Journal of the Geological Society, London, Vol. **170**, 2013, pp. 291–300. doi: 10.1144/jgs2012-025.

Completeness of the fossil record and the validity of sampling proxies: a case study from the Triassic of England and Wales

A. M. DUNHILL[1], M. J. BENTON[1], A. J. NEWELL[2] & R. J. TWITCHETT[3]
[1]*School of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK*
[2]*British Geological Survey, Maclean Building, Crowmarsh Gifford, Wallingford OX10 8BB, UK*
[3]*School of Geography, Earth and Environmental Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK*
**Corresponding author (e-mail: alex.dunhill@bristol.ac.uk)*

Abstract: Many studies have highlighted correlations between palaeodiversity and sampling proxies. These correlations have been interpreted as evidence for bias, common cause, or redundancy between signals. Here, we compare a number of sampling proxies representing sedimentary rock volume, rock accessibility and worker effort with palaeodiversity through the predominantly terrestrial Triassic System in England and Wales. We find that proxies for sedimentary rock volume and accessibility do not correlate with palaeodiversity until the removal of facies-related preservational and palaeoecological factors. This indicates that a weak sampling signal may be present, but the effects of changing palaeoenvironments are far more important at the regional scale. Significant correlations between worker effort and palaeodiversity are detected, although this is likely to be a result of the preferential sampling of formations already known to be rich in fossils. The fact that there is little evidence for sedimentary rock bias in the fossil record of the Triassic of England and Wales suggests that either (1) sampling bias is not a major source of error at the regional scale or (2) sampling proxies are inadequate representations of geological and human sampling bias.

Supplementary material: Correlation test results and raw time series data from the study are available at www.geolsoc.org.uk/SUP18567.

The fossil record provides our best resource to study evolutionary patterns through deep time by observing past patterns of diversity (e.g. Benson *et al*. 2010; Butler *et al*. 2010; Upchurch *et al*. 2011) and disparity (e.g. Butler *et al*. 2012). However, palaeontologists must consider the inadequacies of the fossil record that arise from differing preservation and sampling (e.g. Raup 1972; Peters & Foote 2001; Crampton *et al*. 2003; Smith 2007; Benson *et al*. 2010; Benton *et al*. 2011). Raup (1972) was the first to identify correlations between the fossil and rock records and interpreted these patterns as a geological megabias that had overprinted the true diversity pattern in the fossil record (Raup 1976). Since then, many other studies have found covariation between palaeodiversity and various proxies for sampling (Peters & Foote 2001, 2002; Smith 2001; Smith *et al*. 2001; Crampton *et al*. 2003; Smith & McGowan 2005, 2007; Wang & Dodson 2006; Fröbisch 2008; Barrett *et al*. 2009; Butler *et al*. 2009, 2010; Wall *et al*. 2009; Benson *et al*. 2010). These examples of rock record–fossil record covariation at various scales have been interpreted as evidence for: (1) a sampling bias on palaeodiversity estimates (Raup 1972, 1976; Peters & Foote 2001, 2002; Smith 2001; Smith & McGowan 2005, 2007; Fröbisch 2008; Barrett *et al*. 2009; Butler *et al*. 2009, 2010; Wall *et al*. 2009; Benson *et al*. 2010); or (2) a common cause (e.g. sea level) having driven the fossil and rock records simultaneously (Sepkoski 1976; Peters 2005, 2006; Peters & Heim 2010; Hannisdal & Peters 2011; Heim & Peters 2011); or (3) redundancy between sampling proxies and apparent diversity (Benton 2010; Benton *et al*. 2011; Dunhill 2012). Most palaeontologists now accept that the diversity signal in the fossil record represents a combination of both evolutionary patterns and biases associated with sampling and preservation (Kalmar & Currie 2010; Dunhill *et al*. 2012), and that it is very difficult to distinguish between biological signals and sampling noise.

Almost all published studies investigating the adequacy of the fossil record have been carried out on a global (Raup 1972, 1976; Lloyd *et al*. 2008; Barrett *et al*. 2009; Butler *et al*. 2009, 2010; Wall *et al*. 2009; Benson *et al*. 2010) or continental scale (Smith 2001; Peters 2005, 2006; Smith & McGowan 2005, 2007; Marx 2009; Peters & Heim 2010, 2011; Heim & Peters 2011), where both the fossil occurrence data and sampling proxies are often, at best, vague approximations (Twitchett *et al*. 2000; Crampton *et al*. 2003; Benton 2010; Benton *et al*. 2011; Dunhill 2011, 2012; Lloyd *et al*. 2011; Dunhill *et al*. 2012). The majority of these large-scale studies have discovered positive correlations between palaeodiversity and sampling proxies. However, few studies have been carried out at local or regional scales using well-constrained sampling proxies, and these have generally found little evidence for strong sampling bias (Wignall & Benton 1999; Benton *et al*. 2004; Mander & Twitchett 2008; Dunhill *et al*. 2012), the only notable exception being that by Crampton *et al*. (2003), who detected correlations between mollusc palaeodiversity and outcrop area and the number of fossil collections through the Cenozoic of New Zealand.

In this study we assess sampling bias in a single system, the Triassic, across nine basins in England and Wales (Figs 1 and 2). The constrained temporal and geographical scale allows the compilation of accurate data on sampled palaeodiversity and precisely measured sampling proxies, and eliminates the risk of comparing like with unlike, a problem of many larger-scale studies (Barnosky 2001; Benton *et al*. 2011).

The Triassic System of England and Wales

The Triassic System of England and Wales represents largely terrestrial rocks, with marine formations only in the upper portion of the Mercia Mudstone Group and the Penarth Group. The system crops out across nine sedimentary basins (Fig. 1; Howard *et al*. 2008) and consists of four lithostratigraphic groups: the Aylesbeare Mudstone Group, Sherwood Sandstone Group, Mercia Mudstone Group, and Penarth Group (Fig. 2; Benton *et al*. 2002; Howard *et al*. 2008). The Aylesbeare Mudstone Group, in the lowest Triassic

