Palaeogeography, Palaeoclimatology, Palaeoecology 404 (2014) 1–11

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Testing the fossil record: Sampling proxies and scaling in the British Triassic–Jurassic

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ARTICLE INFO

Article history:
Received 23 April 2013
Received in revised form 17 March 2014
Accepted 19 March 2014
Available online 30 March 2014

Keywords:
Palaeodiversity
Fossil record
Sampling
Proxy
Triassic
Jurassic

ABSTRACT

The quality of the fossil record varies immensely across taxa, geographic regions, environments and time intervals. Because much of this variation can be confounded when examining global patterns, we present a detailed investigation of the British Triassic and Jurassic, one of the most intensively studied pairs of systems in the world. Marine Jurassic palaeodiversity is at least partly controlled by rock availability and accessibility. The terrestrial record is patchier, and effects of rock availability are overprinted by a stronger signal of sporadic preservation. These results also fit a sea-level driven common-cause explanation, as one would expect to see close correlation between rock availability and palaeodiversity in the marine realm, but less so in the terrestrial. Formation counts and palaeodiversity do not correlate, a surprising result given the number of earlier studies that have found close correlations. However, this study differs from most others in that formation counts and palaeodiversity metrics are derived from independent data sources, and so within-study redundancy is avoided. The study confirms the complexity of rock-fossil time series, and the likelihood that the fossil record documents a complex mix of potential biological signal, common cause signal, and rock record and sampling bias. It may be impossible to identify a useful simple sampling proxy for the fossil record that captures every bias and sampling error. Ironically, when preservation is good, sampling proxies representing rock availability, such as outcrop area, can be used to predict palaeodiversity, but are ineffectual when the fossil record is patchy.

1. Introduction

A major question facing palaeobiologists is whether patterns of raw biodiversity observed in the fossil record can be trusted (Raup, 1972, 1976; Smith and McGowan, 2011). Many recent publications have attempted to address this issue and have identified positive correlations between fossil occurrences and postulated proxies for sampling (Raup, 1972, 1976; Peters and Foote, 2001; Smith, 2001; Smith and McGowan, 2005, 2007; Fröbisch, 2008; Barrett et al., 2009; Butler et al., 2009; Wall et al., 2009; Benson et al., 2010). There have been four, non-mutually exclusive, explanations for this persistent covariation: (1) the fossil record is severely biased by the amount of sedimentary rock preserved per time period (Raup, 1972, 1976; Peters and Foote, 2001, 2002; Smith, 2001; Smith and McGowan, 2005, 2007; Fröbisch, 2008; Barrett et al., 2009; Wall et al., 2009; Benson et al., 2010); (2) the fossil record has been unevenly sampled by palaeontologists, both stratigraphically (Sheehan, 1977) and geographically (Jackson and Johnson, 2001; Johnson, 2003); (3) time series for both the rock and fossil records have been driven simultaneously by an environmental common-cause mechanism (Peters, 2005, 2006; Peters and Heim, 2010, 2011, 2012; Hannisdal, 2011; Hannisdal and Peters, 2011; Heim and Peters, 2011); or (4) sampling proxies and fossil diversity are not independent variables and are therefore at least partly redundant with each other (Benton, 2010, 2012; Benton et al., 2011; Dunhill, 2012; Benton et al., 2013). It is generally accepted that the relationship between the rock and fossil records most likely represents a complicated mix of evolutionary patterns and biases associated with sampling and preservation (Miller, 2000; Foote, 2003; Kalmar and Currie, 2010; Benson and Butler, 2011; Dunhill et al., 2012; Benson and Upchurch, 2013; Dunhill et al., 2013) and it is therefore extremely difficult, if not impossible, to extract a pure biological signal.

The majority of studies that have demonstrated a close correlation between sampling proxies and fossil diversity have been carried out at global or continental scales, using sampling proxies that are arguably imprecise, such as rock outcrop area (Smith, 2001; Smith and McGowan, 2005, 2007; Wall et al., 2009; Wall et al., 2011) and counts

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http://dx.doi.org/10.1016/j.palaeo.2014.03.026
0031-0182/

of fossiliferous formations (Peters and Foote, 2001, 2002; Wang and Dodson, 2006; Fröbisch, 2008; Barrett et al., 2009; Butler et al., 2009; Benson et al., 2010; Benson and Butler, 2011; Butler et al., 2011; Upchurch et al., 2011). In contrast, the majority of studies carried out at finer geographic and stratigraphic scales have found little evidence for a strong correlation between the rock and fossil records (Benton et al., 2004; Mander and Twitchett, 2008; Benton, 2012; Dunhill et al., 2012, 2013), with the exception of Crampton et al. (2003). This mismatch of results could be a result of imprecise or redundant sampling proxies available for use in large scale studies, or that the fossil-proxy covariation only becomes apparent at larger continental and global scales.

Here, we compare fossil diversity with a number of proxies representing different aspects of sampling in the well studied Triassic–Jurassic systems of Great Britain at well-constrained temporal and geographical scales in an attempt to understand the nature of the biasing factors affecting apparent diversity preserved in the fossil record. This case study records a transition from a predominantly terrestrial Triassic system to a predominantly marine Jurassic system. Therefore, we are able to test the quality of, and compare, both the terrestrial and marine fossil records. The fossil record of Great Britain has been intensively studied for well over two centuries and represents one of the most heavily sampled systems in the world. In addition, the activities of the British Geological Survey (BGS) over the past century and a half have resulted in a unique and extremely detailed set of geological maps and databases that are now available in digital format.

2. Data and methods

Fossil generic occurrence data of all animal groups were obtained from a detailed literature search of over 1400 journal papers, books, field guides, and monographs (Appendix B). Taxic occurrences were recorded at the levels of stratigraphic stages and formations for both the marine and terrestrial realms. Sampling proxies were developed to represent the three aspects of sampling identified by Raup (1972): (1) sedimentary rock volume; (2) accessibility; and (3) worker effort. In addition, formation counts were also devised for each stage. All sampling proxies were applied to both the marine and terrestrial realms.

2.1. Sedimentary rock volume

Maximum and minimum measures of outcrop area were calculated from the BGS digital bedrock geology map *DiGMapGB-50* of the UK (1:50,000) for each stage using ArcGIS 9.3. It was not possible to calculate a single outcrop area figure as the BGS *DiGMapGB-50* data is compiled at the formation level and many formations straddle stage boundaries, either because they truly include rock deposited during multiple stage intervals, or because, although they really belong to a single stage, they cannot be accurately dated, and cannot be assigned confidently to one or the other, or appropriately divided. The only suitable method for dealing with this was to record a maximum outcrop area measurement that includes the entire map area in each stage for multi-stage formations, and a minimum outcrop area measurement that assumes the entire area belongs in the alternate stage. At the formation level, average thickness values were obtained from the BGS lexicon (http://www.bgs.ac.uk/lexicon/) and BGS field reports. Outcrop area measurements were obtained from BGS *DiGMapGB-50* in ArcGIS 9.3. Formation volumes were then calculated by multiplying thickness by outcrop area. In the formation level data set, the Penarth Group was not subdivided into its constituent Westbury and Lilstock formations as neither is sufficiently thick to map at 1:50,000 throughout Great Britain.

