

Uncovering the diversification history of marine tetrapods: ecology influences the effect of geological sampling biases

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Abstract: Mesozoic terrestrial vertebrates gave rise to sea-going forms independently among the ichthyosaurs, sauropterygians, thalattosaurs, crocodyliforms, turtles, squamates, and other lineages. Many passed through a shallow marine phase before becoming adapted for open ocean life. This allows quantitative testing of factors affecting our view of the diversity of ancient organisms inhabiting different oceanic environments. We implemented tests of correlation using generalized difference transformed data, and multiple regression models. These indicate that shallow marine diversity was driven by changes in the extent of flooded continental area and more weakly influenced by uneven fossil sampling. This is congruent with studies of shallow marine invertebrate diversity and suggests that ‘common cause’ effects are influential in the shallow marine realm. In contrast, our view of open ocean tetrapod diversity is strongly distorted by temporal heterogeneity in fossil record sampling, and has little relationship with continental flooding. Adaptation to open ocean life allowed plesiosaurs, ichthyosaurs and sea turtles to ‘escape’ from periodic extinctions driven by major marine regressions, which affected shallow marine taxa in the Late Triassic and over the Jurassic–Cretaceous boundary. Open ocean taxa declined in advance of the end-Cretaceous extinction. Shallow marine taxa continued diversifying in the terminal stages due to increasing sea-level.

Supplementary material: The data series and full analytical results are available at <http://www.geolsoc.org.uk/SUP18486>

Documenting the diversification history of extinct organisms is a fundamental goal of palaeobiology (e.g. Valentine 1969; Sepkoski 1981, 1982), but recent work has raised serious concerns that uneven temporal sampling of the fossil record may limit our ability to distinguish genuine and artifactual patterns (e.g. Raup 1972, 1976; Peters & Foote 2001, 2002; Smith 2001, 2007; Smith *et al.* 2001; Crampton *et al.* 2003; Peters 2005; Smith & McGowan 2005, 2007; Alroy *et al.* 2008). Most work examining the influence of sampling on perceived diversity patterns has focused on the record of shallow marine invertebrates. Vertebrates have been relatively neglected, with the significant exceptions of Permo-Triassic Russian tetrapods (Benton *et al.* 2004), Cenozoic mammals (e.g. Alroy 2000; Uhen & Pyenson 2007; Marx 2008; Marx & Uhen 2010), anomodont therapsids (Fröbisch 2008), pterosaurs (Butler *et al.* 2009, 2011*b*) and dinosaurs (Wang & Dodson 2006; Lloyd *et al.* 2008; Barrett *et al.* 2009; Mannion *et al.* 2010; Butler *et al.* 2011*a*). As a result, studies of vertebrate palaeodiversity do not routinely consider sampling biases

(Slack *et al.* 2006; Benton & Emerson 2007; Sahney *et al.* 2010) despite the fact that the vertebrate record (which is dominantly terrestrial) is generally thought to be less complete than that of shallow marine invertebrates (but see Benton 2001) and thus might be subject to more severe biases.

Vertebrates have the potential to provide a unique perspective on heterogeneity (temporal, spatial and ecomorphological) in the nature of sampling biases because they occupy a broad range of habitats, and thus depositional environments, and are ecomorphologically diverse. For example, contemporaneous groups of Mesozoic vertebrates occupied open ocean (e.g. plesiosaurians, chelonoid turtles), shallow marine (e.g. thalattosaurs, placodonts, see below), coastal and fully terrestrial (e.g. pterosaurs, dinosaurs) habitats. In addition, the marine tetrapods of the Mesozoic formed at least twelve independent radiations into the marine realm from terrestrial ancestors, often passing through a shallow marine phase early in their adaptation to open ocean life (Fig. 1; Storrs 1993*a*; Rieppel 2000; Bell & Polcyn 2005; Motani 2005, 2009).

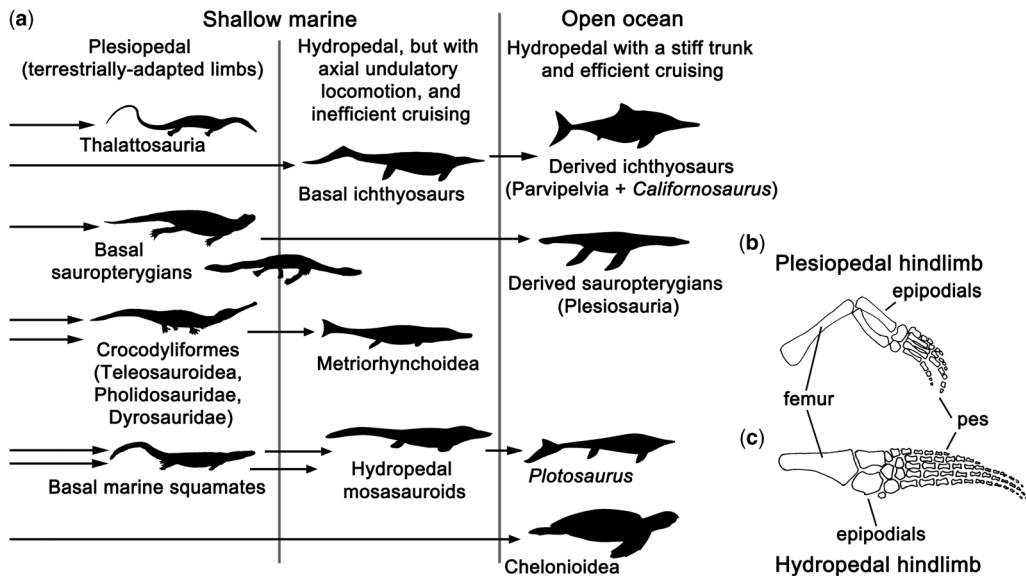


Fig. 1. The evolution of Mesozoic marine tetrapods. (a) schematic representation of transitions (represented by arrows) from the terrestrial to shallow marine and open ocean habitats by independent tetrapod groups. (b, c) diagrams showing plesioipedal (terrestrially-adapted), (b) (modified from Caldwell 1997, fig. 2K: *Serpianosaurus*, a basal sauropterygian), and hydropedal, (c) (modified from Caldwell 1997, fig. 3D: *Hydrorion*, a plesiosaurian), hindlimb morphologies.