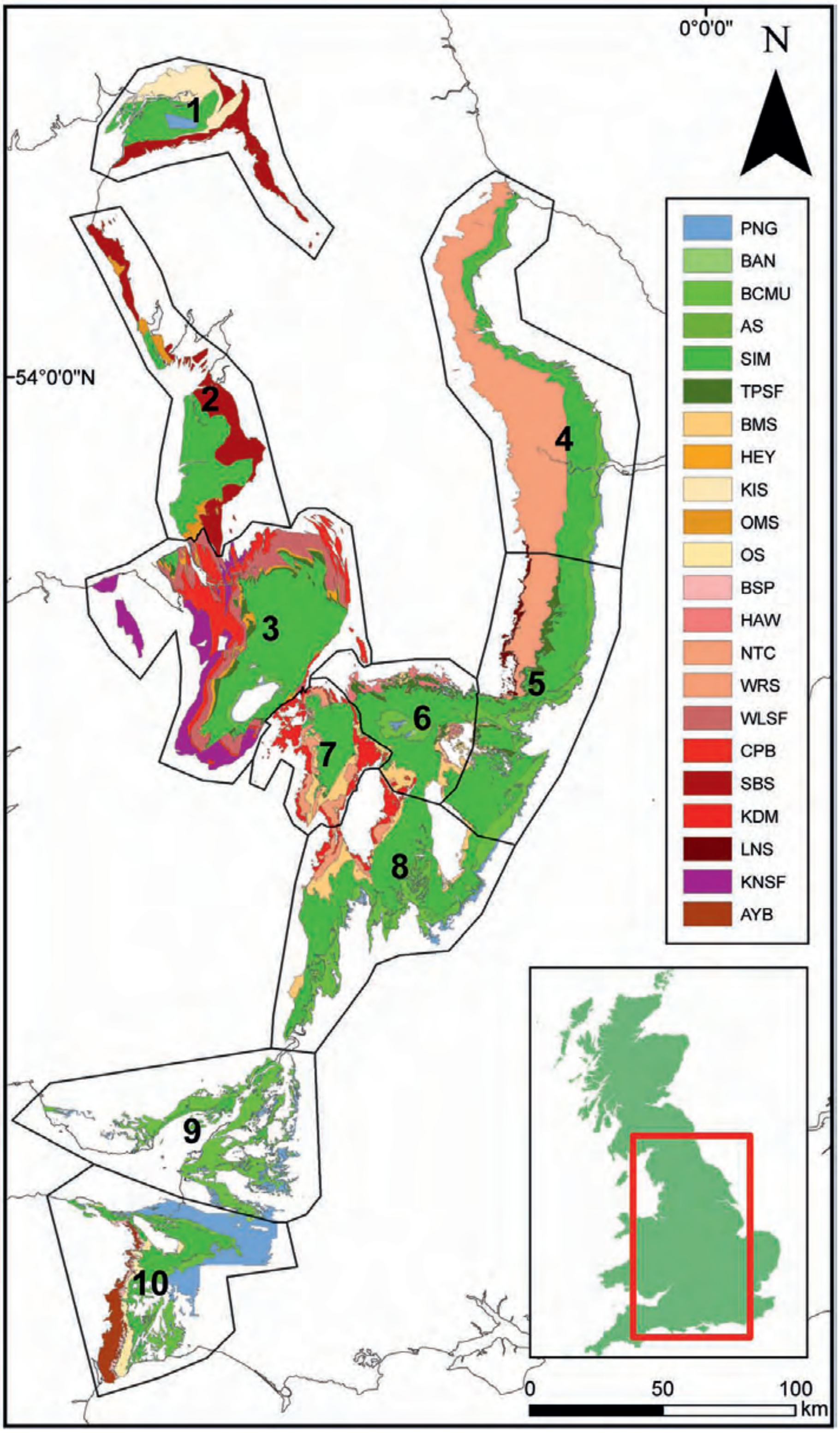

Fig. 1. Location and lithostratigraphy of the Triassic basins of England and Wales. (**1**) Carlisle; (**2**) Lancashire; (**3**) Cheshire; (**4**) East Midlands (North); (**5**) East Midlands (South); (**6**) Needwood; (**7**) Stafford; (**8**) Worcester–Knowle; (**9**) Bristol–South Wales; (**10**) Wessex. AYB, Aylesbeare Mudstone Group; KNSF, Kinnerton Sandstone Formation; LNS, Lenton Sandstone Formation; KDM, Kidderminster Formation; SBS, St. Bees Sandstone Formation; CPB, Chester Pebble Beds Formation; WLSF, Wilmslow Sandstone Formation; WRS, Wildmoor Sandstone Formation; NTC, Nottingham Castle Formation; HAW, Hawksmoor Formation; BSP, Budleigh Salterton Pebble Bed Formation; OS, Otter Sandstone; OMS, Ormskirk Sandstone Formation; KIS, Kirklinton Sandstone Formation; HEY, Helsby Sandstone Formation; BMS, Bromsgrove Sandstone Formation; TPSF, Tarporley Siltstone Formation; SIM, Sidmouth Mudstone Formation; AS, Arden Sandstone Formation; BCMU, Branscombe Mudstone Formation; BAN, Blue Anchor Formation; PNG, Penarth Group.

(Fig. 2), crops out solely in the Wessex Basin (Fig. 1) and consists of silty mudstones and fine sandstones, representative of fluvial, floodplain and playa-lake environments (Benton *et al*. 2002). The lowest units of the Triassic System in other basins are all fluvial sandstones, the Lenton Sandstone Formation in the East Midlands Basin, Kinnerton Sandstone Formation in the Cheshire Basin, and St. Bees Sandstone Formation in the Lancashire and Carlisle basins (Figs 1 and 2). The Sherwood Sandstone Group crops out throughout all of the basins, apart from the Bristol and South Wales Basin (Figs 1 and 2), and consists of sandstones, some of which are pebbly, representing fluvial conditions in an arid or semi-arid environment (Benton *et al*. 2002; Howard *et al*. 2008). The Mercia Mudstone Group is present throughout all nine basins (Figs 1 and 2), and consists of mudstones, siltstones and thick halite-bearing

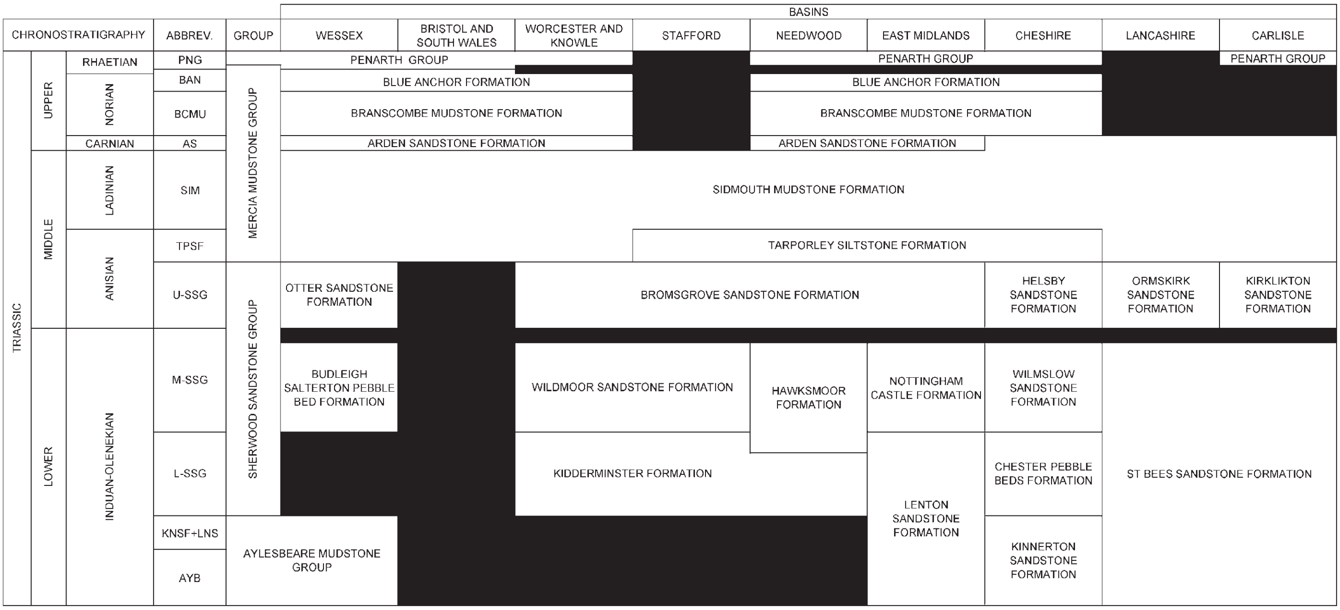

Fig. 2. Chrono- and lithostratigraphy of the Triassic basins of England and Wales shown in Figure 1.

units associated with fluvial, estuarine, ephemeral playa-lake conditions and a transgression to marginal marine environments in the Blue Anchor Formation (Mayall 1981; Benton *et al*. 2002; Howard *et al*. 2008; Porter & Gallois 2008). The marine Penarth Group, at the top of the Triassic succession (Fig. 2) consists of mudstones with subordinate sandstones and limestones (Benton *et al*. 2002), representing both lagoonal and offshore environments (Barras & Twitchett 2007). The Penarth Group crops out in all basins apart from the Stafford and Lancashire basins (Figs 1 and 2).

Methods

Stratigraphical framework and datasets

The stratigraphical framework for this study of the Triassic of England and Wales was compiled from Benton *et al*. (2002) and Howard *et al*. (2008), together with data from the BGS Lexicon (http://www.bgs.ac.uk/lexicon/) and BGS digital bedrock geology DiGMapgb-50 of the UK (1:50000). In total, eight datasets were analysed. Time-equivalent units from separate basins were combined to produce a synoptic sequence (SEQ) through the entire Triassic of England and Wales. The data were also divided by groups (GRP) and formations (FRM), and each group or formation from each basin was treated as a separate entity. To limit the effects of facies-controlled biases on the results of the study, the marine Penarth Group was removed from both the groups (GNPNG) and formations (FNPNG) datasets. Also, each group (Sherwood Sandstone Group, Mercia Mudstone Group and Penarth Group) was assessed across basins to test for sampling biases when lithofacies remain constant.

Occurrence data

Taxon occurrence data, for genera and species of all fossil groups, were acquired from a detailed literature search and from museum collection records. The museum collections used were those of the British Geological Survey (BGS) (from Palaeosaurus: http://www.bgs.ac.uk/palaeosaurus/home.cfm), Bristol City Museum (BRSMG), Liverpool Museum (NMGM) and Manchester Museum (MANCH). The literature-based fossil diversity lists are the prime source of data used here, and the museum data were used to check for the comprehensiveness of the recorded data. In the end, thorough investigation of these four major collections of British Triassic fossils added almost no additional fossil occurrence data to the literature search, so it was deemed unnecessary and a poor use of time to further extend the collection search.

Sampling proxies

Various sampling proxies were devised to represent the three aspects of sampling identified by Raup (1972): (1) sedimentary rock volume; (2) accessibility; (3) worker effort.

