Kaili and the Series 2 Chengjiang biota (34), while the Burgess Shale and Chengjiang share 35 genera. The fact that Kaili shares fewer genera with the older, but geographically closer Chengjiang biota, than it does with the Burgess Shale, a locality on a different palaeocontinent but of similar age, suggests that age rather

than geographic distance is having a stronger effect on assemblage composition in this instance, as suggested by Zhao et al. (2011). As might be expected, however, Kaili tends to be the Series 3 site most closely associated with the Series 2 Chinese localities in the ordination plots.

Similarities between the Chengjiang (74 shared genera/158 endemic) and Burgess Shale assemblages (90/75) have been noted before (see Han et al., 2008), although it seems that a large number of their 35 shared genera are those with relatively cosmopolitan distributions as listed previously, e.g. *Selkirkia* (present at 7 sites), *Anomalocaris* (10), *Canadaspis* (5), *Isoxys* (8), *Leancoilia* (5), *Liangshanella* (5), *Naraoia* (6), *Tuzoia* (10), *Lingulella* (6), *Yuknessia* (7), *Wiwaxia* (5), *Choia* (8), *Hazelia* (5) and *Eldonia* (6). Presumably these were good dispersers, although it should be noted that the Lagerstätten considered here are spread through c. 16 million years, implying that these taxa were not only widespread, but also long-lived in geologic time. In addition, the term 'cosmopolitan' is of some limited value in this instance given that the majority of Lagerstätten occur in Laurentia and South China, although many of these taxa also occur at one or more of the singular sites in Sinsk, Sirius Passet and the Emu Bay Shale.

Similarities in biomineralised taxa that are more dependent on age (i.e. have higher turnover) rather than soft-bodied elements of BST biotas that tend to persist through time, appear to be the major cause of Kaili tending to group with Laurentian sites of similar age. Firstly, Kaili and the Burgess Shale share a number of trilobite genera, namely *Burlingia*, *Kootenia*, *Olenoides*, *Oryctocephalus* and *Pagetia*. Kaili also shares all of these, as well as *Peronopsis*, with one or more of the Utah Lagerstätten. In contrast, Chengjiang shares no trilobites with Kaili or any of the sites in Utah simply due to the fact that trilobite genera do not persist across the time gaps

seen between the Series 2 and 3 deposits. Kaili also shares the brachiopods *Lingulella*, *Linnarssonina*, *Micromitra*, *Nisusia*, *Paterina* and *Dictyonina* with the Burgess Shale, as well as the majority of these plus *Acrothele* with the Utah sites, whereas with Chengjiang it shares only *Kutorgina* and *Lingulella*. Other notable similarities with Laurentian sites include the cyanobacteria *Morania* and *Marpolia*, molluscs such as *Latouchella* and *Scenella*, and soft-bodied arthropods *Perspigaris*, *Mollisonia* and *Skania*.

The relationships between the Spence (c. 506 Ma), Wheeler (c. 504 Ma) and Marjum (c. 502 Ma) Shales of Utah, and the Burgess Shale (c. 505 Ma), are of particular interest, as they provide a 'time series' of well-sampled assemblages, present on the same palaeocontinent. It is clear that in this instance time is having the major effect on assemblage composition. The Spence Shale, the oldest of this group of sites, shares a higher number of genera with the Burgess Shale, than it does with the slightly younger Wheeler Shale, and less again with the (even younger) Marjum Formation. The (present-day) geographic distance between the Utah sites and the Burgess Shale (c. 1,500 km) seems to have little effect on this, with site pairings with similar age differences showing comparable amounts of assemblage distance, regardless of whether the Burgess Shale is under consideration. Moreover, the Spence Shale tends to group with the almost contemporaneous Burgess Shale in our various analyses, rather than with its closest neighbours (although this may also reflect more similar environmental settings).