The occurrence of multiple radiations means that inferences drawn from marine tetrapods may be independent of phylogenetic relationships. Although vertebrate fossils are less abundant than invertebrate fossils, exceptional professional and public interest in fossil vertebrates means that their taxonomy and spatiotemporal distributions are often well-understood, and ecological inferences based on their preserved anatomy are often well-constrained.

Here, we focus on the relationship between sampling and diversity for Mesozoic marine reptiles, building on a previous study (Benson *et al.* 2010). Most other previous studies of marine tetrapod diversity only considered sampling biases qualitatively (Bardet 1992, 1994; Pierce *et al.* 2009a (thalattosuchians); Young *et al.* 2010 (metriorhynchoids)). A study of mosasauroids using rarefaction to standardize sample size by (Ross 2009) is one exception, and Storrs (1993a) attempted to quantify the quality of the Triassic sauropterygian record. Our aim here is to test for and examine the nature of ecomorphological heterogeneity in sampling biases. This forms the basis for a refined understanding of trends in marine tetrapod diversity. Nearly all previous work on sampling biases and vertebrate diversity has ignored (or not explicitly considered) ecomorphological variation in the study taxa. Consequently, most hypotheses of Phanerozoic animal diversification are predominantly based on shallow marine invertebrates that make up the bulk of the

fossil record (e.g. Sepkoski 1981, 1982; Alroy *et al.* 2008). This may be problematic if open ocean or terrestrial taxa follow a different diversification trajectory.

Ecology of marine reptiles

Based on Carrier's (1987) observations of running lizards, Cowen (1996) recognized that rapid axial undulatory locomotion in aquatic vertebrates would have impaired the ability to breathe using paired, bilateral lungs. This would have limited the stamina of aquatic vertebrates propelled by axial undulation. This hypothesis is consistent with Massare's (1988) observation that axial undulatory swimmers such as mosasauroids and crocodyliforms have proportionally long, narrow bodies. In principle, this allowed them rapid bursts of acceleration but low sustained swimming speeds that limited them to 'ambush' predation in marginal and shallow marine environments. The axial undulatory mode was inherited from the terrestrial ancestors of most marine tetrapod groups and is therefore plesiomorphic (Cowen 1996; marine mammals, aquatic birds, and turtles are exceptions). Axial undulatory locomotion is inferred for all marine tetrapods with 'plesioipedal' (i.e. terrestrially-proportioned; Fig. 1b; Bell & Polcyn 2005) limbs, including thalattosaurs (e.g. Liu & Rieppel 2001; Jiang *et al.*

2004), basal mosasauroids and related squamate groups (Bell & Polcyn 2005), and most basal sauropterygians (Carroll 1985; Caldwell 1997; Rieppel 2000), as well as many hydropedal taxa (with limbs forming flippers; Fig. 1c) such as basal ichthyosaurs (McGowan 1991; Motani *et al.* 1996; Sander 2000; Motani 2005), derived mosasauroids (Massare 1988; Cowen 1996; other than *Plotosaurus*) and thalattosuchian crocodyliforms (Massare 1988).

In contrast, parvipelvic ichthyosaurs (e.g. Motani 2002a, b, 2005), plesiosaurians (Storrs 1993b; Rieppel 2000), turtles and the mosasauroid *Plotosaurus* (Lindgren *et al.* 2007) had appendicular- or caudally-driven locomotion and rigid trunks that in principle allowed efficient, cruising locomotion over long distances, sometimes at relatively high speeds (Massare 1988). These locomotory functional inferences, combined with facies data, have led several authors to suggest that basal representatives of most clades were limited to shallow water environments on the flooded continental shelf, whereas parvipelvic ichthyosaurs, plesiosaurians, turtles and *Plotosaurus* could cross the open ocean (Rieppel 2000; Motani 2002a, b, 2005; Lindgren *et al.* 2007).

Prediction

We predict that if the ecomorphological inferences discussed above are correct, then the actual taxic diversity of 'shallow marine' tetrapods should be strongly influenced by the extent of continental flooding, which provided habitable area for these taxa. Thus, the origination and extinction of shallow marine tetrapods may be controlled by eustatic sea-level changes. However, because of their inferred capacity to survive in the open ocean, the actual diversity of 'non-undulating' taxa should be less dependent upon shallow marine area and potentially show a stronger correlation with fossil sampling metrics.

Methods

Data series

All data series were assigned to stage-level time bins. The stratigraphic age and total duration of stages was taken from Walker & Geismann (2009). Mesozoic sea-level estimates were drawn from Miller *et al.* (2005, supplementary data) who provided two data series: one for the curve of Haq *et al.* (1987) covering the time period of 0–244 Ma and a novel one spanning 0–172 Ma. Because the points within these data series are not distributed evenly in time, we interpolated equally spaced data points onto linear segments spanning adjacent

points in the original data series at 0.1 million year intervals. To do this we used a freeware function (XIXtrFun) for Microsoft Excel that interpolates data using a third-order piecewise polynomial. We then calculated the mean sea-level for each of our time bins. Data on reconstructed total non-marine surface area were derived from Smith *et al.* (1994, table 3), who generated their data from a series of reconstructed global palaeogeographical maps. Non-marine surface area exactly corresponds to the continental area that is not flooded by shallow seas, and thus varies inversely with the amount of shallow marine habitat available. Non-marine area and sea-level estimates are used here as proxies for the area of shallow marine habitat available.