Sedimentary rock volume. Average unit thicknesses were devised from various literature sources (Benton *et al*. 2002; Howard *et al*. 2008) and the BGS Lexicon. Outcrop areas were obtained from the BGS digital bedrock geology DiGMapgb-50 of the UK (1:50000) using ArcGIS 9.3. Sedimentary rock volume was then calculated by multiplying average thickness by outcrop area.

Accessibility. Dunhill (2011) showed that geological formations in the UK are more likely to be exposed if they crop out on the coast, rather than inland. Therefore, coastal outcrop areas were calculated by placing a 1 km buffer around the UK coastline of the BGS DiGMapgb-50 in ArcGIS 9.3. This 1 km buffer is in line with our previous studies (Dunhill 2011, 2012), and is chosen as the minimum necessary to encompass inlets and coastal slopes, and so to maximize the zone of high exposure. This gives an estimate of the amount of exposed coastal rock of Triassic age in England and Wales. To represent the amount of inland exposure, past and present, numbers of quarries, both active and inactive (no longer operating), were recorded using the BGS BritPits database (Licence 2011/026BP ED) in ArcGIS 9.3.

Worker effort. Worker effort was represented by the number of palaeontological publications and number of palaeontologists who have published on each group or formation. These proxies were then expanded to all publications and all authors who have published on each group or formation, to capture the amount of total effort expended on studying each unit. For example, if a unit is unfossiliferous, the count of palaeontological publications and palaeontologists would be zero, so without also considering the number of

Table 1. *Correlation tests between generic and species diversity throughout the entire Triassic sequence (SEQ), at the group level (GRP) and at the formation level (FRM)*

	Spearman's rank		Kendall's tau	
Dataset	r_s	p	τ	p
SEQ	0.89	0.0003**	0.72	0.002*
GRP	0.97	<0.0001**	0.9	<0.0001**
FRM	0.94	<0.0001**	0.85	<0.0001**

*Significant at $p < 0.05$ before FDR correction.
**Significant after FDR correction.

sedimentological studies and geological memoirs it would appear that the lack of fossils was purely an issue of lack of sampling. Further, the total count of papers allows us to include papers concerned solely with fossils as well as others concerned with sedimentology but that also report fossils as a minor component.

Statistical tests

Spearman rank and Kendall's tau correlation tests were carried out to detect any correlations between different sampling proxies within the whole sequence, group and formation datasets with the aim of assessing whether sedimentary rock volume, accessibility and worker effort all follow the same patterns. Correlation tests were carried out between sampling proxies and palaeodiversity for all the datasets to discover whether the Triassic palaeodiversity signal in England and Wales can be wholly or partly explained by any of the three aspects of sampling. All statistical tests were carried out using R v.2.12.1 (R-Development-Core-Team 2010) and corrections for multiple correlation tests were carried out using the False Discovery Rate (FDR) approach of Benjamini & Hochberg (1995).

Results

Palaeodiversity

Generic and species occurrences correlate very strongly in each dataset (Table 1). Palaeodiversity is very low throughout the Aylesbeare Mudstone Group and lower and middle Sherwood Sandstone Group (Fig. 3). There is a sharp rise in palaeodiversity in the upper Sherwood Sandstone (Fig. 3), marking the fossiliferous Bromsgrove, Helsby and Otter Sandstone formations (Fig. 1). Palaeodiversity drops in the Tarporley Siltstone Formation, and then remains relatively constant throughout the Sidmouth Mudstone, Arden Sandstone and Branscombe Mudstone formations (Fig. 3). There is a significant increase in biodiversity as conditions begin to change from terrestrial to marine in the Blue Anchor Formation, before a final dramatic rise in palaeodiversity in the fully marine Penarth Group (Fig. 3).

Sampling proxies

Sedimentary rock volume. The units of the Sherwood Sandstone Group and the Sidmouth Mudstone Formation display the largest amount of preserved sedimentary rock, whereas the Arden Sandstone Formation, Blue Anchor Formation and the Penarth Group have the least (Fig. 3a). All proxies for sedimentary rock volume correlate strongly through the entire sequence, and when the data are split into groups and formations (Table 2).

Accessibility. The amount of accessible sedimentary rock varies considerably through the system (Fig. 3b). The Sidmouth Mudstone Formation and formations of the Sherwood Sandstone Group are associated with the greatest number of quarries and largest coastal outcrop areas, whereas the Tarporley Siltstone, Arden Sandstone and Blue Anchor formations have the least (Fig. 3b). The proxies for accessibility show varying degrees of correlation. The number of quarries and number of active quarries correlate strongly and consistently through the whole sequence and at the group and formation level (Table 2). However, coastal outcrop area correlates with only the number of quarries and the number of active quarries through the entire sequence (Table 2), and the correlations between coastal outcrop area and the number of active quarries become non-significant after the application of FDR correction (Table 2).

Worker effort. All the proxies for worker effort show a very similar pattern, with low counts of publications and publishing authors through the lower part of the system before a peak in the upper Sherwood Sandstone (Fig. 3c). Worker effort then falls through the Mercia Mudstone Group before an increase in the Blue Anchor Formation, followed by a dramatic increase in the Penarth Group (Fig. 3c). All proxies for worker effort correlate positively with each other through the entire sequence and at the group and formation level (Table 2). All correlations remain significant after the application of FDR corrections at the formation and group level, but the correlations are less robust for the entire Triassic sequence, where correlations between palaeontological publications and authors and all publications and authors become non-significant (Table 2).

Correlations between different aspects of sampling. The proxies for volume of sedimentary rock correlate positively with the proxies for accessibility (Table 2). The correlations are more robust at the formation scale than through the entire sequence or at the group scale (Table 2). There are no positive correlations between the proxy for sedimentary rock volume or accessibility and the proxy for human effort throughout the entire sequence or at the group or formation scale (Table 2). There are, however, negative correlations between thickness and both the number of palaeontological publications and authors, but these correlations both become non-significant after FDR correction (Table 2).

Sampling proxies and palaeodiversity

There are no significant positive correlations between the proxy for sedimentary rock volume or accessibility and palaeodiversity through the entire sequence or at the group or formation scale (Table 3). There are significant negative correlations between thickness and generic diversity at the group and formation scale (Table 3). When the Penarth Group is removed from the analysis there are positive correlations between both outcrop area and the number of active quarries and generic occurrence at the group scale (Table 4). There are also positive correlations with generic diversity for outcrop area and the number of active quarries in the Mercia Mudstone Group (Fig. 4), and outcrop area, rock volume and coastal outcrop area in the Penarth Group (Fig. 4a and b and Table 4). However, all of these correlations become non-significant after the application of FDR correction (Table 4).

The proxies for worker effort generally show significant positive correlation with generic occurrence (Fig. 4c and Tables 3 and 4). This is particularly the case for both the number of palaeontological publications and the number of palaeontological authors, which show consistently strong correlations with generic occurrence that become non-significant after the application of FDR corrections only in the Sherwood Sandstone and Mercia Mudstone groups (Fig. 4c and Table 4). The counts of all publications and all authors show weaker correlations that are non-significant in the Sherwood Sandstone Group and, for all authors only, at the group scale when the Penarth Group is removed (Table 4). The positive correlations between generic occurrence and all publications become non-significant at the group scale, at the group scale with no Penarth Group, and in both the Mercia Mudstone and Penarth groups (Tables 3