The Sirius Passet assemblage, despite its uniqueness (8/32), also gives us potential clues as to how the relationships between sites have changed through time. Sirius Passet shares only the annelid *Hyolithellus* (with the Wheeler and Marjum Formations), as well as the cosmopolitan arthropod *Isoxys* and a small number of

sponges with other sites, despite being thought to have occupied a setting very similar to that of the Burgess Shale, i.e. in relatively deep water immediately adjacent an escarpment representing the outer edge of the carbonate platform (Ineson and Peel, 2011; Peel and Ineson, 2011). It has recently been shown that microbial mats and silica 'death masks' may have played a role in the unique preservation observed at Sirius Passet (Strang et al., 2016). The assemblage (despite anomalous preservation style) also seems to house a relatively representative BST biota, suggesting that perhaps some other reason is responsible for the uniqueness of Sirius Passet. It is illustrative that this site is vastly different from other Series 2 sites of possibly very similar age (e.g. Chengjiang), when Series 3 sites present on different palaeocontinents (e.g. Kaili and the Burgess and Spence Shales) are much more similar to one another, i.e. one might expect Sirius Passet to exhibit similarities to other Series 2 sites. Given that this is not the case, it is possible that at this time, biotas were not yet stable and widespread (as per Zhao et al., 2005), but rather more peculiar and individual, perhaps due to more limited dispersal ability of constituent taxa.

Despite the fact that the Emu Bay Shale (EBS) assemblage (10/23) appears to be relatively unique based on the ordination plots, it is consistently positioned closer to the South Chinese Lagerstätten than to other sites, and groups with these in the cluster, PAE and BAE analyses. This is reflected by a clear link between the EBS biota (East Gondwana) and the Series 2 South Chinese sites in terms of shared taxa. The EBS shares the trilobite *Redlichia* with the contemporaneous Balang and Guanshan Lagerstätten, and the arthropods *Kangacaris*, *Squamacula* and *Tanglangia* with Chengjiang, as well as the problematic *Vetustovermis* (although it is uncertain as to whether these represent the same taxon). A brachiopod assigned to

Diandongia (Paterson et al., 2016) is shared with Chengjiang and Guanshan. The palaeoscolecid *Wronascolex* is shared with all three, as well as the Sinsk biota (it should be noted that there are also uncertain assignments of specimens to this genus from the Spence and Marjum Formations of Utah). In contrast, the EBS shares only the cosmopolitan *Anomalocaris*, *Isoxys* and *Tuzoia* with Laurentian localities (as well as with all of the South Chinese sites), suggesting sufficient separation of East Gondwana and Laurentia by this time to limit dispersal across the Iapetus Ocean. The uniqueness of the Emu Bay Shale is likely due to its relative isolation, and the similarities between this site and the BST biotas of South China also suggest a geographic relationship, however, it is not possible to discount similarity in age as a major factor. The unique inner-shelf depositional setting (Gehling et al., 2011), as well as preservation style (Gaines, 2014), of the Emu Bay Shale could also potentially explain why this assemblage is rather singular, although, as with Sirius Passet, the assemblage does seem to be relatively typical of BST biotas.

The Sinsk biota (14/30) is also similar to Sirius Passet and the Emu Bay Shale in that it appears to be quite distinct from sites of similar age. The biota appears to show a mix of affinities, with certain taxa linked to Laurentia (e.g. *Cambrorhytium*, *Diagoniella*, *Laenigma*) and others more closely aligned with Gondwana (e.g. *Wronascolex*), although the majority of shared genera have representatives on both palaeocontinents, e.g. *Marpolia*, *Linnarssonina*, *Archiasterella*, as well as many of the cosmopolitan taxa mentioned above. This is consistent with palaeogeographic reconstructions placing Siberia between Gondwana and Laurentia at this time (e.g. Fig. 1). The distinctiveness of the Sinsk biota could also be partly due to environmental causes. The Lagerstätte occurs

largely within a relatively thin (c. 0.5m) section of calcareous shale, within the clastic limestones of the Sinsk Formation (Ivantsov et al., 2005). Despite this slightly unusual depositional setting, other factors are consistent with typical BST deposits (i.e. fine sediment rapidly deposited in an outer-shelf setting at or below storm wave base: Gaines, 2014).

The Kinzers Shale of southeastern Pennsylvania (USA) spans the Cambrian Series 2/Series 3 boundary. The basal Emigsville Member is of uppermost Series 2 age and contains a relatively low diversity (14/13) Lagerstätte, that in terms of age, links the Series 2 and Series 3 localities. The NMDS ordinations (Fig. 2) tend to place Kinzers slightly apart from the Series 3 sites (usually close to Kaili), which is consistent with the tree-based methods placing the site as the most basal of the otherwise Series 3 cluster. In terms of shared genera, Kinzers shares *Dalyia*, *Metaspriggina* and *Tubulella* exclusively with the Burgess Shale, *Paterina* with the Burgess Shale and Kaili, *Pelagiella* with the Wheeler Shale, as well as *Morania* and *Yuknessia* with all of the Series 3 Lagerstätten. All other shared taxa are largely cosmopolitan, e.g. *Selkirkia*, *Anomalocaris*, *Tuzoia*, *Haplophrentis*, *Hazelia*, *Kootenia* and *Allonnia*. Kinzers provides an example of how it can be difficult to determine whether assemblage relationships are a result of geographic proximity (i.e. to other Laurentian sites), similarity in age (e.g. with Kaili), or a combination of both. In this case we suspect it is likely some combination of the two.