Taxic diversity counts were extracted from a modified version of the dataset of Benson *et al.* (2010), which is available as an online appendix to Benson *et al.* (2010) and on request from the authors. This includes species occurrences of chelonoid turtles, ichthyosaurs, mosasauroids and other marine squamates, sauropterygians, thalattosaurs and thalattosuchian, dyrosaurid and pholidosaurid crocodyliforms. These were compiled from recent taxonomic compendia or systematic assessments (e.g. Steel 1973; Hirayama 1997; Rieppel 2000; O'Keefe 2001; McGowan & Motani 2003; Bell & Polcyn 2005; Druckenmiller & Russell 2008; Hill *et al.* 2008; Jouve *et al.* 2008; Pierce *et al.* 2009a, b; Young & Andrade 2009; Ketchum & Benson 2010; Young *et al.* 2010) and a review of the wider literature conducted by Benson *et al.* (2010). This data was modified by the removal of Jurassic 'plesiochelyid' turtles, the ecology of which is poorly understood (J. Anquetin pers. comm. 2010; although they may be marginal marine; Billione-Bruyat *et al.* 2005; Fuente & Fernandez 2011). Due to the small number of Jurassic turtle occurrences (one Oxfordian; two Tithonian), this is not expected to have a major impact on the data. This resulted in a total of 570 occurrences by stage. The total taxic diversity of marine tetrapods was divided into two non-overlapping subsets comprising 'open ocean' and 'shallow marine' taxa, identified by locomotor inferences (above). This resulted in three data series: total taxic diversity (TDE_{total} : Benson *et al.* 2010, fig. 2a), shallow marine taxic diversity ($TDE_{\text{shallow marine}}$: Fig. 2) and open ocean taxic diversity ($TDE_{\text{open ocean}}$: Fig. 3).

Counts of fossiliferous marine formations were used as a proxy for geological sampling of marine depositional environments and were downloaded from The Paleobiology Database (Benson *et al.* 2010; accessed 12th May 2009). Use of formation counts as a sampling proxy does not assume that all formations are equal, only that variation in weathering rates, outcrop area, thickness, lithostratigraphic research, and palaeontological sampling

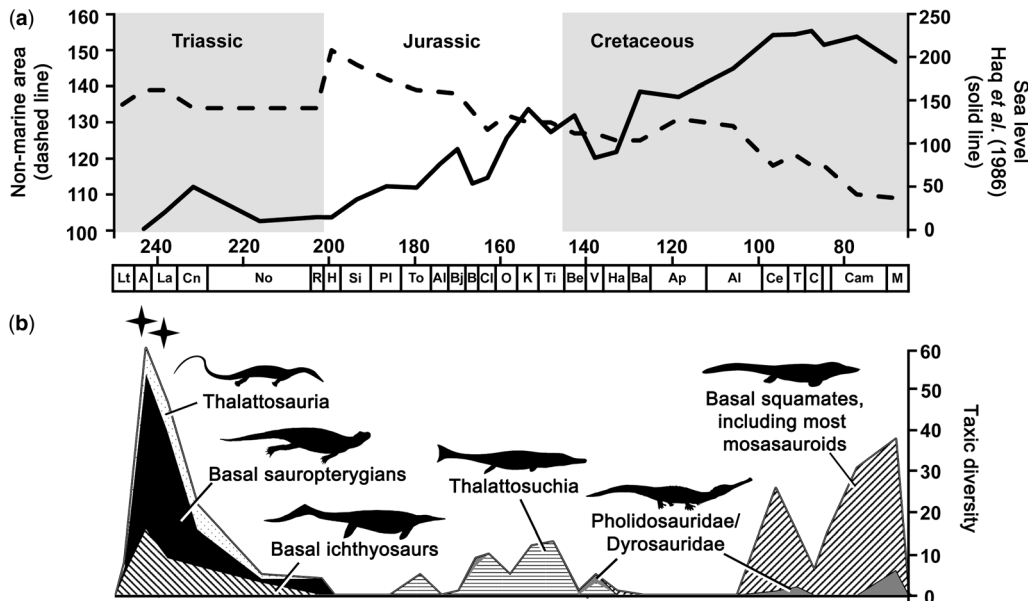


Fig. 2. Continental flooding proxies (a) and shallow marine taxic (b) diversity plotted against geological time (Ma; stage names abbreviated). Stars indicate shallow marine Lagerstätten stages explained in the text.

effort are distributed randomly and do not introduce systematic biases. The fossil record has been sampled over more than two centuries and historic collections are often sparsely documented. Thus, sampling effort can only rarely be measured directly. Although sampling proxies only provide an estimate of sampling effort, they are necessary in quantitative studies of ancient biotic diversity such as this one.

Taxon records and fossiliferous marine formations that span multiple stages were considered to occur within their entire range, even when the range represented uncertainty in dating or provenance (following the arguments of Upchurch & Barrett (2005, pp. 111–112)).

Lagerstätten

Benson *et al.* (2010) identified Lagerstätten within five Triassic–Jurassic intervals. Greater than half of marine tetrapod taxa from these stages were collected from a single formation, or a restricted geographical region characterized by intensive local sampling. Marine tetrapod Lagerstätten include the Anisian (55%) and Ladinian (66%) formations of central Europe (values in parentheses indicate the percentage of taxa from localized deposits), the primarily Sinemurian Lower Lias Group of the UK (100%), the Toarcian Posidonienschiefer Lagerstätte of Germany (52%), the Callovian Peterborough Member of the Oxford Clay Formation

(73%) and the primarily Kimmeridgian Kimmeridge Clay Formation of the UK (55%). Lagerstätten effects present a major challenge to palaeodiversity studies. Despite representing the most extreme form of uneven fossil sampling, Lagerstätten weaken the apparent correlation between most sampling proxies and observed palaeodiversity. They also spuriously inflate taxic diversity estimates for the intervals in which they occur. A basic approach to removing Lagerstätten effects from palaeodiversity data series is to simply exclude Lagerstätten data. Here we propose an alternative approach whereby Lagerstätten are coded as present or absent using a binary variable in multiple regression models (described below) as a coarse attempt to account for their presence without discarding data.