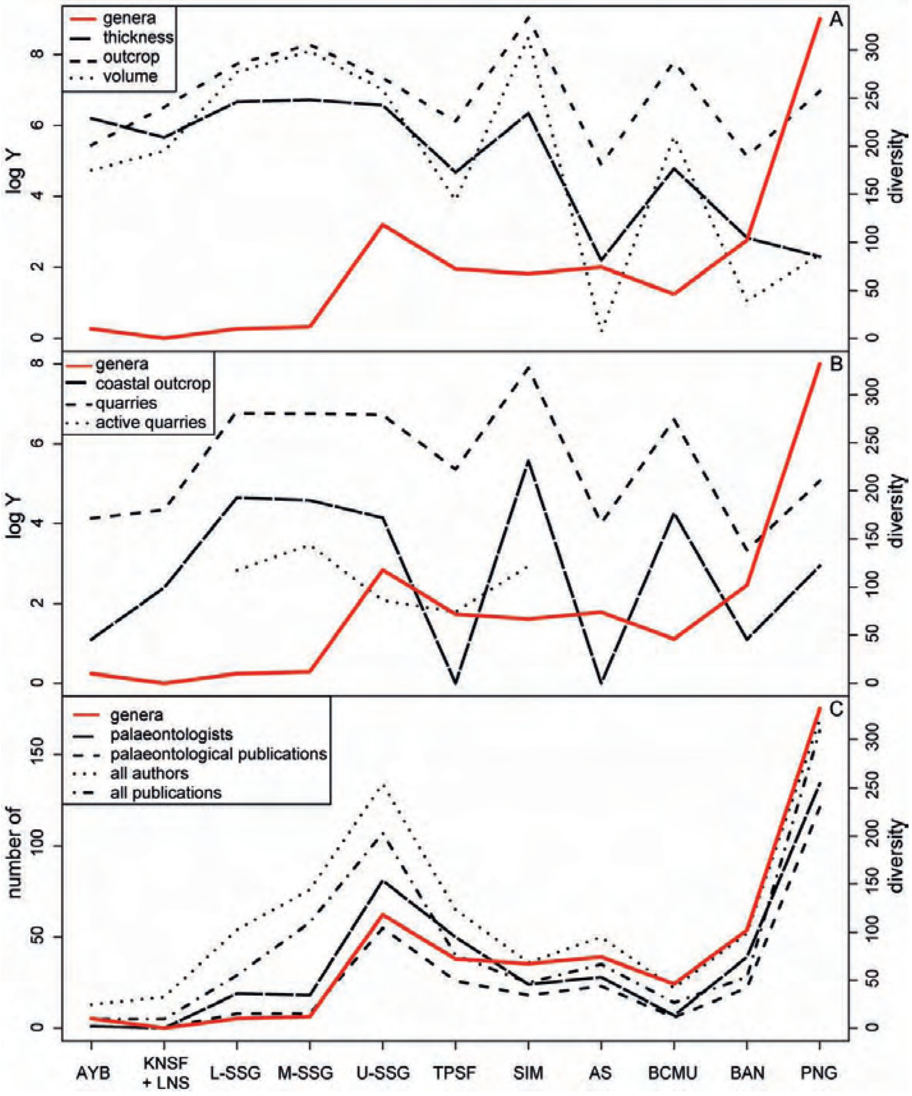

Fig. 3. Sampling proxy and palaeodiversity trends through the entire Triassic System of England and Wales (SEQ). (**a**) Sedimentary rock volume proxies and palaeodiversity; (**b**) rock accessibility and palaeodiversity; (**c**) worker effort and palaeodiversity. AYB, Aylesbeare Mudstone Group; KNSF + LNS, Kinnerton Sandstone Formation and Lenton Sandstone Formation; L-SSG, Lower Sherwood Sandstone Group; M-SSG, Middle Sherwood Sandstone Group; U-SSG, Upper Sherwood Sandstone Group; TPSF, Tarporley Siltstone Formation; SIM, Sidmouth Mudstone Formation; AS, Arden Sandstone Formation; BCMU, Branscombe Mudstone Formation; BAN, Blue Anchor Formation; PNG, Penarth Group.

and 4). The positive correlations between generic occurrence and all authors become non-significant through the entire sequence, at the group level, and in the Mercia Mudstone Group (Tables 3 and 4).

Discussion

Palaeodiversity

The general increase in palaeodiversity through the Triassic System of England and Wales is certainly influenced by the effects of changing facies. The Lower Triassic, represented by the Aylesbeare Mudstone and Sherwood Sandstone groups, is characterized by braided fluvial and playa-lake environments associated with an arid or semi-arid climate (Benton *et al*. 2002). Such environments would be expected both to be low in diversity and to exhibit poor preservation potential. The upper part of the Sherwood Sandstone Group, represented by the Bromsgrove Sandstone, Helsby Sandstone, Otter Sandstone, Ormskirk Sandstone and Kirklinton Sandstone formations, shows a significant jump in palaeodiversity, including a diverse vertebrate (Benton 1990, 1997, 2011; Benton & Spencer 1995) and plant (Warrington 1970; Smith & Warrington 1971) assemblage. This leap in palaeodiversity could be artificial, perhaps a result of more favourable conditions for fossil preservation or increased sampling intensity, or it could be at least partly real, documenting a phase in the recovery of ecosystems following the end-Permian mass extinction event some 6 Ma earlier (Benton & Twitchett 2004; Erwin 2006; Sahney & Benton 2008; Irmis & Whiteside 2011). The formations of the Mercia Mudstone Group show lower palaeodiversity than those of the upper Sherwood Sandstone Group, but levels are consistently higher than in the lower and middle Sherwood Sandstone Group. Again, this could be interpreted as the progressive recovery of ecosystems through the Triassic; however, the drop in diversity from the upper Sherwood Sandstone Group is more probably an artefact of changing palaeoenvironment, preservation or sampling. The final leap in palaeodiversity into the Penarth Group during the uppermost Triassic is almost certainly a combination of changing palaeoenvironment and preservation brought about by the change from terrestrial and marginal marine conditions to a fully marine environment.

Sampling proxies

All of the proxies for sedimentary rock volume correlate strongly with each other and are therefore probably all showing the same signal. The same pattern was observed by Dunhill *et al*. (2012) at a local scale, and shows that unit thickness, outcrop area, and calculated unit volume can all be regarded as reliable proxies for the overall amount of sedimentary rock preserved.

Table 2. *Correlation tests between sampling proxies throughout the entire Triassic sequence (SEQ), at the group level (GRP) and at the formation level (FRM)*