2.2. Accessibility

At the stage level, maximum and minimum measures of coastal outcrop area were calculated by clipping the BGS *DiGMapGB-50* to a 1 km buffer (i.e. outcrop area incorporates an extra 1 km on all sides) around the British coastline in ArcGIS 9.3. The distance of 1 km was used as a conservative measure that was deemed to capture the maximum extent of cliffs and rocky foreshore across all coastal regions. Coastal outcrop was used as a proxy for accessibility, as Dunhill (2011, 2012) showed that formations are more likely to be exposed, and thus easily accessible for sampling, if they outcrop in close proximity to the coast. The maximum and minimum numbers of quarries were also calculated by clipping the BGS *BritPits* database to Triassic–Jurassic formations in the BGS *DiGMapGB-50* in ArcGIS 9.3. Quarry numbers, taken from the BGS *BritPits* database, were used as a proxy for the amount of inland rock exposure. As there is no information available of quarry areas/volumes, a simple count of quarry numbers per time bin/formation is the only suitable metric. At the formation level, coastal outcrop area and the number of quarries were calculated for each formation from BGS *DiGMapGB-50* and BGS *BritPits* database using ArcGIS 9.3. These metrics for accessibility are practical measures, and they highlight the enormous potential differences between outcrop (= map area) and exposure (= rock accessible), and the fact that outcrop and exposure areas do not correlate because of variable cover in the UK (Dunhill, 2011) and in non-desert areas generally (Dunhill, 2012).

2.3. Worker effort

Counts of publications were developed at the stage and formation levels from a detailed literature search (using Web of Knowledge, Google Scholar, and the reference lists of already recorded publications; Appendix B). Publications selected include those that have yielded palaeontological data, but also those that present sedimentological and stratigraphical studies, including the BGS memoirs. The inclusion of non-palaeontological publications allowed the identification of formations that are truly unfossiliferous, rather than those that have not yielded any fossil material because of a lack of sampling. Inclusion of all publications on each geological formation, not just those that report fossils, allowed a balanced measure of worker effort. This has rarely been done in previous studies that tend to report only fossiliferous formations, or even just the formations that yield the particular fossils of interest. It is, however, normal in ecological sampling to count null returns so as to document sampling completely.

2.4. Formation counts

Many recent publications investigating the quality of the fossil record have used formation counts as a sampling proxy (Peters and Foote, 2001, 2002; Wang and Dodson, 2006; Fröbisch, 2008; Barrett et al., 2009; Butler et al., 2009; Benson et al., 2010; Benson and Butler, 2011; Butler et al., 2011; Upchurch et al., 2011; Benson and Mannion, 2012). However, this practice has been criticized because; (1) formations are arbitrary human constructs (Peters and Heim, 2010) and they vary in thickness and coverage over many orders of magnitude (Benton et al., 2011); (2) they do not correlate with rock exposure measurements (Dunhill, 2011); (3) they do not consistently correlate with collection effort (Crampton et al., 2003); and (4) they may depend on fossil abundance and diversity (Wignall and Benton, 1999), and are therefore not independent of fossil diversity (Benton et al., 2011). It is therefore unclear how much formation counts can tell us about sampling intensity and their popularity in recent papers is most likely related to their relative ease of acquisition from sources such as the Paleobiology Database (PaleoDB). However, in some cases, where extensive geological mapping has yet to be carried out, formation counts offer one of the only alternative ways of quantifying the geological record. In this study, three measures of formation counts were used; (1) a total formation count obtained from the BGS *DiGMapGB-50*; (2) a raw fossiliferous formation count obtained directly from the PaleoDB; and (3) a valid PaleoDB formation count, which was standardized for synonymy and subdivisions with regard to current BGS terminology.

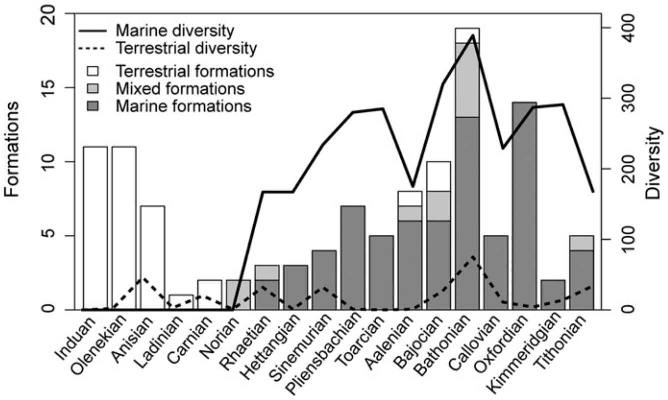

Fig. 1. Marine and terrestrial generic diversities and the number of marine, mixed, and terrestrial valid sedimentary formations (from the BGS lexicon) through the Triassic and Jurassic of Great Britain.

2.5. Statistical tests

Wilcoxon tests were used to test for significant differences in generic diversity between formations of different facies (marine/mixed/terrestrial) and different lithologies within facies (carbonates/fine siliciclastic/coarse siliciclastic). Pairwise Spearman Rank correlation tests were used to test for significant correlations between pairings of all variables, using the R function *pair.cor* provided by M. Sakamoto (Appendix A), which applies the False Discovery Rate (FDR) approach of Benjamini and Hochberg (1995).

We use multiple regression to test the non-independent predictive power of combinations of sampling proxies on generic diversity and to identify which combinations of sampling proxies best predict generic diversity. Here, we use a multiple linear regression using the R function 'lm', which produces regression fits by simple and multiple least-squares regression. The goodness of fit is specified by adjusted r^2 and by Akaike information criterion (AIC). Model fitting is carried out in a stepwise manner using the R function 'step', both backwards and forwards. The best-fitting model is identified by stepwise experimentation and improvements in adjusted r2 and AIC. We carried out the analyses using the R function 'mlm.R' (Appendix A) (Benton et al. 2013).

Generalized differencing was applied to the time series data at the level of stratigraphic stages to help mitigate the effects of autocorrelation, using the R function *gen.diff* of G. Lloyd. All tests were carried out at the stage and formation level for the marine and terrestrial data sets and R functions are available in the Supplementary Material (Appendix A).

3. Results

Unsurprisingly, given the proportion of shelly and skeletonized marine organisms and consistency of conducive preservational environments, total diversity is higher in the predominantly marine Jurassic, than in the predominantly terrestrial Triassic (Fig. 1) as marine formations support a significantly higher palaeodiversity than terrestrial formations (Fig. 2A).

3.1. Marine data

There are no Lower or Middle Triassic marine strata in Great Britain. Marine diversity remains at zero until the Norian–Rhaetian transgression in the Late Triassic (Fig. 1). Marine Jurassic palaeodiversity shows three peaks through the Pliensbachian–Toarcian, Bajocian–Bathonian, and Oxfordian–Kimmeridgian, and troughs in the Aalenian, Callovian, and Tithonian (Fig. 1). Palaeodiversity is significantly higher in fine siliciclastic and carbonate formations than in coarse siliciclastic formations (Fig. 2B).

Stage duration does not correlate with any of the sampling proxies or palaeodiversity (Table 1). At the stage level, the correlation between different sampling proxies is poor; only quarry counts and formation counts show robust correlation (Table 1). Of particular concern is that the time series of maximum and minimum measures of outcrop area, coastal outcrop area, and numbers of quarries differ markedly and do not show robust correlations (Fig. 3ABC; Table 1), questioning whether either the maximum or minimum measurements are accurate figures. Palaeodiversity does not correlate well with any of the sampling proxies, except for publication counts (Fig. 3; Table 1); however, the significance of this correlation does not survive correction for multiple comparisons. At the stage level, multiple regression models show that all variables combined can be used to predict palaeodiversity (Table 2) and only the removal of the BGS formation count increases the significance of the model, although the predictive power improves only very slightly (Tables 2 and 3).