Pairwise tests of correlation

As a preliminary survey, we conducted multiple pairwise tests of correlation between our data series using Pearson's product moment (r). Non-parametric tests (Spearman's ρ , and Kendall's τ) were also performed to corroborate these analyses (Supplementary Material). Tests of correlation were implemented using the computer program PAST (Hammer *et al.* 2001), applied using both the raw data series, and modified versions of the data series after the application of generalized differencing (e.g. McKinney 1990; Alroy 2000; see below). Because of the strong influence of Jurassic

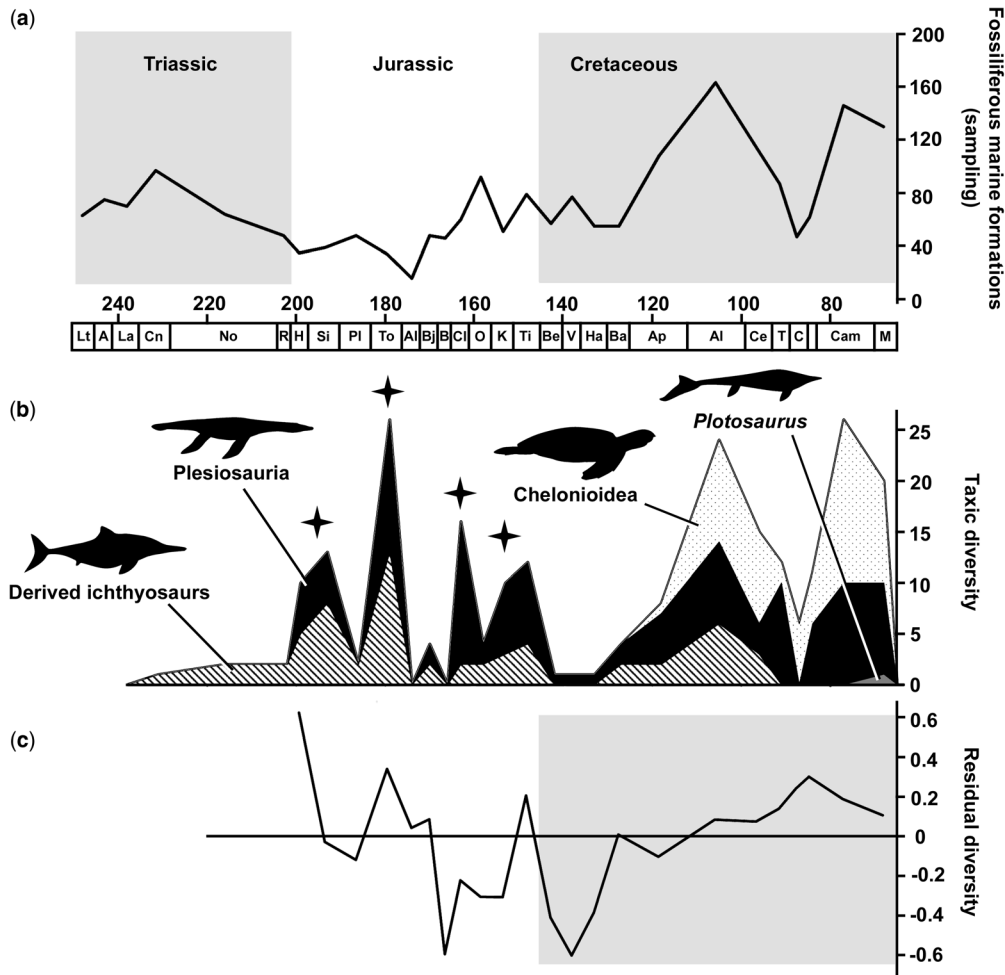


Fig. 3. Fossiliferous marine formations (**a**; sampling proxy), open ocean taxic diversity (**b**), and residual diversity after subtraction of a GLS multiple regression model including stage duration, deep water Lagerstätten, and sampling (**c**; Table 3) plotted against geological time (Ma; stage names abbreviated). Stars indicate deep water Lagerstätten stages explained in the text.

Lagerstätten on total taxic diversity and open ocean taxic diversity, tests of correlation with these data series were also performed excluding Lagerstätten stages. Because each data series was compared to a maximum of four other data series, the threshold for statistical significance was made more stringent ($\alpha = 0.05/4 = 0.0125$; Bonferroni correction) to avoid the increased risk of detecting spurious correlations as a result of making multiple comparisons. Triassic data were not analysed because our objective was to test the strength of correlations between taxic diversity and proxies representing sampling (fossiliferous marine formations) and the area of shallow marine shelf available (sea-level, non-marine area). The Triassic comprises only five

time bins of a total 28 in the Mesozoic and is marked by several events that could confound underlying correlations, including (1) the initial diversification of marine tetrapods, incorporating a necessary rise from zero diversity independent of external factors; (2) the invasion of the open ocean by thunniform or intermediate-grade ichthyosaurs from the Carnian onwards (Motani 2005) and plesiosaurians at least as early as the Rhaetian (e.g. Storrs 1994); (3) the early Late Triassic mass extinction among marine tetrapods (e.g. Bardet 1994; Rieppel 2000; Benson *et al.* 2010) incorporating a dramatic decline in diversity. Note that the Triassic data were included in our generalized least squares multiple regression analyses described below.

One assumption of tests of correlation is that values in each data series are drawn independently from one another. However, for time series data, such as those analysed here, the presence of long-term trend (i.e. a directed change in the mean value through time) or short-term autocorrelation (correlation between successive data points) may violate this assumption and cause overestimation of correlation coefficients. Generalized differencing is a two-stage approach in which data series are first detrended, then corrected for autocorrelation by differencing of successive values, modulated by the observed strength of autocorrelation between successive time bins (McKinney 1990; no differencing is applied if statistically significant autocorrelation is not detected). This technique was applied to fossil vertebrate diversity data by Alroy (2000) and Butler *et al.* (2011a), but most recent authors examining the link between fossil sampling and palaeodiversity in vertebrates have left the data uncorrected (Fröbisch 2008; Barrett *et al.* 2009; Butler *et al.* 2009; Mannion *et al.* 2010) or applied first differencing (Uhen & Pyenson 2007; Marx 2008). In first differencing, each data point is transformed by subtraction of the preceding datum. This results in a data series describing the change in an observation through time (e.g. Chatfield 2003). Benson *et al.* (2010, appendix S2) voiced concerns that first differencing may be an overcorrection of the data and result in loss of signal. However, application of generalized differencing addresses this concern (McKinney 1990; Alroy 2000).

The Jarque–Bera test indicated that all detrended and generalized difference transformed data series were distributed normally. The raw data series for sea-level estimates, non-marine area and fossiliferous marine formations were also distributed normally. However, the raw taxic diversity data series were significantly non-normal. Thus, the raw taxic diversity series were \log_{10} -transformed prior to tests of correlation, resulting in fully normal distributions.