	SEQ				GRP				FRM			
	Spearman’s rank		Kendall’s tau		Spearman’s rank		Kendall’s tau		Spearman’s rank		Kendall’s tau	
Proxy	r_s	*p*	τ	*p*	r_s	*p*	τ	*p*	r_s	*p*	τ	*p*
Thickness and outcrop	0.69	0.02*	0.53	0.03*	0.69	0.0001**	0.49	0.0006**	0.65	<0.0001**	0.47	<0.0001**
Thickness and volume	0.90	0.0002**	0.75	0.0008**	0.85	<0.0001**	0.69	<0.0001**	0.88	<0.0001**	0.70	<0.0001**
Thickness and coastal outcrop	0.72	0.01*	0.50	0.03*	0.48	0.02*	0.34	0.02*	0.46	0.0002**	0.33	0.0006**
Thickness and quarries	0.75	0.01*	0.53	0.03*	0.48	0.01*	0.30	0.04*	0.55	<0.0001**	0.39	<0.0001**
Thickness and active quarries	0.79	0.003*	0.65	0.008*	0.49	0.01*	0.36	0.02*	0.31	0.02*	0.24	0.02*
Thickness and palaeo publications	−0.38	0.25−	0.26	0.27−	0.22	0.3−	0.15	0.31−	0.34	0.007*−	0.24	0.01*
Thickness and all publications−	0.04	0.9−	0.04	0.88−	0.05	0.81	0.01	0.93−	0.06	0.65−	0.05	0.61
Thickness and palaeontologists	−0.36	0.27−	0.24	0.36−	0.32	0.12−	0.21	0.14−	0.39	0.002*−	0.26	0.005*
Thickness and all authors	0.05	0.88	0.02	1−	0.02	0.93	0.01	0.94−	0.11	0.42−	0.07	0.44
Outcrop and volume	0.91	<0.0001**	0.78	0.0003**	0.93	<0.0001**	0.81	<0.0001**	0.92	<0.0001**	0.77	<0.0001**
Outcrop and coastal outcrop	0.93	<0.0001**	0.83	0.0004**	0.63	0.0007**	0.45	0.002*	0.62	<0.0001**	0.48	<0.0001**
Outcrop and quarries	0.92	<0.0001**	0.78	0.0003**	0.77	<0.0001**	0.58	<0.0001**	0.72	<0.0001**	0.55	<0.0001**
Outcrop and active quarries	0.84	0.001*	0.69	0.005*	0.73	<0.0001**	0.59	0.0001	0.42	0.0009*	0.33	0.0009*
Outcrop and palaeo publications−	0.15	0.65−	0.07	0.75	0.02	0.93	0.04	0.8−	0.17	0.18−	0.12	0.21
Outcrop and all publications	0.09	0.79	0.04	0.88	0.12	0.58	0.10	0.48	0.10	0.47	0.08	0.37
Outcrop and palaeontologists−	0.15	0.65−	0.05	0.88−	0.06	0.77−	0.01	0.94−	0.20	0.13−	0.13	0.16
Outcrop and all authors	0.17	0.61	0.13	0.65	0.18	0.4	0.13	0.39	0.06	0.64	0.07	0.46
Volume and coastal outcrop	0.89	0.0002**	0.76	0.001**	0.60	0.002*	0.42	0.005*	0.61	<0.0001**	0.45	<0.0001**
Volume and quarries	0.91	<0.0001**	0.78	0.0003**	0.75	<0.0001**	0.54	0.0002**	0.72	<0.0001**	0.56	<0.0001**
Volume and active quarries	0.87	0.0004**	0.77	0.002*	0.68	0.0002**	0.53	0.0006**	0.42	0.0007**	0.33	0.0009*
Volume and palaeo publications−	0.33	0.32−	0.15	0.53−	0.04	0.84	0.01	0.96−	0.30	0.02*−	0.20	0.03*
Volume and all publications−	0.08	0.82−	0.04	0.88	0.08	0.71	0.10	0.5	0.02	0.89	0.03	0.72
Volume and palaeontologists−	0.33	0.33−	0.13	0.65−	0.14	0.51−	0.05	0.71−	0.33	0.01*−	0.22	0.02*
Volume and all authors	0.01	0.99	0.05	0.88	0.09	0.65	0.09	0.54−	0.02	0.88	0.00	0.97
Coastal outcrop and quarries	0.86	0.0007**	0.76	0.001*	0.17	0.43	0.13	0.38	0.20	0.12	0.15	0.11
Coastal outcrop and active quarries	0.76	0.007*	0.60	0.02*	0.18	0.4	0.12	0.43	0.14	0.28	0.11	0.29
Coastal outcrop and palaeo publications	−0.21	0.54−	0.11	0.64−	0.11	0.6−	0.09	0.55−	0.14	0.29−	0.11	0.29
Coastal outcrop and all publications	0.02	0.96−	0.04	0.88	0.07	0.75	0.02	0.87	0.21	0.11	0.15	0.12
Coastal outcrop and palaeontologists	−0.18	0.59−	0.06	0.81−	0.17	0.43−	0.13	0.39−	0.17	0.2−	0.13	0.2
Coastal outcrop and all authors	0.12	0.73	0.06	0.81	0.16	0.46	0.12	0.42	0.19	0.14	0.14	0.15
Quarries and active quarries	0.92	<0.0001**	0.81	0.001*	0.70	0.0001**	0.57	0.0003**	0.56	<0.0001**	0.46	<0.0001**
Quarries and palaeo publications−	0.01	0.97	0.04	0.88	0.00	1	0.01	0.93−	0.12	0.36−	0.08	0.37
Quarries and all publications	0.21	0.55	0.11	0.64	0.03	0.89	0.04	0.8	0.08	0.55	0.05	0.61
Quarries and palaeontologists−	0.02	0.97	0.02	1−	0.07	0.74−	0.03	0.85−	0.15	0.26−	0.10	0.29
Quarries and all authors	0.27	0.42	0.13	0.65	0.00	0.99−	0.01	0.93	0.02	0.9	0.00	0.98
Active quarries and palaeo publications	−0.01	0.98	0.02	0.93	0.22	0.29	0.17	0.29−	0.11	0.42−	0.09	0.4
Active quarries and all publications	0.25	0.45	0.21	0.41	0.32	0.12	0.25	0.1	0.11	0.39	0.09	0.37
Active quarries and palaeontologists	−0.02	0.96	0.00	1	0.15	0.46	0.14	0.37−	0.11	0.39−	0.09	0.39
Active quarries and all authors	0.31	0.35	0.24	0.32	0.32	0.12	0.25	0.11	0.08	0.53	0.07	0.5
Palaeo publications and all publications	0.85	0.0009*	0.76	0.001*	0.85	<0.0001**	0.70	<0.0001**	0.71	<0.0001**	0.64	<0.0001**
Palaeo publications and palaeontologists	0.99	<0.0001**	0.95	<0.0001**	0.96	<0.0001**	0.86	<0.0001**	0.99	<0.0001**	0.94	<0.0001**
Palaeo publications and all authors	0.80	0.003*	0.66	0.005*	0.79	<0.0001**	0.65	<0.0001**	0.70	<0.0001**	0.61	<0.0001**
All publications and palaeontologists	0.82	0.002*	0.70	0.003*	0.83	<0.0001**	0.68	<0.0001**	0.70	<0.0001**	0.61	<0.0001**
All publications and all authors	0.97	<0.0001**	0.92	<0.0001**	0.96	<0.0001**	0.87	<0.0001**	0.97	<0.0001**	0.89	<0.0001**
Palaeontologists and all authors	0.80	0.005*	0.67	0.003*	0.77	<0.0001**	0.61	<0.0001**	0.71	<0.0001**	0.61	<0.0001**

*Significant at $p < 0.05$ before FDR correction.

**Significant after FDR correction.

Table 3. *Correlation tests between sampling proxies and generic diversity throughout the entire Triassic sequence (SEQ), at the group level (GRP) and at the formation level (FRM)*

	SEQ				GRP				FRM			
	Spearman's rank		Kendall's tau		Spearman's rank		Kendall's tau		Spearman's rank		Kendall's tau	
Proxy	r_s	p	τ	p	r_s	p	τ	p	r_s	p	τ	p
Thickness and genera−	0.51	0.11−	0.37	0.12−	0.42	0.03*−	0.28	0.06−	0.32	0.01*−	0.21	0.02*
Outcrop and genera	−0.21	0.55−	0.11	0.64−	0.11	0.6−	0.05	0.74−	0.16	0.21−	0.12	0.19
Volume and genera	−0.43	0.19−	0.26	0.27−	0.21	0.31−	0.12	0.41−	0.28	0.03*−	0.19	0.04*
Coastal outcrop and genera−	0.23	0.49−	0.15	0.53−	0.14	0.52−	0.08	0.59−	0.04	0.75−	0.03	0.76
Quarries and genera	−0.19	0.58−	0.18	0.43−	0.15	0.48−	0.10	0.5−	0.20	0.12−	0.14	0.13
Active quarries and genera−	0.16	0.63−	0.14	0.56−	0.07	0.75−	0.05	0.75−	0.21	0.11−	0.17	0.1
Palaeo publications and genera	0.92	<0.0001**	0.80	0.0008**	0.79	<0.0001**	0.61	<0.0001**	0.90	<0.0001**	0.76	<0.0001**
All publications and genera	0.71	0.02*	0.57	0.02*	0.60	0.002*	0.43	0.003*	0.56	<0.0001**	0.44	<0.0001**
Palaeontologists and genera	0.92	<0.0001**	0.81	0.0006**	0.86	<0.0001**	0.69	<0.0001**	0.89	<0.0001**	0.74	<0.0001**
All authors and genera	0.66	0.03*	0.55	0.02*	0.50	0.01*	0.35	0.02*	0.56	<0.0001**	0.42	<0.0001**

*Significant at $p < 0.05$ before FDR correction.
**Significant after FDR correction.

The inconsistent correlation between the number of quarries and coastal outcrop area suggests that each is driven by different mechanisms. The number of quarries and coastal outcrop correlate significantly only at the coarsest scale when considering all of the Triassic of England and Wales as a whole sequence. The number of quarries per geological unit is governed by the economic value of each unit, whereas coastal outcrop area is purely a result of the geographical location of each unit outcrop. It is therefore not possible to declare that one proxy is better than the other, and it is necessary to consider the accessibility of rock units in terms of both natural and human influences. The number of active quarries in each formation or group is only a small percentage of the total number of quarries that have ever been active. It is therefore evident that, in England and Wales at least and perhaps more widely, historical exposures have probably had much more influence on sampling than current exposures. This would suggest that the number of quarries represents a better proxy for sampling than the remote sensing methods employed by Dunhill (2011, 2012), which considered only extant exposure area. However, the total number of quarries and the number of currently active quarries correlate very well at all scales, so it can be said that the pattern of quarry outcrop has not changed significantly over time.

All the proxies for worker effort correlate well at the sequence, group and formation level, with correlations becoming more robust at the finer scale (i.e. formations). As would be expected, the number of palaeontologists and the number of palaeontological publications correlate very strongly at all stratigraphical scales, as do the number of all authors and number of all publications. The correlations between the number of palaeontologists and all authors and the number of palaeontological publications and all publications show weaker but significant correlations after FDR correction at the group and formation scale, but not at the sequence level where the correlation becomes non-significant. This suggests that the number of palaeontologists and palaeontological publications do not always correlate with the total number of publications and authors and thus suggests that a better measure of human worker effort should include all references to the geological units in question, not just those that have recorded the presence of fossils. Therefore, measures of worker effort should include sedimentological studies and geological memoirs that have rigorously sampled units, such as those that describe completely unfossiliferous units (e.g. Chester Pebble Bed and Lenton Sandstone formations). If the number of palaeontologists or palaeontological publications were used alone this would imply that such unfossiliferous units were devoid of recorded collections because nobody had sampled them, rather than that they have been extensively studied and yet are apparently barren of fossil material.