At the formation level, the majority of sampling proxies correlate well with one another and all sampling proxies correlate well with palaeodiversity, apart from thickness and number of quarries, which become non-significant after correction for multiple comparisons (Table 4). At the formation level, multiple regression models show that all variables combined can be used to predict palaeodiversity (Table 2), and a model consisting of outcrop, volume and publication count offers the most predictive power (Tables 2 and 3). At the formation level, publication count is by far the most significant predictor of palaeodiversity (Table 2).

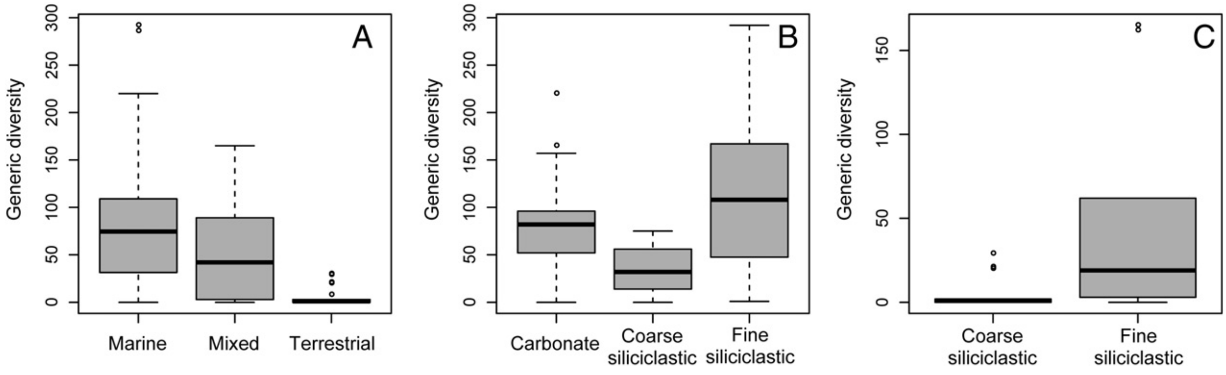

Fig. 2. (A) Generic diversity of valid BGS formations by facies (Wilcoxon tests: marine ~ mixed, W = 310, $p = 0.3$; marine ~ terrestrial, W = 1147, $p < 0.001$; mixed ~ terrestrial, W = 164, $p = 0.004$), (B) generic diversity of marine formations by lithology (Wilcoxon tests: carbonate ~ coarse siliciclastic, W = 81.5, $p < 0.001$; carbonate ~ fine siliciclastic, W = 364, $p = 0.12$; coarse siliciclastic ~ fine siliciclastic, W = 64, $p < 0.001$), (C) generic diversity of terrestrial formations by lithology (Wilcoxon test: coarse siliciclastic ~ fine siliciclastic, W = 31.5, $p = 0.003$).

Table 1
Correlation coefficients for generalized differenced stage level marine data. Significant at ($p < 0.05$)* and significant after correction for multiple comparison** using false discovery rate method of Benjamini and Hochberg (1995) are indicated.

Comparison	Spearman rank	
	r_s	p
Stage duration ~ max outcrop	0.12	0.65
Stage duration ~ min outcrop	0.14	0.58
Stage duration ~ max coastal outcrop	−0.11	0.68
Stage duration ~ min coastal outcrop	0.01	0.96
Stage duration ~ min quarries	−0.29	0.26
Stage duration ~ min quarries	−0.14	0.60
Stage duration ~ BGS formations	−0.12	0.65
Stage duration ~ paleoDB formations	−0.40	0.12
Stage duration ~ valid PaleoDB formations	−0.30	0.24
Stage duration ~ coarse siliciclastic formations	0.09	0.72
Stage duration ~ fine siliciclastic formations	−0.01	0.98
Stage duration ~ carbonate formations	−0.08	0.76
Stage duration ~ publications	0.05	0.86
Stage duration ~ genera	−0.03	0.90
Max outcrop ~ min outcrop	0.46	0.07
Max outcrop ~ max coastal outcrop	0.15	0.57
Max outcrop ~ min coastal outcrop	0.06	0.81
Max outcrop ~ min quarries	0.19	0.46
Max outcrop ~ min quarries	−0.01	0.97
Max outcrop ~ BGS formations	0.32	0.21
Max outcrop ~ paleoDB formations	0.42	0.10
Max outcrop ~ valid PaleoDB formations	0.41	0.10
Max outcrop ~ coarse siliciclastic formations	0.49	0.05*
Max outcrop ~ fine siliciclastic formations	0.54	0.03*
Max outcrop ~ carbonate formations	0.11	0.67
Max outcrop ~ publications	0.37	0.15
Max outcrop ~ genera	0.31	0.22
Min outcrop ~ max coastal outcrop	−0.37	0.14
Min outcrop ~ min coastal outcrop	0.14	0.59
Min outcrop ~ min quarries	0.43	0.09
Min outcrop ~ min quarries	0.63	0.008*
Min outcrop ~ BGS formations	0.65	0.006*
Min outcrop ~ paleoDB formations	0.58	0.02*
Min outcrop ~ valid PaleoDB formations	0.55	0.02*
Min outcrop ~ coarse siliciclastic formations	0.31	0.23
Min outcrop ~ fine siliciclastic formations	0.44	0.08
Min outcrop ~ carbonate formations	0.63	0.007*
Min outcrop ~ publications	0.13	0.62
Min outcrop ~ genera	0.35	0.17
Max coastal outcrop ~ min coastal outcrop	0.43	0.09
Max coastal outcrop ~ min quarries	−0.10	0.72
Max coastal outcrop ~ min quarries	−0.51	0.04*
Max coastal outcrop ~ BGS formations	−0.22	0.40
Max coastal outcrop ~ paleoDB formations	−0.13	0.61
Max coastal outcrop ~ valid PaleoDB formations	−0.06	0.82
Max coastal outcrop ~ coarse siliciclastic formations	−0.40	0.11
Max coastal outcrop ~ fine siliciclastic formations	0.27	0.29
Max coastal outcrop ~ carbonate formations	−0.31	0.23
Max coastal outcrop ~ publications	0.46	0.07
Max coastal outcrop ~ genera	0.43	0.09
Min coastal outcrop ~ min quarries	−0.11	0.68
Min coastal outcrop ~ min quarries	0.15	0.55
Min coastal outcrop ~ BGS formations	−0.01	0.98
Min coastal outcrop ~ paleoDB formations	0.18	0.50
Min coastal outcrop ~ valid PaleoDB formations	0.22	0.40
Min coastal outcrop ~ coarse siliciclastic formations	−0.05	0.85
Min coastal outcrop ~ fine siliciclastic formations	0.12	0.65
Min coastal outcrop ~ carbonate formations	0.22	0.39
Min coastal outcrop ~ publications	0.22	0.40
Min coastal outcrop ~ genera	0.09	0.72
Max quarries ~ min quarries	0.65	0.005*
Max quarries ~ BGS formations	0.80	<0.001**
Max quarries ~ paleoDB formations	0.63	0.008*
Max quarries ~ valid palaeoDB formations	0.66	0.005*
Max quarries ~ coarse siliciclastic formations	0.05	0.84
Max quarries ~ fine siliciclastic formations	0.57	0.02*
Max quarries ~ carbonate formations	0.58	0.02*
Max quarries ~ publications	0.25	0.34
Max quarries ~ genera	0.27	0.29
Min quarries ~ BGS formations	0.77	<0.001**
Min quarries ~ paleoDB formations	0.63	0.008*
Min quarries ~ valid PaleoDB formations	0.70	0.002**
Min quarries ~ coarse siliciclastic formations	0.30	0.24
Min quarries ~ fine siliciclastic formations	0.21	0.43
Min quarries ~ carbonate formations	0.91	<0.001**
Min quarries ~ publications	−0.01	0.97
Min quarries ~ genera	0.02	0.95
BGS formations ~ paleoDB formations	0.64	0.007*
BGS formations ~ valid PaleoDB formations	0.76	0.001**
BGS formations ~ coarse siliciclastic formations	0.35	0.17
BGS formations ~ fine siliciclastic formations	0.45	0.07
BGS formations ~ carbonate formations	0.80	<0.001**
BGS formations ~ publications	0.36	0.15
BGS formations ~ genera	0.38	0.14
PaleoDB formations ~ valid PaleoDB formations	0.94	<0.001**
PaleoDB formations ~ coarse siliciclastic formations	0.08	0.77
PaleoDB formations ~ fine siliciclastic formations	0.46	0.06
PaleoDB formations ~ carbonate formations	0.69	0.003**
PaleoDB formations ~ publications	−0.03	0.92
PaleoDB formations ~ genera	0.25	0.32
Valid paleoDB formations ~ coarse siliciclastic formations	0.12	0.65
Valid paleoDB formations ~ fine siliciclastic formations	0.47	0.06
Valid paleoDB formations ~ carbonate formations	0.83	<0.001**
Valid paleoDB formations ~ publications	0.13	0.63
Valid paleoDB formations ~ genera	0.36	0.16
Coarse siliciclastic formations ~ Fine siliciclastic formations	−0.11	0.67
Coarse siliciclastic formations ~ carbonate formations	0.25	0.33
Coarse siliciclastic formations ~ publications	0.15	0.57
Coarse siliciclastic formations ~ genera	−0.24	0.35
Fine siliciclastic formations ~ carbonate formations	0.25	0.32
Fine siliciclastic formations ~ publications	0.33	0.19
Fine siliciclastic formations ~ genera	0.31	0.23
Carbonate formations ~ publications	0.10	0.69
Carbonate formations ~ genera	0.26	0.32
Publications ~ genera	0.62	0.01*