Generalized differencing: implementation

Generalized differencing was implemented manually following the protocol described by McKinney (1990). Concomitant statistical procedures were carried out in PAST (Hammer *et al.* 2001). Initially, values of each data series were regressed against the midpoint ages of the time bins. In those cases where the Durbin–Watson test statistic indicated a significant fit of the least squares regression line, long-term trend was inferred. This was removed by subtraction of the regression slope from values in the data series, resulting in detrended versions of all series other than time bin duration and open ocean taxic diversity (which did not

show statistically significant evidence for long-term trend).

The presence of Lagerstätten, yielding high values of taxic diversity, and concentrated in the Triassic and Jurassic may affect estimates of trend in taxic diversity estimates (Benson *et al.* 2010). Thus, the regression slope (trend line) was also calculated excluding Jurassic stages in which Lagerstätten effects were observed by Benson *et al.* (2010; Sinemurian, Toarcian, Callovian, Kimmeridgian). In most cases, the regression slope calculated excluding Lagerstätten was closely similar to the slope calculated from the complete data series, as expected for sea-level, non-marine surface area and fossiliferous marine formations (these variables are not oversampled in Lagerstätten). Correspondingly, data series calculated using the two methods were strongly correlated (Pearson's $r > 0.99$) in most cases, including those for shallow marine taxic diversity (N.B. Jurassic Lagerstätten represent deep water facies; Hudson *et al.* 1991; Röhl *et al.* 2001; Martill *et al.* 2006). The correlation was lower for total taxic diversity ($r = 0.97$), and for open ocean taxic diversity a significant regression slope, indicating long-term trend, was only detected when Lagerstätten were excluded. This indicates a strong impact of Lagerstätten on the inference of long-term trend in total and open ocean taxic diversities. Thus, the trend slope estimated excluding Lagerstätten was used exclusively for these latter two data series (although pairwise correlation test were applied both to the full data series, and to the data series excluding Lagerstätten; see Results). Next, the autocorrelation coefficient at a time lag of one interval was estimated by regressing the values of each data series (t_i) against a series comprising values from the immediately preceding time bins (t_{i-1}). A significant fit of the least squares regression line was absent for most data series, including both open ocean and total taxic diversity (both including or excluding Lagerstätten stages). A significant fit was indicated for non-marine area and shallow marine taxic diversity, for both of which generalized differences were thus calculated. The slope of the regression line represents the autocorrelation coefficient (a). This was used to remove autocorrelation via the following equation yielding the generalized differenced values (t_{GD}):

$$t_{GD} = t_i - at_{i-1}$$

Generalized least squares

Generalized least squares (GLS) is a multiple regression technique that does not assume independence of data series or points within a data series. For instance, the problem of autocorrelation described above was accounted for by an underlying

autoregressive model (e.g. Box *et al.* 1994; Chatfield 2003) in our GLS analyses. GLS was previously applied to palaeontological time series data by Hunt *et al.* (2005), Marx & Uhen (2010), Benson & Mannion (2011) and Butler *et al.* (2011b). One advantage of GLS over pairwise tests of correlation is that it allows multiple explanatory variables to be examined simultaneously, and the effect of adding additional variables to be assessed quantitatively. We used GLS to examine the relationship between sampling (fossiliferous marine formations), shallow marine area (using sea-level estimates or the amount of non-marine area as proxies), taxic diversity of shallow marine and open ocean tetrapods, and the total taxic diversity. For each taxic diversity series, the best combinations of explanatory variables were identified using an information criterion (AICc; Sugiura 1978). This is a measure that rewards goodness fit of the regression model (combination of explanatory variables; Table 1) but penalizes models incorporating higher numbers of variables. Thus, the best model is deemed to be one that explains the highest proportion of variation in taxic diversity using the fewest explanatory variables. GLS and associated statistical tests were implemented in R version 2.10.1 (R Development Core Team 2009) with the packages *lmtest* (Zeileis & Hothorn 2002), *nlme* version 3.1–96 (Pinheiro *et al.* 2009), *qpcR* version 1.2–7 (Spiess & Ritz 2010) and *tseries* version 0.10–22 (Trapletti & Hornik 2009). Because it was possible to take account of multiple explanatory variables (e.g. Lagerstätten, continental flooding) that otherwise confound pairwise correlation tests (described above; also see Benson & Mannion 2011), Triassic data were included in our GLS analyses. GLS analyses excluding Triassic data can be found in the supplementary material.

Table 1. List of regression models including various factors that may explain observed taxic diversity

Regression models (combinations of explanatory variables)
Stage duration [null model]
Stage duration + sampling*
Stage duration + shallow marine area [†]
Stage duration + sampling* + shallow marine area [†]
Stage duration + Lagerstätten + sampling*
Stage duration + Lagerstätten + shallow marine area [†]
Stage duration + Lagerstätten + sampling* + shallow marine area [†]

*Sampling is measured by a proxy, the number of fossiliferous marine formations.

[†]Shallow marine area is measured by one of three proxies described in the text.

Due to the importance of Lagerstätten stages (as detected during application of generalized differencing and preliminary tests of correlation, see above, and Results), Lagerstätten stages observed by Benson *et al.* (2010) were coded for presence or absence by a binary variable. The Triassic (Anisian–Ladinian) deposits that have yielded the majority of discoveries are European formations (Benson *et al.* 2010), in which marine reptiles are abundant in shallow and marginal facies with carbonate and terrigenous input (Hagdorn & Rieppel 1999). These stages were scored for a ‘shallow marine Lagerstätten’ variable used in comparison with shallow marine taxic diversity (Fig. 2b). Contrastingly, the Jurassic Lagerstätten represent deeper water facies with fully marine fauna and virtually no terrigenous input (Hudson *et al.* 1991; Röhl *et al.* 2001; Martill *et al.* 2006). These stages were scored for a ‘deep marine Lagerstätten’ variable used in comparison with open ocean taxic diversity (Fig. 3b).