There are consistent positive correlations between the proxies for sedimentary volume and accessibility (Table 2). This shows that accessibility to sedimentary rocks, whether via man-made quarry or natural coastal exposure, is proportional to the total amount of preserved sedimentary rock and thus contradicts the findings of Dunhill (2011, 2012) in regional studies of rocks of all ages. However, this does not necessarily show that proxies such as outcrop area are good representations of sampling, just that the number of quarries and coastal outcrop are proportional to the total outcrop area of geological units in the Triassic of England and Wales.

There are no positive significant correlations between sedimentary rock volume or accessibility proxies and worker effort proxies. However, there were some negative correlations between unit thickness and the number of palaeontological publications and the number of palaeontologists at the formation scale. This is driven by very thick formations within the Sherwood Sandstone and Mercia Mudstone groups that are either unfossiliferous or yield a sparse fauna, and the relatively thin Penarth Group, which contains a very rich fossil assemblage. It may be noted that this example bears out a point made before (e.g. Crampton *et al.* 2003; Smith 2007; Benton *et al.* 2011) that geological formations are named according to rock heterogeneity and fossiliferousness. The fact that there are no positive correlations between preserved sedimentary rock volumes or accessibility and worker effort shows that palaeontologists have not preferentially sampled formations that have the most rock preserved or formations that are most accessible.

Evidence for sampling bias

There are no positive correlations between any of the proxies for sedimentary rock volume and palaeodiversity at the sequence, group or formation level, suggesting that there is no evidence that the amount of sedimentary rock influences the diversity of fossils recovered from geological units. However, there are positive correlations between outcrop area and generic occurrence when the marine Penarth Group is removed from the group-level data and when considering only the Mercia Mudstone Group and Penarth Group outcrop across the nine basins. However, these observed correlations are deemed non-significant once the FDR tests are applied. This suggests that once the effects of different facies (i.e. palaeoecological

Table 4. *Correlation tests between sampling proxies and generic diversity excluding the Penarth Group at the group (GNPNG) and formation level (FNPNG), and in the Sherwood Sandstone Group (SSG), Mercia Mudstone Group (MMG) and Penarth Group (PNG) across different basins*

	GNPNG				FNPNG				SSG				MMG				PNG			
	Spearman's rank		Kendall's tau		Spearman's rank		Kendall's tau		Spearman's rank		Kendall's tau		Spearman's rank		Kendall's tau		Spearman's rank		Kendall's tau	
Proxy	r_s	p	τ	p	r_s	p	τ	p	r_s	p	τ	p	r_s	p	τ	p	r_s	p	τ	p
Thickness and genera	0.11	0.67	0.08	0.65–	0.12	0.38–	0.09	0.39	0.12	0.79	0.00	1	0.13	0.73	0.08	0.75	0.07	0.88	0.05	0.88
Outcrop and genera	0.51	0.03*	0.36	0.04*–	0.11	0.43–	0.08	0.4	0.04	0.93	0.11	0.71	0.70	0.03*	0.59	0.03*	0.81	0.03*	0.68	0.03*
Volume and genera	0.47	0.05*	0.28	0.11–	0.14	0.3–	0.10	0.3	0.10	0.84	0.07	0.9	0.30	0.44	0.11	0.76	0.89	0.01*	0.81	0.01*
Coastal outcrop and genera	0.04	0.89	0.05	0.76–	0.03	0.84–	0.02	0.82–	0.10	0.82–	0.04	0.9–	0.05	0.9	0.03	0.92	0.78	0.04*	0.70	0.04*
Quarries and genera	0.40	0.1	0.28	0.1–	0.08	0.57–	0.05	0.59	0.23	0.59	0.11	0.71	0.35	0.35	0.31	0.25	0.38	0.4	0.29	0.36
Active quarries and genera	0.47	0.05*	0.33	0.07–	0.09	0.52–	0.08	0.49	0.58	0.13	0.46	0.12	0.75	0.02*	0.59	0.04*	–	–	–	–
Palaeo publications and genera	0.76	0.0002**	0.56	0.002**	0.88	<0.0001**	0.74	<0.0001**	0.85	0.007*	0.76	0.009*	0.80	0.01*	0.55	0.04*	0.92	0.003**	0.78	0.02*
All publications and genera	0.52	0.03*	0.34	0.05*	0.47	0.0003**	0.36	0.0003**	0.57	0.15	0.43	0.18	0.79	0.01*	0.54	0.05*	0.88	0.008*	0.78	0.02*
Palaeontologists and genera	0.78	0.0001**	0.58	0.0009**	0.87	<0.0001**	0.71	<0.0001**	0.74	0.05*	0.64	0.03*	0.81	0.008*	0.61	0.03*	0.95	0.0008**	0.88	0.006*
All authors and genera	0.38	0.12	0.24	0.17	0.46	0.0006**	0.34	0.0007**	0.29	0.5	0.21	0.55	0.74	0.02*	0.57	0.04*	0.95	0.0008**	0.88	0.006*

*Significant at $p < 0.05$ before FDR correction.
**Significant after FDR correction.

and preservational effects) are removed from the equation it is possible to detect some evidence of rock-record-driven sampling bias, but it appears that the evidence for geologically controlled sampling bias is very weak in the Triassic of England and Wales.

There is also only limited evidence for correlation between any of the accessibility proxies and palaeodiversity. Positive correlations between coastal outcrop and generic occurrence in the Penarth Group and positive correlations between the number of active quarries and generic occurrence in the Mercia Mudstone Group and at the group level once the Penarth Group has been removed become non-significant after correction for FDR. It can therefore be said that there is only very limited evidence that the accessibility of sedimentary rock is a major driving force of documented palaeodiversity.

Proxies for worker effort correlate strongly and consistently with palaeodiversity across most of the datasets. The numbers of palaeontological publications and palaeontologists show the strongest correlation with generic occurrence, becoming non-significant only after correction for FDR in the Sherwood Sandstone and Mercia Mudstone groups. It is inevitable that these measures of palaeontological worker effort should correlate with palaeodiversity as the two metrics are non-independent. For example, if formation X contains a rich fossil fauna whereas formation Y contains a more sparse assemblage, formation X will attract a greater number and wider variety of palaeontologists than formation Y. Although formation X will inevitably be more rigorously sampled than formation Y, this stems directly from the fact that formation X is richer in fossils in the first place. This view is in line with Raup's suggestion that 'systematists follow the fossils' (Raup 1977; Dunhill *et al.* 2012), rather than that palaeontological study drives apparent palaeodiversity (Sheehan 1977). This interpretation is supported by the fact that counts of total publications and authors (including sedimentological studies and geological memoirs) do not correlate as well with palaeodiversity as the number of palaeontological publications and palaeontologists. However, it is not possible to explicitly determine the direction of causality between worker effort proxies and palaeodiversity without identifying an unequivocal sampling proxy. It is highly likely that a number of other factors are also linked to this correlation, such as the sampling and publishing habits of vertebrate and invertebrate palaeontologists. For example, the peak in sampling in the middle Sherwood Sandstone Group (Fig. 3c) is heightened by the fact that vertebrate palaeontologists have published extensively and repeatedly on single taxa whereas the invertebrate-dominated faunas of the Mercia Mudstone Group have been recorded as occurrence lists in relatively few publications (Fig. 3c).