4.3 Higher-level taxonomic diversity

The analysis of generic diversity based on the number of genera per phylum (or other higher level taxonomic group in the case of trilobites, algae/cyanobacteria,

and *incertae sedis* taxa) shows a number of patterns. There is a large and significant increase in the proportion of trilobites, whilst non-trilobite arthropods decrease (although less dramatically) through time (Fig. 6). The total proportion of arthropods within the assemblages increases slightly across the same period, although this trend is not significant. The increase in trilobites reflects the fossil record in general, which shows a dramatic increase in diversity following their appearance in the mid-early Cambrian through to the end of the period (Fortey and Owens, 1997). An exception to this trend in our dataset is the Sinsk Biota, a possible cause for which was noted by Ivantsov et al. (2005) in that this Lagerstätte occurs predominantly in carbonate facies. This may have represented a more hospitable environment for trilobites (as predominantly benthic inhabitants) compared to the anoxic/dysoxic conditions inferred for many other Lagerstätten. This suggests increasing tolerance for low-oxygen conditions as an alternative explanation for the increasing trilobite proportions in BST biotas through time. The Burgess Shale is also something of an exception and tends to group with the older sites, in particular Chengjiang, Guanshan and the Emu Bay Shale, mainly based on a relatively low trilobite:non-trilobite arthropod ratio, and low relative arthropod diversity in general compared to other localities. This may simply be an artifact of the higher number of taxa known from this locality, essentially 'diluting' the proportion of trilobites. For preservational reasons these are likely to be well-sampled even during the early stages of an investigation, or at sites with lower collection effort (with the exception of extremely rare species); we could expect therefore that the proportion of trilobites (and biomineralised taxa in general) to fall over the course of investigations into a BST biota. We also note that these differences may be a result of data bias due to

relatively poor constraints on the sections that exhibit exceptional preservation within the other Series 3 formations compared to the Burgess Shale.

There is an increase in the proportion of echinoderms across the period in question, which also mirrors the pattern suggested by the echinoderm fossil record in general, which shows increasing diversity from an appearance in Stage 3 through Stage 5 (Zamora et al., 2013). There is also a decline in the proportion of chordates (driven largely by the pattern in vetulicolians that were more prevalent in early Cambrian BST biotas), priapulids, and *incertae sedis* taxa, suggesting that this was a critical period where the rapid evolution of communities was occurring, and that the variable success of major lineages of animals was playing a significant role.

5. Conclusions

Both space and time have important effects on the taxonomic composition of Cambrian Lagerstätten assemblages. Early Cambrian (Series 2) Lagerstätten from different geographic regions are highly distinct, but later (Series 3) localities appear to be more globally homogenous. This pattern seems to be driven largely by a general increase in the number of biomineralised taxa such as trilobites and brachiopods shared between sites, occurring against a backdrop of ‘cosmopolitan’ taxa that are pervasive both in space and time. This pattern might be related to a general increase in dispersal ability, possibly linked to an increased development of pelagic larvae in certain groups. There is also evidence of higher-level taxonomic turnover through time, with certain groups (e.g. trilobites, echinoderms) becoming more prevalent, while others seem to disappear (e.g. vetulicolians). The reduction in *incertae sedis* taxa through time is also illustrative, suggesting that more

'recognisable' taxa were emerging during this time, and that this was indeed an important period in the evolution of modern lineages and communities. The proposed link between the Cambrian Lagerstätten assemblages of Laurentia and South China (e.g. Chengjiang and Burgess Shale) is not particularly evident, partly because these relationships have been proposed mainly on the basis of large numbers of shared cosmopolitan taxa, and also due to a lack of context, i.e. there is a limited number of other sites with which to make meaningful comparisons. The discovery of new deposits and further investigation of the lesser-known localities would help to resolve this. It should also be noted that the exclusion of endemic (singleton) taxa may not always be the best approach in biogeographic studies, particularly from a palaeontological perspective where sample sizes may vary greatly. Adopting metrics that better accommodate endemic taxa might be a more productive approach.