Because both taxic diversity and fossiliferous marine formations may accumulate through longer stages (Sepkoski & Koch 1996), uneven stage duration may cause a spurious increase in correlation between these variables. To counter this effect, stage duration was included as a non-optional explanatory variable in all models, including the null model. Sea-level estimates are only available from the Anisian (Middle Triassic) onwards (Haq *et al.* 1987) and the Bajocian (Middle Jurassic) onwards (Miller *et al.* 2005). Therefore, we implemented GLS on the full duration of each taxic diversity series (i.e. Triassic–Cretaceous for shallow marine and total taxic diversity; Jurassic–Cretaceous or open ocean taxic diversity (excluding a small number of Triassic open ocean ichthyosaurs)) only when comparing with non-marine area (Smith *et al.* 1994), shorter subsets of each data series were compared with the sea-level estimates (Haq *et al.* 1987; Miller *et al.* 2005). However, because the sea-level estimates showed substantially worse fit to taxic diversity estimates than did non-marine area in all cases, these results are presented in the supplementary material. Because open ocean marine tetrapods only appeared late in the Triassic and were not well-established until the Jurassic, we analysed open ocean taxic diversity only for the Jurassic–Cretaceous and shorter time intervals.

Autoregressive models (e.g. Box *et al.* 1994; Chatfield 2003) of order zero, one or two were fit to combinations of explanatory variables used to predict taxic diversity (Table 1). This was implemented using the ‘GLS’ function of *nlme*. The modified version of Akaike’s information criterion introduced by Sugiura (1978) for small sample sizes (AICc; ‘AICc’ function of *qpcR*) was used to calculate Akaike weights (Burnham & Anderson

2001) to identify the best combination of explanatory variables. The generalized coefficient of determination (R^2) introduced by Cox & Snell (1989; Magee 1990; Nagelkerke 1991) was calculated manually from the output of the GLS analysis. This coefficient indicates the proportion of variance in taxic diversity explained by the combination of variables in the regression model. The Jarque–Bera ('jarque.bera.test' function of tseries) and Breusch–Pagan ('bptest' function of lmtest) tests were used to assess the normality and homoscedasticity of residuals. The residuals were normally distributed in all cases after \log_{10} transformation of the data series prior to analysis (only stage duration and the presence or absence of Lagerstätten were not transformed). In a few cases the Breusch–Pagan test indicated heteroskedasticity and this could not be removed by prior transformation of the dependent data series. Heteroskedasticity may cause overestimation of regression fit (e.g. Burnham & Anderson 2001). However, in most cases it was only present in the residuals from regression models

with low Akaike weights, in which case it should not affect the interpretation of our results.

Results

Pairwise tests of correlation

Almost all pairwise tests of correlation between the raw, untransformed data series recovered statistically significant results with correlation coefficients ranging from 0.5–0.9 (Table 2). Thus, non-marine surface area is correlated negatively with both sea-level estimates, counts of fossiliferous marine formations are correlated negatively with non-marine surface area and positively with both sea-level estimates, although the correlation with the sea-level estimate of Miller *et al.* (2005) is rendered non-significant after correction for multiple comparisons (Table 2).

Shallow marine taxic diversity correlates negatively with non-marine area, and positively with

Table 2. Summary of pairwise tests of correlation over the Jurassic–Cretaceous interval

		Fossiliferous marine formations (sampling) $N = 23$ (19)	Non-marine area $N = 23$ (19)	Sea-level (Haq <i>et al.</i> 1987) $N = 23$ (19)	Sea-level (Miller <i>et al.</i> 2005) $N = 18$ (16)
<i>'Raw' data comparisons</i>					
Taxic diversity (\log_{10} transformed)	Shallow marine	0.366 ^{ns}	–0.706**	0.503*	0.543*
	Open ocean	0.513** (0.735**)	–0.261 ^{ns} (–0.458*)	0.380 ^{ns} (0.655**)	0.709** (0.804**)
	Total	0.574** (0.733**)	–0.480* (–0.626**)	0.462* (0.654**)	0.739** (0.819**)
Shallow marine area proxy	Sea-level (Haq <i>et al.</i> 1987)	0.631**	–0.852**		
	(Miller <i>et al.</i> 2005)	0.568*	–0.825**		
	Non-marine area (Smith <i>et al.</i> 1994)	–0.609**			
<i>Generalized differenced (or detrended) data comparisons</i>					
Taxic diversity	Shallow marine	0.220 ^{ns}	–0.545**	–0.160 ^{ns}	0.570*
	Open ocean	0.449* (0.721**)	–0.0467 ^{ns} (0.164 ^{ns})	–0.0359 ^{ns} (–0.0319 ^{ns})	0.409 ^{ns} (0.388 ^{ns})
	Total	0.369 ^{ns} (0.499*)	–0.338 ^{ns} (–0.256 ^{ns})	–0.125 ^{ns} (–0.132 ^{ns})	0.546* (0.514*)
Shallow marine area proxy	Sea-level (Haq <i>et al.</i> 1987)	–0.0964 ^{ns}	0.113 ^{ns}		
	(Miller <i>et al.</i> 2005)	0.167 ^{ns}	–0.335 ^{ns}		
	Non-marine area (Smith <i>et al.</i> 1994)	0.160 ^{ns}			

Correlation coefficients are derived from Pearson's product moment (r), suffixed by^{ns}, non-significant; *significant at $\alpha = 0.05$; **, significant at $\alpha = 0.0125$ (i.e. incorporating a correction for multiple comparisons). Results in brackets were calculated excluding Lagerstätten stages. Shaded cells contain results that were significant after correction for multiple comparisons.

both sea-level estimates, but not with fossiliferous marine formations, and the correlations with sea-level are rendered non-significant after correction for multiple comparisons. Total taxic diversity and open ocean taxic diversity both correlate positively with counts of fossiliferous marine formations and the sea-level estimate of Miller *et al.* (2005). After exclusion of Lagerstätten stages, both of these series also correlate positively with the sea-level estimate of Haq *et al.* (1987) and total taxic diversity correlates negatively with non-marine area. This is consistent with the strong Lagerstätten effect on these data series over the Jurassic–Cretaceous interval for which correlations were tested.

Many of these pairwise tests of correlation are rendered insignificant after the application of generalized differencing. A few significant correlations remain (Table 2): diversity of shallow marine taxa is negatively correlated with non-marine area ($\rho = -0.545$); diversity of open ocean taxa is positively correlated with counts of fossiliferous marine formations ($\rho = 0.721$), but only when Lagerstätten stages are excluded. The intermediate strength of these correlations suggests that neither non-marine area nor our sampling proxy provide a complete explanation of either taxic diversity series. Neither sea-level series is correlated with either non-marine area or counts of fossiliferous marine formations, and non-marine area is not correlated with counts of fossiliferous marine formations.