The validity of sampling of proxies

Previous studies investigating Phanerozoic palaeodiversity have used a number of proxies for sampling, including outcrop area (Smith 2001; Crampton *et al.* 2003; Smith & McGowan 2005, 2007; Mander & Twitchett 2008; Marx 2009; Wall *et al.* 2009; Peters & Heim 2010; Dunhill *et al.* 2012), sedimentary rock volume (Raup 1972, 1976; Kalmar & Currie 2010; Dunhill *et al.* 2012), and palaeontological worker effort (Sheehan 1977; Purnell & Donoghue 2005; Dunhill *et al.* 2012). In this study we have compared the fossil record of the Triassic of England and Wales with a number of sampling proxies. The results suggest that the palaeodiversity curve of the Triassic of England and Wales is not significantly biased by the amount of sedimentary rock preserved or by its accessibility. The strong correlations between worker effort and palaeodiversity probably show that palaeontologists preferentially work on units that bear rich fossil assemblages rather than that the number of palaeontologists who work on different rock units by

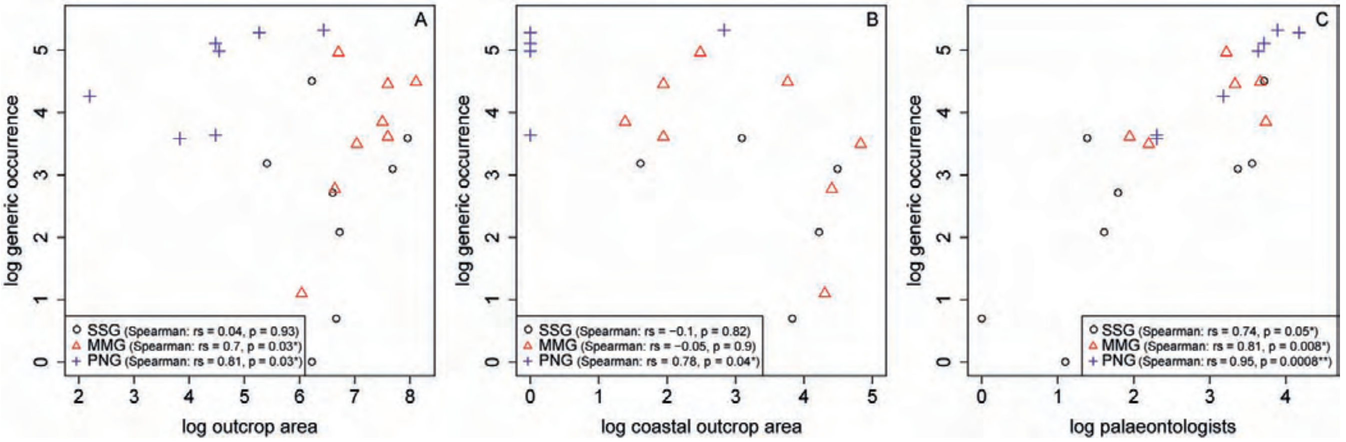

Fig. 4. Correlation plots showing (**a**) outcrop area, (**b**) coastal outcrop area and (**c**) number of palaeontologists against generic occurrence within the Sherwood Sandstone Group (SSG), Mercia Mudstone Group (MMG) and Penarth Group (PEN).

chance drives the fossil diversity signal, as well as being representative of differing sampling and publishing practices between vertebrate and invertebrate palaeontologists. These results closely resemble those obtained from a local-scale study carried out on the Lower Jurassic of SW England (Dunhill *et al*. 2012).

However, it is also possible that the sampling proxies used in this, and other, studies are simply not effective representations of sampling regimes. Several previous studies have questioned the validity of commonly used sampling proxies such as outcrop area (Benton *et al*. 2011; Dunhill 2011, 2012; Dunhill *et al*. 2012), number of sedimentary formations (Crampton *et al*. 2003; Smith 2007; Benton 2010; Benton *et al*. 2011; Dunhill 2011), and worker effort (Raup 1977; Dunhill *et al*. 2012), and there has yet to be unequivocal proof of the validity of any proxy that has been used to identify and correct for sampling bias in the fossil record. This study shows that, in the case study of the Triassic of England and Wales, preservational and palaeoecological influences associated with changing facies have a much greater influence on palaeodiversity than the amount of sedimentary rock that is preserved or accessible, or the worker effort expended per geological formation. However, there is also likely to be an issue of scale, and when larger study areas are investigated the increased beta diversity sampled over larger areas may result in a species–area effect and thus a correlation developing between sampled outcrop area and palaeodiversity (Smith 2007; Wall *et al*. 2009). However, the assumption made by many that the error in the fossil record caused by uneven sampling can be corrected using a single metric of sampling seems overambitious and, thus far, unsupported.

Conclusions

This is the first study to carry out a rigorous analysis of the effects of sampling biases on palaeodiversity through a single geological period on a national scale. The results obtained bear close resemblance to those of Dunhill *et al*. (2012), as no robust correlations were obtained between proxies for sedimentary rock volume or accessibility and palaeodiversity. However, as with the Lower Jurassic study by Dunhill *et al*. (2012), significant correlations were obtained between worker effort and palaeodiversity. This is interpreted as a bonanza effect where palaeontologists are drawn to collect in proportion to the richness of fossils in different formations and locations. The appearance of weak correlations between certain proxies for sedimentary rock volume and accessibility and palaeodiversity after the removal of preservational and palaeoecological effects suggests that sampling biases are present in the data, but are far less influential than facies effects. This is supported by the leap in palaeodiversity observed during the transition from the terrestrial Mercia Mudstone Group to the marine Penarth Group.

It appears that the scale of an investigation is the main factor influencing the degree of correlation between sampling proxies and palaeodiversity. Investigations carried out at a small scale show no or little correlation and the strength of correlations seems to increase in proportion to the geographical and stratigraphical scale of the study. This has been attributed to an increase in beta diversity associated with the increased number of palaeohabitats sampled (Smith 2007, Wall *et al*. 2009), both geographically and temporally.

It is also possible that sampling proxies used in palaeodiversity studies are simply not effective representations of sampling regimes through time. The lack of a clear correlation between sampling and palaeodiversity in the Triassic of England and Wales lends support to the hypothesis that many or most so-called sampling proxies are ineffectual and cannot guarantee to distinguish sampling from redundancy and common cause.

Thanks go to E. Crew (BGS), D. Gelsthorpe (MANCH), W. Simkiss (NMGM) and R. Vaughan (BRSMG) for the provision of palaeodiversity and sampling proxy data. We also thank I. Sansom, N. Pyenson and an anonymous reviewer for their insightful and constructive comments. This work was funded by NERC doctoral training grant NE/H525111/1 and BGS CASE grant to A.M.D.

References

Barnosky, A.D. 2001. Distinguishing the effects of the Red Queen and Court Jester on Miocene mammal evolution in the northern Rocky Mountains. *Journal of Vertebrate Paleontology*, **21**, 172–185.

Barras, C.G. & Twitchett, R.J. 2007. Response of the marine infauna to Triassic–Jurassic environmental change: Ichnological data from southern England. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **244**, 223–241.

Barrett, P.M., McGowan, A.J. & Page, V. 2009. Dinosaur diversity and the rock record. *Proceedings of the Royal Society of London, Series B*, **276**, 2667–2674.

Benjamini, Y. & Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, Series B*, **57**, 289–300.

Benson, R.B.J., Butler, R.J., Lindgren, J. & Smith, A.S. 2010. Mesozoic marine tetrapod diversity: mass extinctions and temporal heterogeneity in geological megabiases affecting vertebrates. *Proceedings of the Royal Society of London, Series B*, **277**, 829–834.

Benton, M.J. 1990. The species of Rhynchosaurus, a rhynchosaur (Reptilia, Diapsida) from the Middle Triassic of England. *Philosophical Transactions of the Royal Society of London, Series B*, **328**, 213–306.

Benton, M.J. 1997. The Triassic reptiles from Devon. *Proceedings of the Ussher Society*, **9**, 141–152.

Benton, M.J. 2010. The origins of modern biodiversity on land. *Philosophical Transactions of the Royal Society of London, Series B*, **365**, 3667–3679.

Benton, M.J. 2011. Archosaur remains from the Otter Sandstone Formation (Middle Triassic, late Anisian) of Devon, southern UK. *Proceedings of the Geologists' Association*, **122**, 25–33.

Benton, M.J. & Spencer, P.S. 1995. *Fossil Reptiles of Great Britain*. Geological Conservation Review Series, **10**.

Benton, M.J. & Twitchett, R.J. 2004. How to kill (almost all life: the end-Permian extinction event. *Trends in Ecology and Evolution*, **18**, 358–365.

Benton, M.J., Cook, E. & Turner, P. 2002. *Permian and Triassic Red Beds and the Penarth Group of Great Britain*. Joint Nature Conservation Committee, Geological Conservation Review Series, **24**.

Benton, M.J., Dunhill, A.M., Lloyd, G.T. & Marx, F.G. 2011. Assessing the quality of the fossil record. insights from vertebrates. *In*: McGowan, A.J. & Smith, A.B. (eds) *Comparing the Geological and Fossil Records: Implications for Biodiversity Studies*. Geological Society, London, Special Publications, **358**, 63–94.

Benton, M.J., Tverdokhlebov, V.P. & Surkov, M.V. 2004. Ecosystem re-modelling among vertebrates at the Permian–Triassic boundary in Russia. *Nature*, **432**, 97–100.

Butler, R.J., Barrett, P.M., Nowbath, S. & Upchurch, P. 2009. Estimating the effects of the rock record on pterosaur diversity patterns: Implications for hypotheses of bird/pterosaur competitive replacement. *Paleobiology*, **35**, 432–446.