3.2. Terrestrial data

Terrestrial palaeodiversity remains fairly low throughout the entire Triassic–Jurassic, with peaks in the Anisian and Bajocian–Bathonian, when terrestrial rocks were most abundant (Fig. 1). Palaeodiversity is significantly higher in fine siliciclastic formations than in coarse siliciclastic formations (Fig. 2C).

Stage duration does not correlate with any of the sampling proxies or palaeodiversity, apart from a weak correlation with the number of BGS formations, although this correlation becomes non-significant after correction for multiple comparisons (Table 5). At the stage level, there are correlations between outcrop and coastal outcrop area, outcrop area and numbers of quarries, outcrop area and numbers of publications, coastal outcrop area and formation counts, and formation counts and publications (Table 5). However, many of these correlations are influenced by the high numbers of zeros in the 'minimum' data sets. As with the marine data, the maximum and minimum measures of outcrop area, coastal outcrop area and numbers of quarries differ markedly and do not correlate (Fig. 4ABC; Table 5). Palaeodiversity does not correlate well with any of the sampling proxies, except for publication count (Fig. 4; Table 5). At the stage level, a multiple regression model containing all variables does not predict palaeodiversity (Table 2), but after the stepwise removal of stage duration, minimum outcrop area, maximum coastal outcrop area and valid PaleoDB formations, the explanatory power of the model increases and palaeodiversity can be predicted (Tables 2 and 3).

At the formation level, sampling proxies do not correlate well with one another, with the exception of thickness and volume and outcrop and volume (Table 6). None of the sampling proxies correlates at all with palaeodiversity, apart from the publication count, which shows a very strong, highly significant correlation (Table 6). At the formation level, multiple regression models show that all variables combined can be used to predict palaeodiversity (Table 2), but only the publication

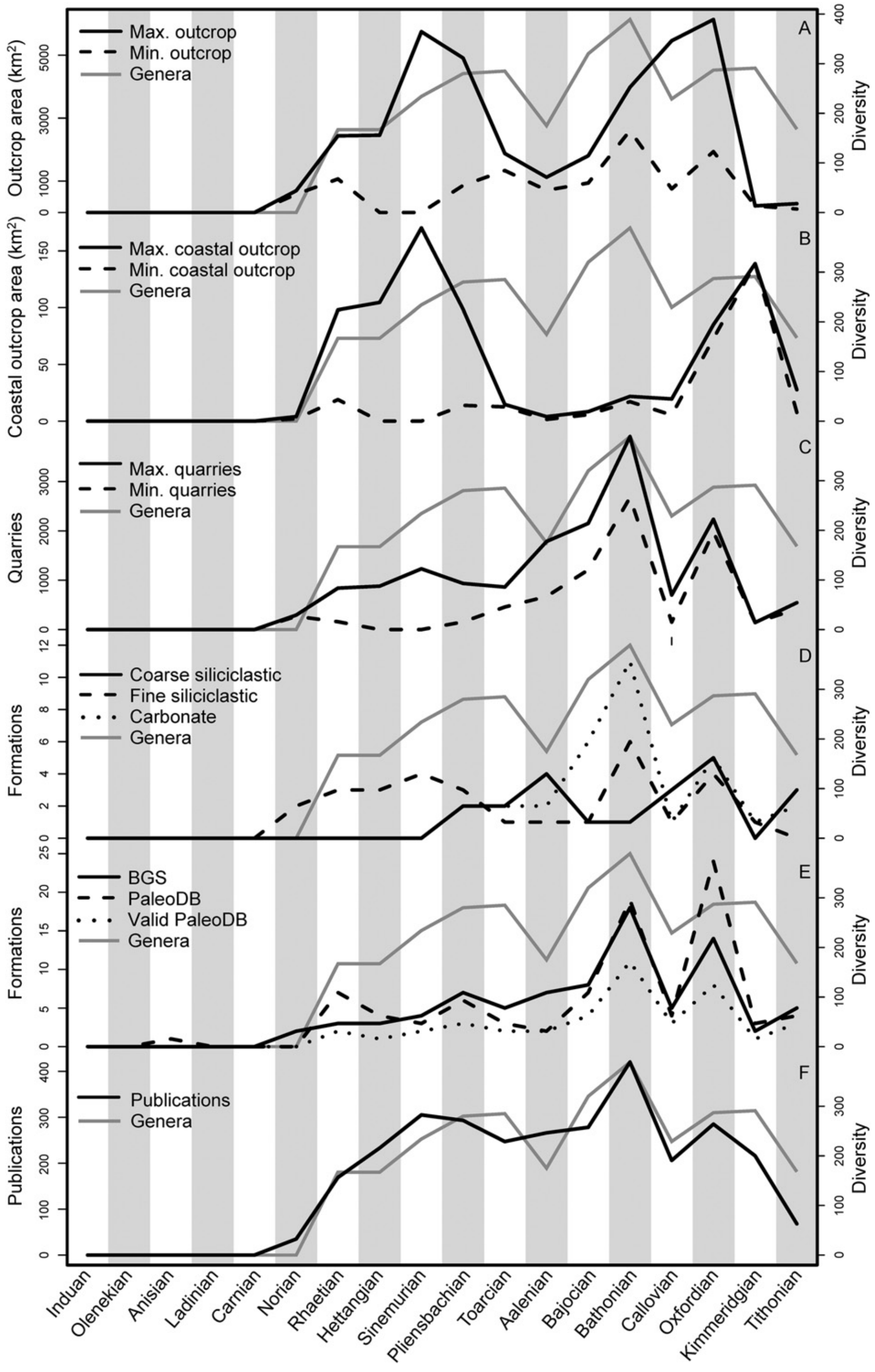

Fig. 3. Generic diversity compared to sampling proxies through the marine Triassic and Jurassic of Great Britain (A) Outcrop area, (B) Coastal outcrop area, (C) Quarry count, (D) Formations by lithology, (E) Formation count and (F) Publication count.

count offers significant predictive power over palaeodiversity and the best fitting model consists of only the publication count (Tables 2 and 3).