Generalized least squares

Among generalized least squares regression models, neither sea-level estimate (Haq *et al.* 1987; Miller *et al.* 2005) fits any taxic diversity data as well as the estimates of non-marine area calculated from palaeogeographical maps by Smith *et al.* (1994) (Supplementary Material). Thus, sea-level is not included in any well-supported explanatory model of taxic diversity, and only analyses that use non-marine area as a proxy for the extent of habitable shallow marine area are presented here (Table 3).

Shallow marine taxic diversity across the whole Mesozoic (Induan–Maastrichtian) is best explained by a regression model including the presence or absence of shallow marine Lagerstätten, and the amount of non-marine surface area (Table 3). Including the number of fossiliferous marine formations in the model results in a slight improvement of fit (Table 3), yielding an approximately equivalent, but slightly lower Akaike weight. Excluding the presence or absence of shallow marine Lagerstätten from either model results in a lower, but non-negligible Akaike weight (Table 3). However, residuals of the model including fossiliferous marine formations and non-marine area, but excluding Lagerstätten, are heteroskedastic,

suggesting that the model fit is overestimated. Furthermore, within this model, none of the explanatory variables has a statistically significant slope (Table 4). Among the best models, only the intercept, Lagerstätten, and non-marine area have a statistically significant slope (Table 4). These results suggest that non-marine surface area and shallow marine Lagerstätten are the key determinants of observed shallow marine tetrapods palaeodiversity, and the influence of sampling is correspondingly weakened.

Open ocean taxic diversity through the Jurassic and Cretaceous is best explained by a model including the presence or absence of deep water Lagerstätten, a count of fossiliferous marine formations, and the amount of non-marine surface area. Models including Lagerstätten and one of either fossiliferous marine formations or non-marine area also have high Akaike weights, although residuals from the latter (weaker) model show heteroskedasticity, suggesting that its fit is overestimated (Table 3). Within the stronger two models, Lagerstätten and fossiliferous marine formations have statistically significant, positive slopes. Within the weaker model (Lagerstätten + non-marine area), all explanatory variables, including stage duration, have statistically significant slopes (Table 4). Despite this conflicting signal from the weakest (and heteroskedastic) model, these results suggest that deep water Lagerstätten and fossiliferous marine formations are the key determinants of observed open ocean tetrapod diversity and any fluctuations in underlying biological diversity driven by continental flooding are very weak.

Total taxic diversity is best explained by regression models minimally including the presence or absence of Lagerstätten (both shallow and deep water as a single variable) and a count of fossiliferous marine formations. Including the amount of non-marine area yields equivalent, though slightly higher AICc scores (Table 3). Within these models, only Lagerstätten and fossiliferous marine formations have statistically significant (positive) slopes. These results suggest that fossiliferous marine formations and Lagerstätten are the primary determinants of the observed palaeodiversity of all Mesozoic marine tetrapods and are consistent with results from pairwise correlation analyses (Table 2). This is similar to the pattern observed among open ocean marine tetrapods and suggests that the strength of the signal is strongest among open ocean taxa, despite the fact that these represent a lower proportion of the total data (40.7%). This is congruent with the slightly higher correlation coefficients (Table 2) and R^2 values (Table 3) recovered from analyses of open ocean taxic diversity when compared to those from shallow marine taxic diversity.

Table 3. Summary of GLS multiple regression models for taxic diversity during the Mesozoic (shallow marine taxic diversity, total taxic diversity) and Jurassic–Cretaceous (open ocean taxic diversity). All models include stage duration. AR order indicates the order of the autoregressive model. ‘Model rank’ indicates the rank order of models based on Akaike weights. Models with Akaike weight less than 1/8th that of the best model are not ranked. Model ranks in brackets indicate heteroskedasticity of model residuals, suggesting that the model’s fit is overestimated

Dependent variable	Regression model	AR order	R ²	Log likelihood	AICc	AIC weight	Model rank
TDE _{shallow marine}	Null	1	–	–21.918	52.797	0.00324	
	Sampling	1	0.135	–19.816	51.298	0.00687	
	Non-marine area	1	0.286	–17.038	45.742	0.110	3
	Sampling + non-marine area	1	0.349	–15.697	46.003	0.0970	(4)
	Lagerstätten	1	0.0860	–20.614	52.894	0.00309	
	Lagerstätten + sampling	1	0.226	–18.209	51.026	0.00787	
	Lagerstätten + non-marine area	1	0.415	–14.151	42.910	0.455	1
	Lagerstätten + non-marine area + sampling	1	0.463	–12.911	43.641	0.316	2
TDE _{open ocean}	Null	0	–	–15.639	38.541	0.0148	
	Sampling	0	0.129	–14.046	38.313	0.0166	
	Non-marine area	0	0.204	–13.0175	36.257	0.0465	
	Sampling + non-marine area	0	0.279	–11.883	37.296	0.0276	
	Lagerstätten	0	0.111	–14.288	38.799	0.0130	
[residuals: Fig. 3C]	Lagerstätten + sampling	1	0.458	–8.590	32.710	0.274	2
	Lagerstätten + non-marine area	0	0.377	–10.197	33.923	0.149	(3)
	Lagerstätten + non-marine area + sampling	1	0.554	–6.349	31.948	0.401	1
TDE _{total}	Null	1	–	–20.717	50.394	<0.0001	
	Sampling	0	0.298	–15.579	40.825	0.000498	
	Non-marine area	0	0.144	–18.465	46.596	<0.0001	
	Sampling + non-marine area	1	0.397	–13.377	39.929	0.000780	
	Lagerstätten	2	0.321	–15.108	43.883	0.000108	
	Lagerstätten + sampling	1	0.629	–6.347	27.302	0.430	2
	Lagerstätten + non-marine area	0	0.405	–13.187	38.984	0.00125	
	Lagerstätten + non-marine area + sampling	1	0.674	–4.466	26.750	0.567	1

Discussion

Determinants of marine reptile palaeodiversity

Lagerstätten effects have an influential role in determining the observed palaeodiversity of marine tetrapods. This is indicated by (1) the confounding effect of Lagerstätten on the ability to estimate long-term trend in diversity (calculated during the process of generalized differencing) and (2) on pairwise correlation of open ocean and total taxic diversity with other data series (data for detrending and correlation tests spanned only the Jurassic–Cretaceous and thus excluded shallow water Lagerstätten so pairwise correlations involving shallow marine taxa are not affected), and (3) the universal inclusion of a variable describing the presence or absence of

Lagerstätten in the best predictive models for taxic diversity (Table 3).