Butler, R.J., Benson, R.B.J., Carrano, M.T., Mannion, P.D. & Upchurch, P. 2010. Sea level, dinosaur diversity and sampling biases: Investigating the 'common cause' hypothesis in the terrestrial realm. *Proceedings of the Royal Society of London, Series B*, **278**, 1165–1170.

Butler, R.J., Brusatte, S.L., Andres, B. & Benson, R.B.J. 2012. How do geological sampling biases affect studies of morphological evolution in deep time? A case study of the Pterosauria (Reptilia: Archosauria). *Evolution*, **66**, 147–162.

Crampton, J.S., Beu, A.G., Cooper, R.A., Jones, C.A., Marshall, B. & Maxwell, P.A. 2003. Estimating the rock volume bias in paleobiodiversity studies. *Science*, **301**, 358–360.

Dunhill, A.M. 2011. Using remote sensing and a GIS to quantify rock exposure area in England and Wales: implications for paleodiversity studies. *Geology*, **39**, 111–114.

Dunhill, A.M. 2012. Problems with using rock outcrop area as a paleontological sampling proxy: Rock outcrop and exposure area compared to coastal proximity, topography, land use and lithology. *Paleobiology*, **38**, 840–857.

Dunhill, A.M., Benton, M.J., Twitchett, R.J. & Newell, A.J. 2012. Sampling and completeness of the marine Lower Jurassic of the Dorset and East Devon coast, Southwest England. *Palaeontology*, **55**, doi: 10.1111/j.1475-4983.2012.01149.x.

Erwin, D.H. 2006. *Extinction! How Life Nearly Ended 250 Million Years ago*. Princeton University Press, Princeton, NJ.

Fröbisch, J. 2008. Global taxonomic diversity of Anomodonts (Tetropoda, Therapsida) and the terrestrial rock record across the Permian–Triassic boundary. *PLoS ONE*, **3**, e3733.

Hannisdal, B. & Peters, S.E. 2011. Phanerozoic Earth system evolution and marine biodiversity. *Science*, **334**, 1121–1124.

Heim, N.A. & Peters, S.E. 2011. Covariation in macrostratigraphic and macroevolutionary patterns in the marine record of North America. *Geological Society of America Bulletin*, **123**, 620–630.

Howard, A.S., Warrington, G., Ambrose, K. & Rees, J.G. 2008. *A formational framework for the Mercia Mudstone Group (Triassic) of England and Wales*. British Geological Survey Research Report, **RR/08/04**.

Irmis, R.B. & Whiteside, J.H. 2011. Delayed recovery of non-marine tetrapods after the end-Permian mass extinction tracks global carbon cycle. *Proceedings of the Royal Society of London, Series B*, **279**, 1310–1318.

Kalmar, A. & Currie, D.J. 2010. The completeness of the continental fossil record and its impact on patterns of diversification. *Paleobiology*, **36**, 51–60.

Lloyd, G.T., Davis, K.E., *et al.* 2008. Dinosaurs and the Cretaceous terrestrial revolution. *Proceedings of the Royal Society of London, Series B*, **275**, 2483–2490.

Lloyd, G.T., Young, J.R. & Smith, A.B. 2011. Taxonomic structure of the fossil record is shaped by sampling bias. *Systematic Biology*, **61**, 80–89.

Mander, L. & Twitchett, R.J. 2008. Quality of the Triassic–Jurassic bivalve fossil record in Northwest Europe. *Palaeontology*, **51**, 1213–1223.

Marx, F.G. 2009. Marine mammals through time: When less is more in studying palaeodiversity. *Proceedings of the Royal Society of London, Series B*, **276**, 887–892.

Mayall, M.J. 1981. The Late Triassic Blue Anchor Formation and the initial Rhaetian marine transgression in south-west Britain. *Geological Magazine*, **118**, 377–384.

Peters, S.E. 2005. Geologic constraints on the macroevolutionary history of marine animals. *Proceedings of the National Academy of Sciences of the USA*, **102**, 12326–12331.

Peters, S.E. 2006. Genus extinction, origination, and the durations of sedimentary hiatuses. *Paleobiology*, **32**, 387–407.

Peters, S.E. & Foote, M. 2001. Biodiversity in the Phanerozoic: a reinterpretation. *Paleobiology*, **27**, 583–601.

Peters, S.E. & Foote, M. 2002. Determinants of extinction in the fossil record. *Nature*, **416**, 420–424.

Peters, S.E. & Heim, N.A. 2010. The geological completeness of paleontological sampling in North America. *Paleobiology*, **36**, 61–79.

Peters, S.E. & Heim, N.A. 2011. Stratigraphic distribution of marine fossils in North America. *Geology*, **39**, 259–262.

Porter, R.J. & Gallois, R.W. 2008. Identifying fluvio-lacustrine intervals in thick playa-lake successions: An integrated sedimentology and ichnology of arenaceous members in the mid–late Triassic Mercia Mudstone Group of south-west England, UK. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **270**, 381–398.

Purnell, M.A. & Donoghue, M.J. 2005. Between death and data: Biases in the interpetation of the fossil record of conodonts. *Special Papers in Palaeontology*, **73**, 7–25.

Raup, D.M. 1972. Taxonomic diversity during the Phanerozoic. *Science*, **177**, 1065–1071.

Raup, D.M. 1976. Species diversity in the Phanerozoic: An interpretation. *Paleobiology*, **2**, 289–297.

Raup, D.M. 1977. Systematists follow the fossils. *Paleobiology*, **3**, 328–329.

Sahney, S. & Benton, M.J. 2008. Recovery from the most profound mass extinction of all time. *Proceedings of the Royal Society of London, Series B*, **275**, 759–765.

Sepkoski, J.J. 1976. Species diversity in the Phanerozoic: species–area effects. *Paleobiology*, **2**, 298–303.

Sheehan, P.M. 1977. A reflection of labor by systematics? *Paleobiology*, **3**, 325–328.

Smith, A.B. 2001. Large-scale heterogeneity of the fossil record: Implications for Phanerozoic biodiversity studies. *Philosophical Transactions of the Royal Society of London, Series B*, **356**, 351–367.

Smith, A.B. 2007. Marine diversity through the Phanerozoic: problems and prospects. *Journal of the Geological Society, London*, **164**, 731–745.

Smith, A.B. & McGowan, A.J. 2005. Cyclicity in the fossil record mirrors rock outcrop area. *Biology Letters*, **1**, 443–445.

Smith, A.B. & McGowan, A.J. 2007. The shape of the Phanerozoic marine palaeodiversity curve: How much can be predicted from the sedimentary rock record of Western Europe? *Palaeontology*, **50**, 765–774.

Smith, E.G. & Warrington, G. 1971. The age and relationships of the Triassic rocks assigned to the lower part of the Keuper in north Nottinghamshire, north-west Lincolnshire and South Yorkshire. *Proceedings of the Yorkshire Geological Society*, **38**, 201–227.

Smith, A.B., Gale, A.S. & Monks, N.E.A. 2001. Sea-level change and rock-record bias in the Cretaceous: A problem for extinction and biodiversity studies. *Paleobiology*, **27**, 241–253.

Twitchett, R.J., Wignall, P.B. & Benton, M.J. 2000. Discussion on lazarus taxa and fossil abundance at times of biotic crisis. *Journal of the Geological Society, London*, **157**, 511–512.

Upchurch, P., Mannion, P.D., Benson, R.B.J., Butler, R.J. & Carrano, M.T. 2011. Geological and anthropogenic controls on the sampling of the terrestrial fossil record: a case study from the Dinosauria. *In*: McGowan, A.J. & Smith, A.B. (eds) *Comparing the Geological and Fossil Records: Implications for Biodiversity Studies*. Geological Society, London, Special Publications, **358**, 209–240.

Wall, P.D., Ivany, L.C. & Wilkinson, B.H. 2009. Revisiting Raup: Exploring the influence of outcrop area on diversity in light of modern sample-standardization techniques. *Paleobiology*, **35**, 146–167.

Wang, S.C. & Dodson, P. 2006. Estimating the diversity of dinosaurs. *Proceedings of the National Academy of Sciences of the USA*, **103**, 13601–13605.

Warrington, G. 1970. The stratigraphy and palaeontology of the 'Keuper' Series of the central Midlands of England. *Quarterly Journal of the Geological Society of London*, **126**, 183–223.

Wignall, P.B. & Benton, M.J. 1999. Lazarus taxa and fossil abundance at times of biotic crises. *Journal of the Geological Society, London*, **156**, 453–456.

Received 21 February 2012; revised typescript accepted 17 September 2012.
Scientific editing by I