4. Discussion

The disparity in diversity between the Triassic and Jurassic systems of Great Britain is largely facies-controlled, with the predominantly terrestrial Triassic system showing a markedly lower diversity than the predominantly marine Jurassic system. It is also evident that within broader marine and terrestrial facies, the taphonomic processes associated with different lithologies also influence diversity. As expected, carbonate and fine siliciclastic deposits preserve a higher diversity than coarse siliciclastic rocks, the latter being most often associated with high energy and marginal marine or terrestrial environments where life would have been rare or biological remains at least would have been more likely to be destroyed or winnowed away.

The correlations between different sampling proxies are not consistent across different facies and stratigraphic scales. This is particularly evident when comparing the maximum and minimum values of proxies. None of the maximum values correlates with the minimum values,

Table 2

Results of multiple linear modelling for A. Stage and B. formation level marine and terrestrial data sets. Results are displayed for the model containing all variables (FULL) and the best fitting model (BEST) after stepwise elimination. Significance levels are indicated as $^{***}p < 0.001$, $^{**}p < 0.01$ and $^{*}p < 0.05$.

	Estimate	Standard error	t-Value	p
A. Stage				
Marine FULL (adj. $R^2 = 0.76$, AIC = 117.68, $p = 0.04$)				
Intercept	1.8584	7.6022	0.244	0.82
Max outcrop	−0.0452	0.0178	−2.546	0.052
Min outcrop	0.0997	0.0296	3.367	0.02*
Max coast outcrop	2.6065	0.6447	4.043	0.01*
Min coast outcrop	−4.1974	1.5222	−2.757	0.04*
Max quarries	−0.2191	0.0709	−3.091	0.03*
Min quarries	0.2464	0.103	2.391	0.06
BGS formations	−5.4598	17.0488	−0.32	0.76
PaleoDB formations	22.6473	11.6141	1.95	0.11
Valid paleoDB formations	−50.9132	32.7292	−1.556	0.18
Publications	1.32	0.547	2.413	0.06
Duration	−4.378	3.74	−1.17	0.29
Marine BEST (adj. $R^2 = 0.79$, AIC = 116.02, $p = 0.01$)				
Intercept	1.8622	7.0106	0.266	0.8
Max outcrop	−0.0467	0.0158	−2.949	0.03*
Min outcrop	0.0972	0.0263	3.69	0.01*
Max coast outcrop	2.5773	0.5886	4.379	0.005**
Min coast outcrop	−4.0275	1.3158	−3.061	0.02*
Max quarries	−0.2222	0.0647	−3.411	0.01*
Min quarries	0.23	0.0825	2.788	0.03*
PaleoDB formations	22.8638	10.6922	2.138	0.08
Valid paleoDB formations	−52.4055	29.8749	−1.754	0.13
Publications	1.3	0.5021	2.596	0.04*
Duration	−4.0393	3.3087	−1.221	0.27
Terrestrial FULL (adj. $R^2 = 0.61$, AIC = 89.68, $p = 0.1$)				
Intercept	−0.8081	3.1976	−0.253	0.81
Max outcrop	0.0081	0.0187	0.435	0.68
Min outcrop	−0.0183	0.0983	−0.186	0.86
Max coast outcrop	0.1202	0.4907	0.245	0.82
Min coast outcrop	−1.0968	2.8185	−0.389	0.71
Max quarries	−0.067	0.0668	−1.002	0.36
Min quarries	0.0864	0.1419	0.609	0.57
BGS formations	6.879	9.6119	0.716	0.51
PaleoDB formations	−5.9643	5.2357	−1.139	0.31
Valid paleoDB formations	6.2453	13.5474	0.468	0.66
Publications	0.1252	0.6699	0.187	0.86
Duration	0.4033	3.2118	0.126	0.91
Terrestrial BEST (adj. $R^2 = 0.77$, AIC = 82.91, $p = 0.002$)				
Intercept	−0.6203	2.4047	−0.258	0.8
Max outcrop	0.0118	0.0059	2.011	0.08
Min coast outcrop	−1.7638	0.7938	−2.222	0.053
Max quarries	−0.0913	0.0311	−2.934	0.02*
Min quarries	0.0754	0.0323	2.329	0.04*
BGS formations	7.963	3.4549	2.305	0.05*
PaleoDB formations	−5.3661	3.311	−1.621	0.14
Publications	0.3232	0.201	1.608	0.14
B. Formations				
Marine FULL (adj. $R^2 = 0.74$, AIC = 465.51, $p < 0.001$)				
Intercept	15.7355	7.5248	2.091	0.04*
Thickness	0.0414	0.0764	0.541	0.59
Outcrop	−0.0178	0.018	−0.992	0.33
Volume	0.1096	0.0721	1.52	0.13
Coast outcrop	0.1266	0.3118	0.406	0.69
Quarries	0.0209	0.0185	1.135	0.26
Publications	1.1055	0.1661	6.655	<0.001***
Marine BEST (adj. $R^2 = 0.75$, AIC = 461.82, $p < 0.001$)				
Intercept	17.1949	6.7935	2.531	0.01*
Outcrop	−0.0215	0.0153	−1.406	0.16
Volume	0.1311	0.0589	2.228	0.03*
Publications	1.2274	0.1189	10.323	<0.001***
Terrestrial FULL (adj. $R^2 = 0.67$, AIC = 204.99, $p < 0.001$)				
Intercept	−18.05	9.827	−1.837	0.08
Thickness	0.0122	0.0282	0.435	0.67
Outcrop	−0.0054	0.0292	−0.186	0.85
Volume	−0.00093	0.0163	−0.057	0.96
Coast outcrop	−0.1959	0.4141	−0.473	0.64
Quarries	0.0082	0.0391	0.211	0.83
Publications	1.47	0.2478	5.932	<0.001***
Terrestrial BEST (adj. $R^2 = 0.72$, AIC = 196.04, $p < 0.001$)				
Intercept	−18.6128	6.1631	−3.02	0.005**
Publications	1.503	0.1705	8.818	<0.001**

Table 3
Results of multiple linear modelling for A. Stage and B. formation level marine and terrestrial data sets. 'Model' indicates variable is present in best-fitting model and numbers (e.g. 1st) indicate where a variable has been omitted during the step elimination procedure and in which order i.e. worst fitting variables being omitted '1st'.