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Figure 1. Cambrian continental reconstruction (modified from Torsvik and Cocks, 2013: Fig. 2.8) showing hypothesised locations of the 12 Lagerstätten considered in this study, as at 510 Ma. Note that all sites are located within approximately 20 degrees of the equator.

Figure 2. Non-metric multidimensional scaling (NMDS) ordination plots of major BST biotas based on presence/absence of genera. A, using the Ochiai coefficient with singletons included. B, Ochiai coefficient, singletons excluded. C, Jaccard coefficient, singletons included. D, Jaccard coefficient, singletons excluded. Sites in *italics* = Series 3. Point colours; red = South China, blue = Laurentia, purple = East Gondwana, green = Siberia. Note that polarity of axes is arbitrary and are all oriented here to match 2A for ease of comparison.

Figure 3. UPGMA cluster analysis dendrograms depicting assemblage distance between major BST biotas based on presence/absence of genera. A, using the Ochiai coefficient with singletons included. B, Ochiai coefficient, singletons excluded. C, Jaccard coefficient, singletons included. D, Jaccard coefficient, singletons excluded. Sites in *italics* = Series 3. Text colours; red = South China, blue = Laurentia, purple = East Gondwana, green = Siberia (c = cophenetic correlation).

Figure 4. A. Parsimony Analysis of Endemicity (PAE) phylogram (single shortest tree of 755 steps). Branch lengths reflect number of steps (scale bar = 30 steps), with terminal branch lengths reflecting number of singleton taxa within each assemblage; numbers refer to bootstrap values of area groupings ("clades"). Chengjiang branch has been shortened, actual length = 201 units. B. Bayesian

Analysis of Endemicity (BAE) majority-rule consensus tree. Branch lengths are proportional to percentage divergence (scale bar = 2%); numbers refer to posterior probabilities of area groupings ("clades"). Chengjiang branch shortened, actual length = 13.31% (for comparison Burgess Shale = 7.26%). Sites in *italics* = Series 3. Text colours; red = South China, blue = Laurentia, purple = East Gondwana, green = Siberia.

Figure 5. Composition of the 12 Cambrian Lagerstätten assemblages considered in this study in order of age, based on number of genera per phylum (or other higher level taxonomic group in the case of trilobites, algae/cyanobacteria, and *incertae sedis* taxa). Older sites generally exhibit low trilobite:non-trilobite arthropod ratios, low echinoderm and algal/cyanobacterial diversity, presence of chordates (including vetulicolians), and high proportions of *incertae sedis* taxa, with younger sites showing the reverse. Estimated age/total number of genera at each locality is shown in parentheses.

Figure 6. Relative proportions and linear regression trendlines for trilobites and non-trilobite arthropods through time for the assemblages under consideration. There is a significant increase ($p = 0.004$) in the proportion of trilobites, and a significant decrease ($p = 0.05$) in non-trilobite arthropods across the period.

Table 1. Estimated age, location, number of genera, and number of shared/endemic genera (excluding questionable assignments) for each of the 12 Cambrian Lagerstätten considered in this study.