A. Stage

Explanatory variables	Max outcrop	Min outcrop	Max coast outcrop	Min coast outcrop	Max quarries	Min quarries	BGS formations	PaleoDB formations	Valid paleoDB formations	Publications	Duration
Number in file	1	2	3	4	5	6	7	8	9	10	11
Marine	Model	Model	Model	Model	Model	Model	1st	Model	Model	Model	Model
Terrestrial	Model	2nd	3rd	Model	Model	Model	Model	Model	4th	Model	1st

B. Formations

Explanatory variables	Thickness	Outcrop	Volume	Coast outcrop	Quarries	Publications
Number in files	1	2	3	4	5	6
Marine	2nd	Model	Model	1st	3rd	Model
Terrestrial	4th	3rd	1st	5th	2nd	Model

and so neither can be relied upon as precise, or even accurate, measures of rock availability or accessibility. The sampling proxies for rock volume and accessibility correlate well with one another at the formation scale, particularly in the marine data, suggesting that the amount of exposed rock is roughly proportional to the amount of rock outcropping at the surface, thus contradicting the findings of Dunhill (2011, 2012). However, Dunhill (2011, 2012) used measures of rock exposure from remote sensing imagery, while this study uses the number of quarries and amount of coastal outcrop area as proxies for exposed rock area. The stronger correlations between sampling proxies when working at the finer, formation scale support the idea that the use of sampling proxies at coarse scales, both stratigraphically and geographically, is poorly supported. As data are scaled up and generalized, from the formation to stage or epoch level, it becomes difficult to obtain precise sampling proxies because of uncertainties in dating accuracy (Benton et al., 2011; Dunhill, 2012; Dunhill et al., 2012, 2013). Therefore, studies that have used generalized, large-scale measures of the geological record (Raup, 1976; Uhen and Pyenson, 2007; Wall et al., 2009; Kalmar and Currie, 2010; Wall et al., 2011) may suffer from using highly inaccurate and imprecise measures of rock availability: there is a risk of false correlations as both sampling proxy and diversity time series are amalgamated and generalized, masking small-scale sharp variations which may be in- or out of phase, as found for example in a study of the Permian tetrapod fossil record (Benton, 2012). In this latter study, a well-correlated pair of fossil and rock record time series went out of correlation at finer time scales because the peaks and troughs, which had been synchronous at the coarse time scale, ceased to be synchronous when time bins were divided. The inconsistency observed in the correlations between different sampling proxies and the imprecision of sampling proxy measurements at coarse scales casts doubt on the effectiveness of using singular sampling proxies to capture all the biasing effects within the fossil record.

Table 4
Correlation coefficients for raw formation level marine data. Significant at ($p < 0.05$)* and significant after correction for multiple comparison** using false discovery rate method of Benjamini and Hochberg (1995) are indicated.

Comparison	Spearman's rank	
	r_s	p
Thickness ~ outcrop area	0.45	0.001*
Thickness ~ volume	0.7	<0.001**
Thickness ~ coastal outcrop area	0.57	<0.001**
Thickness ~ number of quarries	0.24	0.08
Thickness ~ number of publications	0.32	0.02*
Thickness ~ genera	0.37	0.005*
Outcrop area ~ volume	0.94	0**
Outcrop area ~ coastal outcrop area	0.45	0.001*
Outcrop area ~ number of quarries	0.68	<0.001**
Outcrop area ~ number of publications	0.51	<0.001**
Outcrop area ~ genera	0.53	<0.001**
Volume ~ coastal outcrop area	0.55	<0.001**
Volume ~ number of quarries	0.63	<0.001**
Volume ~ number of publications	0.53	<0.001**
Volume ~ genera	0.54	<0.001**
Coastal outcrop area ~ number of quarries	0.06	0.65
Coastal outcrop area ~ number of publications	0.4	0.002*
Coastal outcrop area ~ genera	0.5	<0.001**
Number of quarries ~ number of publications	0.47	<0.001*
Number of quarries ~ genera	0.43	0.001*
Number of publications ~ genera	0.76	<0.001**

The correlations between sampling proxies and palaeodiversity show different patterns in the marine and terrestrial data sets (Rook et al. 2013). In the marine data, the correlations improve as the stratigraphic resolution improves from the stage to the formation level, whilst correlation is poor at all scales in the terrestrial data. It is likely that this pattern is a result of differences in data quality. The marine record is very rich, particularly in the Jurassic, and it appears that palaeodiversity is at least partly controlled by rock availability and accessibility. The terrestrial record is far more sparse and patchy, so the effects of rock availability are overprinted by a stronger signal of generally poor and sporadic preservation. Therefore it appears that, when preservation is consistently good, sampling proxies representing rock availability, such as outcrop area, can be used to predict palaeodiversity (e.g. Crampton et al. 2003). However, it is unclear whether such a result would hold true for a less intensively studied part of the world.

These results, however, do not rule out a common-cause mechanism where relative sea level drives both palaeodiversity and rock availability by altering the area of shallow shelf seas through time (Peters, 2005, 2006). The presence of strong correlations between sampling proxies and palaeodiversity in the marine realm, whilst being less clear in the terrestrial realm, fits with a common-cause mechanism. It is unclear whether relative sea-level influences terrestrial diversity, and as yet, evidence of common-cause in the terrestrial realm is lacking (Fara, 2002; Butler et al., 2011). Note, however, that these latter authors considered only a sea-level common-cause model for terrestrial diversity. The fact that a terrestrial common cause model has not been identified could mean that it does not exist, or that it is more complex than simply the inverse of the sea-level curve (Hannisdal and Peters, 2011), possibly involving elements of continental subdivision, topographic relief, latitudinal distribution of land, temperature regimes, vegetation distribution, and other factors. Despite the picture commonly painted in the scientific literature (Wall et al., 2009; Butler et al., 2011), there is no logical reason why the bias and common-cause hypotheses need be mutually exclusive, and in all likelihood, the palaeodiversity patterns we see in the fossil record are influenced significantly by both (Benson and Butler, 2011).

Worker effort correlates well with palaeodiversity in all data sets, suggesting that the amount of sampling effort by palaeontologists influences diversity (Sheehan, 1977). However, it must also be considered that the abundance and diversity of fossil material influences the

Table 5
Correlation coefficients for generalized differenced stage level terrestrial data. Significant at ($p < 0.05$)* and significant after correction for multiple comparison** using false discovery rate method of Benjamini and Hochberg (1995) are indicated.

Comparison	Spearman's rank	
	r_s	p
Stage duration ~ max outcrop	−0.25	0.32
Stage duration ~ min outcrop	0.21	0.42
Stage duration ~ max coastal outcrop	−0.42	0.09
Stage duration ~ min coastal outcrop	0.17	0.52
Stage duration ~ min quarries	−0.13	0.63
Stage duration ~ min quarries	0.17	0.52
Stage duration ~ BGS formations	−0.56	0.02*
Stage duration ~ paleoDB formations	−0.14	0.60
Stage duration ~ valid PaleoDB formations	−0.02	0.95
Stage duration ~ coarse siliciclastic formations	−0.58	0.02
Stage duration ~ fine siliciclastic formations	−0.04	0.88
Stage duration ~ publications	−0.31	0.22
Stage duration ~ genera	−0.13	0.62
Max outcrop ~ min outcrop	0.34	0.19
Max outcrop ~ max coastal outcrop	0.87	<0.001**
Max outcrop ~ min coastal outcrop	0.38	0.13
Max outcrop ~ min quarries	0.81	<0.001**
Max outcrop ~ min quarries	0.41	0.10
Max outcrop ~ BGS formations	0.55	0.02*
Max outcrop ~ paleoDB formations	0.04	0.89
Max outcrop ~ valid PaleoDB formations	0.13	0.62
Max outcrop ~ coarse siliciclastic formations	0.67	0.004*
Max outcrop ~ fine siliciclastic formations	0.43	0.09
Max outcrop ~ publications	0.68	0.003**
Max outcrop ~ genera	0.41	0.11
Min outcrop ~ max coastal outcrop	0.31	0.23
Min outcrop ~ min coastal outcrop	0.72	0.001**
Min outcrop ~ min quarries	0.46	0.06
Min outcrop ~ min quarries	0.99	<0.001**
Min outcrop ~ BGS formations	0.42	0.10
Min outcrop ~ paleoDB formations	0.65	0.006*
Min outcrop ~ valid PaleoDBformations	0.50	0.04*
Min outcrop ~ Coarse siliciclastic formations	0.43	0.09
Min outcrop ~ Fine siliciclastic formations	0.44	0.08
Min outcrop ~ Publications	0.53	0.03*
Min outcrop ~ genera	0.37	0.14
Max coastal outcrop ~ min coastal outcrop	0.21	0.43
Max coastal outcrop ~ min quarries	0.75	0.001**
Max coastal outcrop ~ Min quarries	0.38	0.13
Max coastal outcrop ~ BGS formations	0.59	0.01*
Max coastal outcrop ~ paleoDB formations	−0.04	0.88
Max coastal outcrop ~ valid PaleoDB formations	−0.07	0.78
Max coastal outcrop ~ coarse siliciclastic formations	0.79	<0.001**
Max coastal outcrop ~ fine siliciclastic formations	0.19	0.47
Max coastal outcrop ~ publications	0.71	0.002**
Max coastal outcrop ~ genera	0.41	0.10
Min coastal outcrop ~ min quarries	0.15	0.55
Min coastal outcrop ~ min quarries	0.79	<0.001**
Min coastal outcrop ~ BGS formations	0.24	0.35
Min coastal outcrop ~ paleoDB formations	0.60	0.01*
Min coastal outcrop ~ valid PaleoDB formations	0.74	0.001**
Min coastal outcrop ~ coarse siliciclastic formations	0.25	0.32
Min coastal outcrop ~ fine siliciclastic formations	0.60	0.01*
Min coastal outcrop ~ publications	0.43	0.08
Min coastal outcrop ~ genera	0.32	0.21
Max quarries ~ min quarries	0.48	0.06
Max quarries ~ BGS formations	0.65	0.006*
Max quarries ~ paleoDB formations	0.06	0.83
Max quarries ~ valid PaleoDB formations	0.01	0.97
Max quarries ~ coarse siliciclastic formations	0.71	0.002**
Max quarries ~ fine siliciclastic formations	0.25	0.32
Max quarries ~ publications	0.64	0.007*
Max quarries ~ genera	0.38	0.13
Min quarries ~ BGS formations	0.45	0.07
Min quarries ~ paleoDB formations	0.62	0.009*
Min quarries ~ valid PaleoDB formations	0.54	0.03*
Min quarries ~ coarse siliciclastic formations	0.46	0.06
Min quarries ~ fine siliciclastic formations	0.48	0.05*
Min quarries ~ publications	0.58	0.02*
Min quarries ~ genera	0.41	0.10
BGS formations ~ paleoDB formations	0.37	0.15
BGS formations ~ valid PaleoDB formations	0.45	0.07
BGS formations ~ coarse siliciclastic formations	0.86	<0.001**
BGS formations ~ fine siliciclastic formations	0.48	0.05*
BGS formations ~ publications	0.78	<0.001**
BGS formations ~ genera	0.44	0.08
PaleoDB formations ~ valid PaleoDB formations	0.75	0.001**
PaleoDB formations ~ coarse siliciclastic formations	0.25	0.34
PaleoDB formations ~ fine siliciclastic formations	0.60	0.01*
PaleoDB formations ~ publications	0.42	0.10
PaleoDB formations ~ genera	0.35	0.17
Valid paleoDB formations ~ coarse siliciclastic formations	0.21	0.42
Valid paleoDB formations ~ fine siliciclastic formations	0.77	0.001**
Valid paleoDB formations ~ publications	0.43	0.08
Valid paleoDB formations ~ genera	0.44	0.08
Coarse siliciclastic formations ~ fine siliciclastic formations	0.20	0.45
Coarse siliciclastic formations ~ publications	0.66	0.005*
Coarse siliciclastic formations ~ genera	0.36	0.16
Fine siliciclastic formations ~ publications	0.71	0.002**
Fine siliciclastic formations ~ genera	0.55	0.02*
Carbonate formations ~ publications	0.68	0.003**
Publications ~ genera	0.68	0.004**

intensity of sampling a time period or formation receives (Raup, 1977; Benton et al., 2011; Dunhill et al., 2012, 2013). Therefore, it is unlikely that a simple metric of worker effort, such as publication counts, can tell us anything meaningful about sampling biases, as such sampling proxies are not statistically independent of, and are therefore redundant with, palaeodiversity, as they both undoubtedly drive each other. It is therefore not possible to show whether the sampling proxy is driving diversity, vice versa, or whether they are redundant with one another without utilizing a statistical technique such as Information Transfer (Hannisdal and Peters, 2011). Unfortunately, there is no way of effectively implementing such a technique as the data set consists of too few time bins.

Many previous studies have used a count of fossiliferous formations as a sampling proxy, and close correlations are often found between such proxies and palaeodiversity (Peters and Foote, 2001, 2002; Wang and Dodson, 2006; Barrett et al., 2009; Butler et al., 2009; Benson et al., 2010; Benson and Butler, 2011; Butler et al., 2011; Upchurch et al., 2011). Despite claims that fossiliferous formation counts offer a way of quantifying rock volume, facies heterogeneity, and human worker effort (Benson and Upchurch, 2013), they also undoubtedly share a common statistical signal with palaeodiversity, especially when obtained from the same source (i.e. PaleoDB) (Benton et al., 2011). Here, we show there are no correlations between either total formations (obtained from BGS) or fossiliferous formations (obtained from PaleoDB) and palaeodiversity; a pattern recorded previously when fossil occurrences and sampling proxies are obtained from independent data sources (Pearson et al., 2013). However, there is likely to be an increased correlation between formations and diversity across larger geographic areas, as when one samples more and more biogeographic areas, the formation counts will increase as more palaeohabitats are sampled, causing an increase in beta diversity.

Multivariate models offer an alternative and powerful approach to assessing the influence of biasing factors on palaeodiversity in the fossil record (Benson and Mannion, 2012). Multiple regression models confirm that worker effort, in the form of publication counts, is strongly linked to palaeodiversity, and is the strongest predictor of diversity at the formation level. At the stage level, the picture is more complicated in both the marine and terrestrial data and, despite relatively high R^2 values, the best fitting models consist of a complicated mix of many variables. At the formation level, publication counts are the strongest predictor, but other variables, including outcrop area and rock volume, can also predict marine palaeodiversity when included within the same model. In the terrestrial realm, only publication counts offer any predictive power over palaeodiversity. The multivariate approach