Figure 1

ACCEPTED MANUSCRIPT

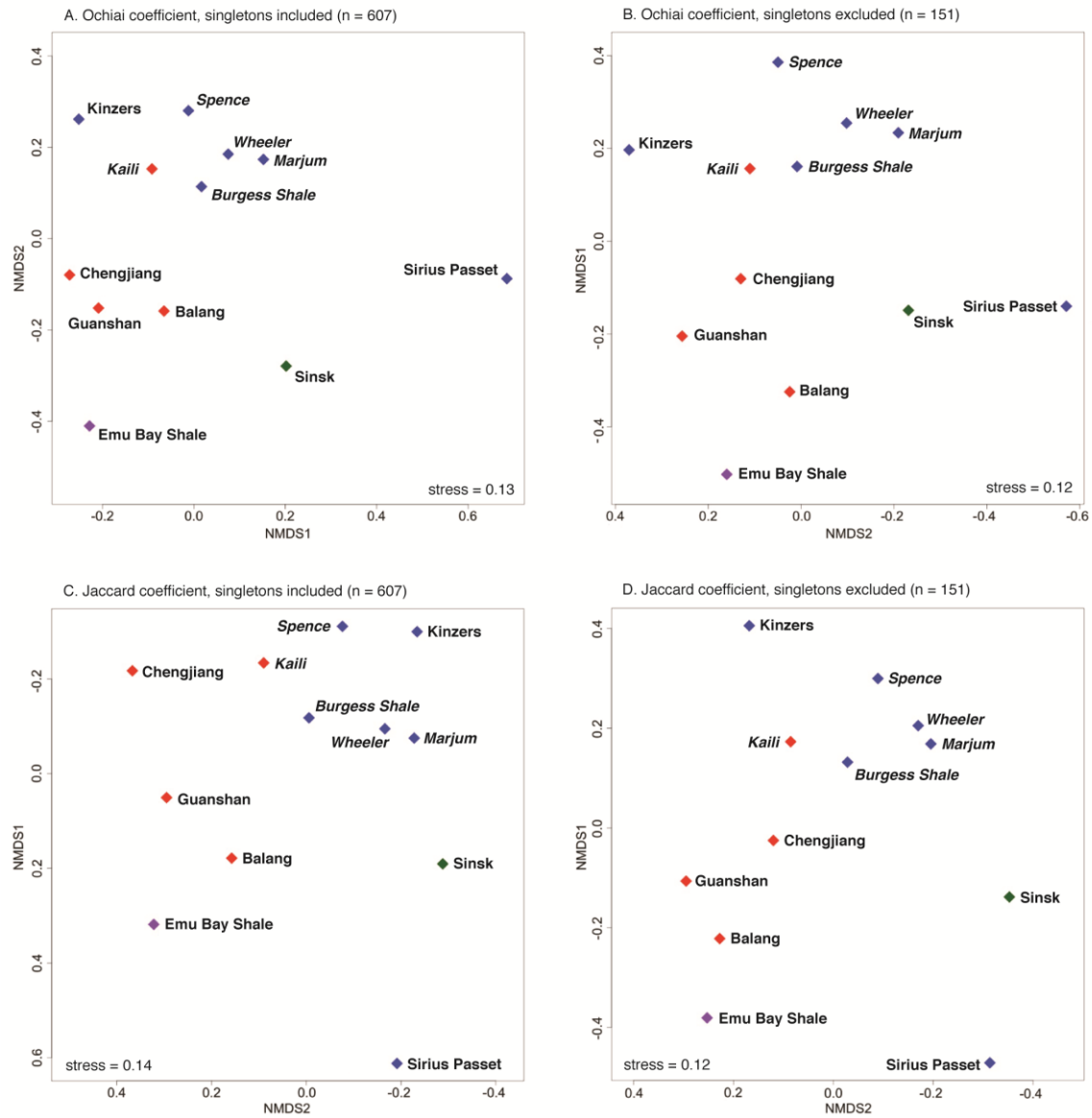


Figure 2

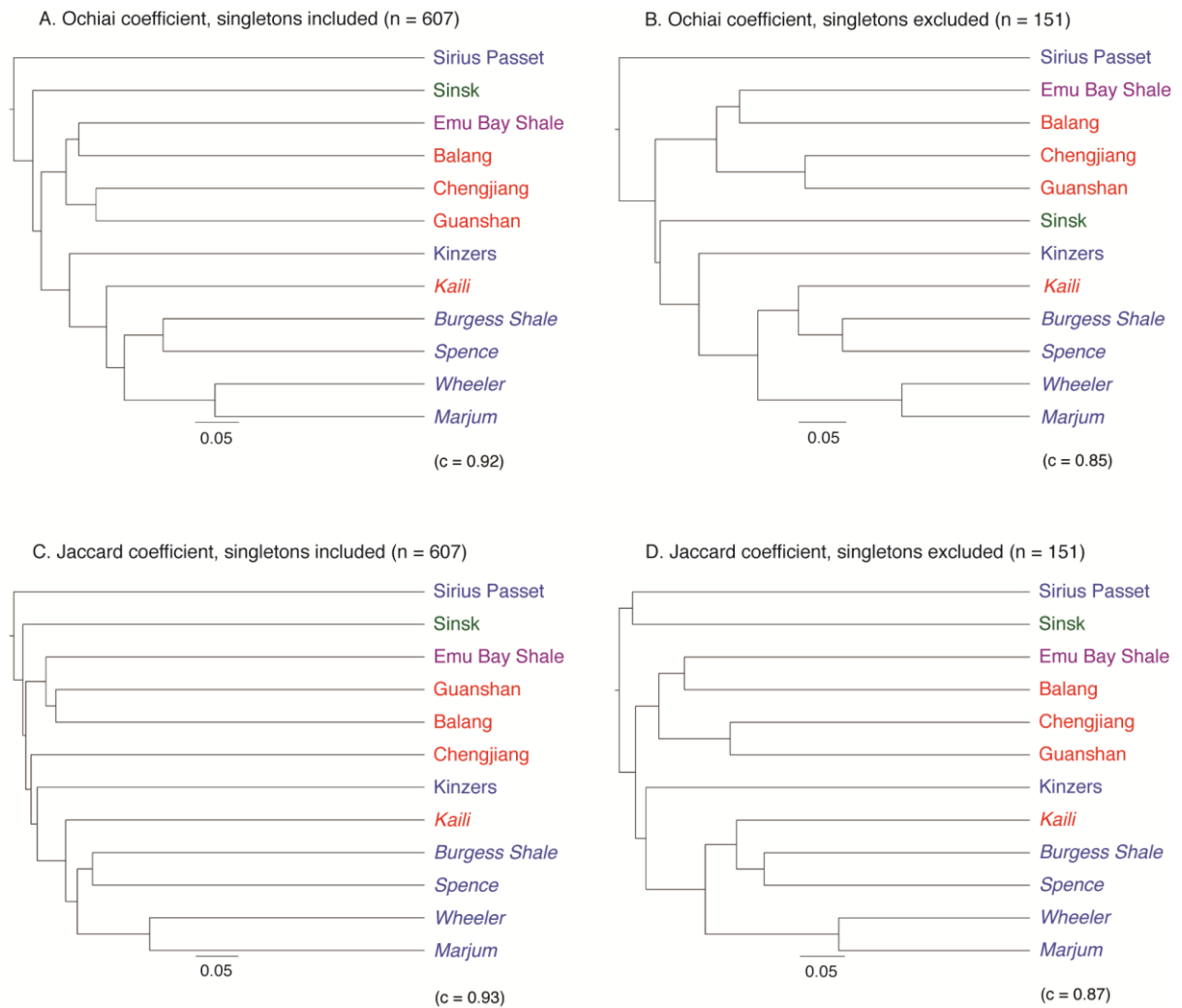


Figure 3

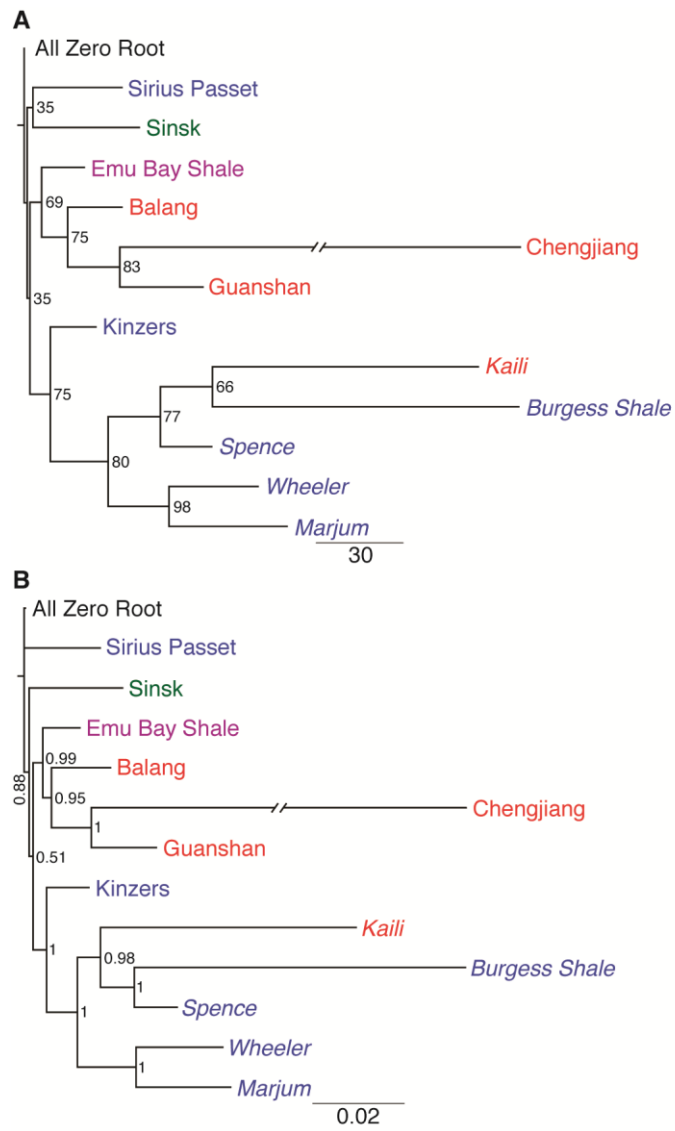


Figure 4

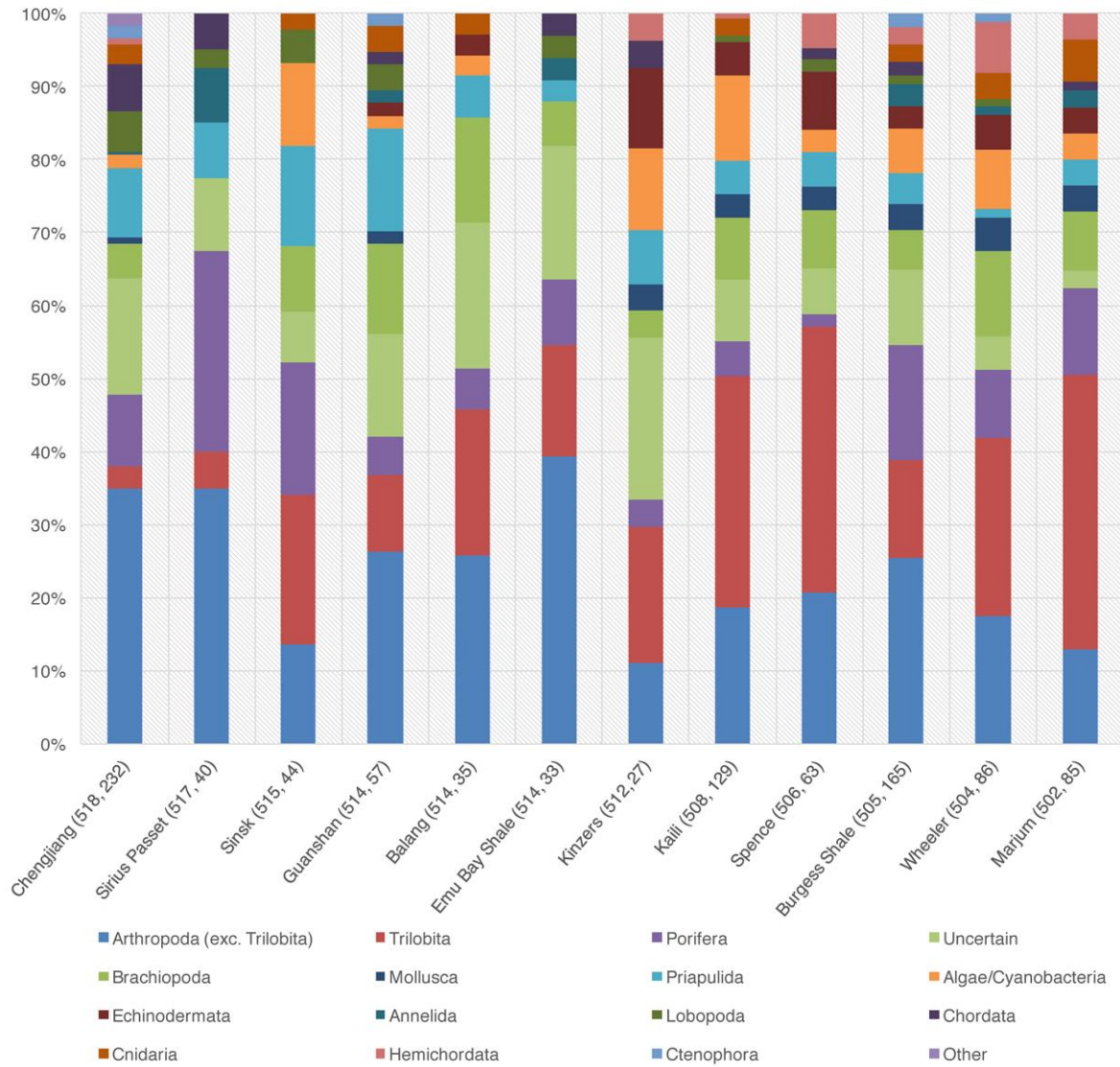


Figure 5

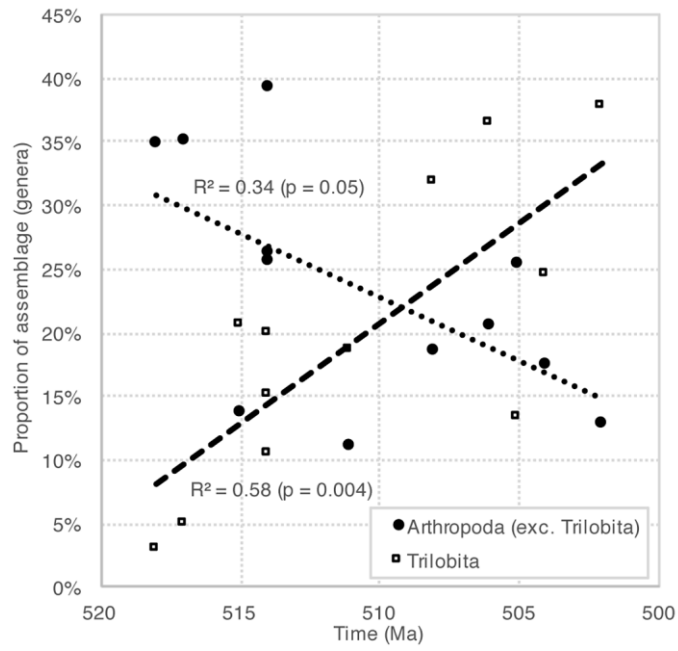
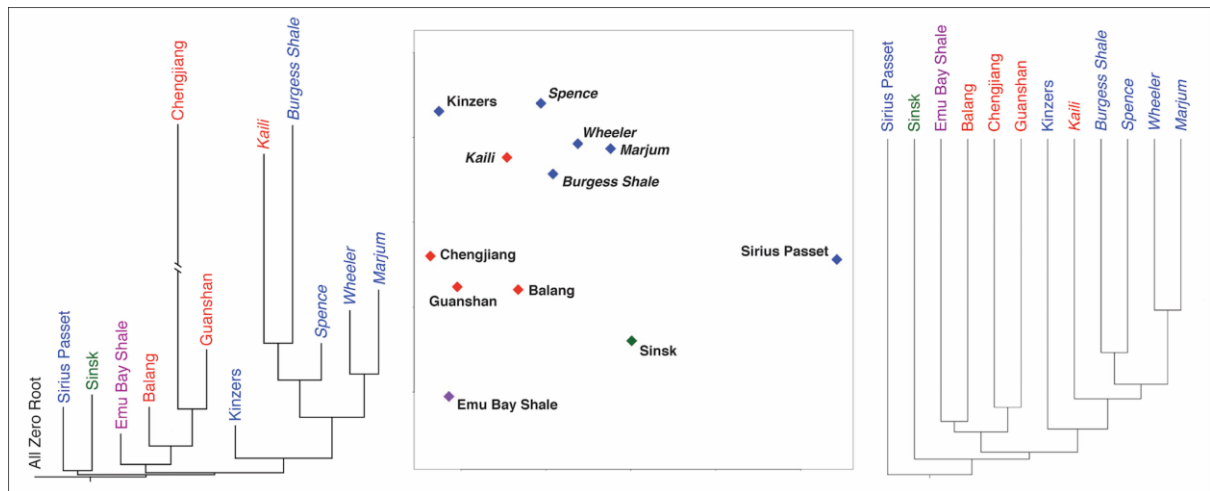


Figure 6



Graphical abstract

Table 1

Locality	Age	Location	No. of genera	Shared / Endemic
Chengjiang	518	Gondwana (South China)	232	74/158
Sirius Passet	517	Laurentia (Greenland)	40	8/32
Sinsk	515	Siberia	44	14/30
Guanshan	514	Gondwana (South China)	57	34/23
Balang	514	Gondwana (South China)	35	20/15
Emu Bay Shale	514	Gondwana (East)	33	10/23
Kinzers	512	Laurentia (South)	27	14/13
Kaili	508	Gondwana (South China)	129	65/64
Spence	506	Laurentia (North)	63	44/19
Burgess Shale	505	Laurentia (North)	165	90/75
Wheeler	504	Laurentia (North)	86	59/27
Marjum	502	Laurentia (North)	85	47/38

Highlights

- Space and time have important effects on Cambrian Lagerstätten assemblages
- Age becomes an increasing determinate of BST assemblage composition over the period
- Taxonomic turnover confirms an important period in evolution of early communities

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