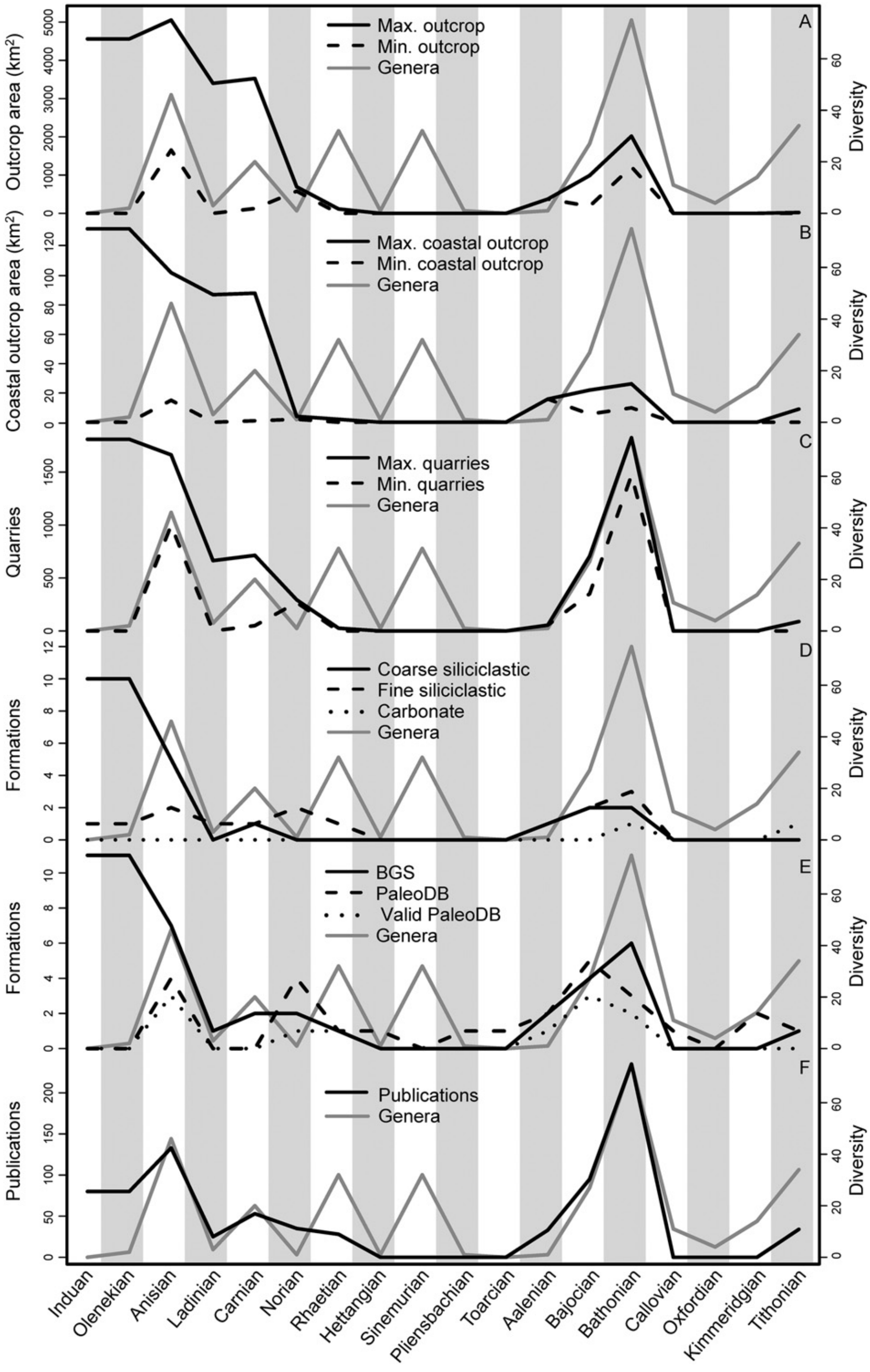

Fig. 4. Generic diversity compared to sampling proxies through the terrestrial Triassic and Jurassic of Great Britain (A) Outcrop area, (B) Coastal outcrop area, (C) Quarry count, (D) Formations by lithology, (E) Formation count and (F) Publication count.

highlights the complexities of factors influencing palaeodiversity patterns in the fossil record, and that no singular proxy or combination of sampling proxies can predict all of the recorded variation in palaeodiversity. It is therefore most likely that the fossil record reflects a complex mix of real diversity signal and confounding sampling effects (Benson and Upchurch, 2013; Fröbisch, 2013; Lloyd and Friedman, 2013).

5. Conclusions

This is the first study to carry out a detailed sampling analysis of coeval marine and terrestrial environments in a well-studied stratigraphic system at a constrained temporal and geographical scale using both pairwise correlation and multivariate modeling approaches.

The results show that facies and lithologies preserved have a considerable effect on the palaeodiversity recorded in the fossil record and are arguably as important as rock area and accessibility effects when determining palaeodiversity in the fossil record (Dunhill et al., 2013). Differences between the marine and terrestrial record are likely a product of sedimentary processes where consistently better preservation in the marine record results in a species-area effect on palaeodiversity, whilst the terrestrial record is too patchy. Sampling proxies become less precise as data are scaled up stratigraphically and proxies representing

Table 6
Correlation coefficients for raw formation level terrestrial data. Significant at ($p < 0.05$)* and significant after correction for multiple comparison** using false discovery rate method of Benjamini and Hochberg (1995) are indicated.

Comparison	Spearman's rank	
	r_s	p
Thickness ~ outcrop area	0.46	0.03*
Thickness ~ volume	0.86	<0.001**
Thickness ~ coastal outcrop area	0.2	0.36
Thickness ~ number of quarries	0.39	0.07
Thickness ~ number of publications	−0.22	0.32
Thickness ~ genera	−0.05	0.84
Outcrop area ~ volume	0.84	<0.001**
Outcrop area ~ coastal outcrop area	0.22	0.32
Outcrop area ~ number of quarries	0.57	0.006*
Outcrop area ~ number of publications	0.01	0.96
Outcrop area ~ genera	0.002	0.99
Volume ~ coastal outcrop area	0.26	0.24
Volume ~ number of quarries	0.55	0.009*
Volume ~ number of publications	−0.14	0.52
Volume ~ genera	−0.08	0.73
Coastal outcrop area ~ number of quarries	0.14	0.54
Coastal outcrop area ~ number of publications	0.29	0.19
Coastal outcrop area ~ genera	0.06	0.81
Number of quarries ~ number of publications	0.37	0.09
Number of quarries ~ genera	0.36	0.1
Number of publications ~ genera	0.82	<0.001**

different aspects of sampling show an inconsistent record of correlation. As it is unclear which proxies best represent sampling regimes and when, it seems illogical to assume that any of these may be used with confidence as a singular sampling proxy to detect and correct for bias in the fossil record.

This study highlights the difficulties involved in obtaining accurate biodiversity patterns from the fossil record by showing the complicated nature of the interplay between biological signal and biasing factors. In reality, the fossil record most likely represents a composite signal of genuine diversity patterns distorted by biasing factors arising from a number of non-mutually exclusive sources. The complex nature of the problem means it is incredibly difficult to interpret diversity patterns through deep-time and highlights that the use of singular sampling proxies, such as outcrop area or formation counts, are insufficient for detecting and removing bias from long-term palaeodiversity curves.

Acknowledgments

We thank Manabu Sakamoto for helping with statistical testing in *R* and for the provision of the *R* function *pair.cor* and Graeme Lloyd for the provision of the *R* function *gen.diff*. We thank Pete Wagner and one anonymous reviewer for helpful constructive criticisms which helped improve the manuscript. We also thank BGS for the provision of the *BritPits* database (license to AMD 2011/026BP ED). We thank various colleagues who have entered data into the Paleobiology Database, this is Paleobiology Database publication number 199. This work was funded by NERC doctoral training grant NE/H525111/1 to AMD. AJN publishes with the permission of the Executive Director of the British Geological Survey (NERC).

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2014.03.026.

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