Pairwise tests of correlation on log₁₀- and generalized difference-transformed data indicate a strong, statistically significant negative correlation between the taxic diversity of shallow marine tetrapods and non-marine area (Table 2). This relationship is confirmed by the strong and statistically significant fit of non-marine area within generalized least squares multiple regression models (Tables 3 & 4). A statistically significant correlation with our sampling proxy, the number of fossiliferous marine formations, is absent (Table 2). However, multiple regression models including sampling as an additional variable are approximately as good as those excluding it (Table 3). This suggests that sampling still has a weak influence on the observed taxic diversity of shallow marine tetrapods. The quantity of

Table 4. Summary of explanatory variables within the best GLS multiple regression models for taxic diversity (indicated in Table 3)

	Slope	SE	<i>P</i>		Slope	SE	<i>P</i>
TDE _{shallow marine} (<i>N</i> = 29 stages)				TDE _{open ocean} (<i>N</i> = 23)			
1 Intercept	25.547	7.881	0.0034*	1 Intercept	-6.295	7.432	0.408
Stage duration	-0.0107	0.0147	0.472	Stage duration	-0.0121	0.0260	0.646
Lagerstätten	0.882	0.328	0.0126*	Lagerstätten	0.725	0.144	0.0001*
Non-marine area	-11.689	3.730	0.0044*	Non-marine area	2.0250	3.362	0.0555
				Sampling	1.586	0.459	0.0028*
2 Intercept	21.428	8.637	0.0205*	2 Intercept	-1.775	0.686	0.0180*
Stage duration	-0.0167	0.0146	0.264	Stage duration	-0.00568	0.0254	0.8254
Lagerstätten	0.827	0.319	0.0160*	Lagerstätten	0.704	0.146	0.0001*
Non-marine area	-10.314	3.966	0.0157*	Sampling	1.426	0.407	0.0024*
Sampling	0.687	0.452	0.1412				
3 Intercept	22.420	9.389	0.0245*	3 Intercept	11.142	4.757	0.0302*
Stage duration	-0.0135	0.0155	0.3927	Stage duration	0.0586	0.0255	0.0329*
Non-marine area	-10.172	4.443	0.0304*	Lagerstätten	0.578	0.205	0.0109*
				Non-marine area	-5.0786	2.251	0.0360*
4 Intercept	17.861	9.669	0.0766				
Stage duration	-0.0197	0.0157	0.222				
Non-marine area	-8.642	4.463	0.0642				
Sampling	0.745	0.492	0.1424				
TDE _{total} (<i>N</i> = 29)				TDE _{total}			
1 Intercept	0.976	4.997	0.847	2 Intercept	-1.901	0.513	0.0011*
Stage duration	-0.0142	0.0110	0.207	Stage duration	-0.0152	0.0106	0.165
Lagerstätten	0.632	0.111	<0.0001*	Lagerstätten	0.626	0.108	<0.0001*
Non-marine area	-1.295	2.236	0.568	Sampling	1.655	0.285	<0.0001*
Sampling	1.576	0.319	<0.0001*				

*Indicates statistical significance of slope or intercept at $\alpha = 0.05$. SE = standard error.

non-marine area is inversely correlated with flooding of the continental shelf, and therefore provides a proxy for the areal extent of shallow marine habitats. Decreases in non-marine area result from increased continental flooding and are strongly correlated with increases in shallow marine taxic diversity, providing strong support for a species diversity-area relationship in this ecomorphological grouping.

In contrast, non-marine area and sea-level have little influence on the diversity of open ocean taxa. Although some tests detect a statistically significant correlation with sea-level (Table 2), correlation with non-marine surface area is absent. Furthermore, after generalized difference transformation, only fossiliferous marine formations show a statistically significant (positive) correlation with the taxic diversity of open ocean marine tetrapods (Table 2). This relationship is confirmed by the strong and statistically significant fit of fossiliferous marine formations within generalized least squares multiple regression models (Tables 3 & 4). Counts of fossiliferous marine formations form a proxy for (1) the amount of rock available for fossil sampling, (2) the geographical extent of sampled

formations (different sedimentary basins have different formations), (3) the heterogeneity of facies available for fossil sampling, and (4) the amount of geological study that has been undertaken (e.g. Raup 1976; Peters & Foote 2001; Peters & Heim 2010). Thus, a strong relationship with fossiliferous marine formations, and weak relationship with non-marine area confirms that observed open ocean taxic diversity is profoundly influenced by heterogeneous temporal sampling of the fossil record. Any underlying fluctuations in genuine biological diversity are evidently too weak to obscure the relationship between open ocean taxic diversity and sampling.

Our multiple regression models explain a higher proportion of variance in total taxic diversity than they do in either of the other taxic diversity data series (Table 3). The best explanatory models yield statistically significant (positive) slopes for Lagerstätten and fossiliferous marine formations, and the *P*-values of these slopes are the most strongly significant of any in the present study. This confirms the conclusions of Benson *et al.* (2010), who suggested that fossil sampling was influential in

determining observed palaeodiversity of marine reptiles, and that Lagerstätten in the Jurassic and Middle Triassic confounded quantitative analyses of palaeodiversity.

Correlation between sea-level and sampling data series

Many previous studies have predicted or recovered a relationship between sea-level or continental flooding, and fossil sampling metrics (e.g. Sepkoski 1976; Peters & Foote 2001; Smith *et al.* 2001; Peters 2005, 2006a; Benton & Emerson 2007). However, we only found a correlation between our sampling metric (fossiliferous marine formations) and estimates of non-marine area or eustatic sea-level, prior to generalized differencing of the data series (Table 2). This indicates that the data series share general features such as a long-term trend of increase over the Jurassic–Cretaceous, but that the pattern of peaks and troughs differs. This lack of detailed correspondence was also observed for the terrestrial Mesozoic record by Butler *et al.* (2011a), and may be genuine or reflect inadequacy of either the estimates of sea-level/continental flooding (Haq *et al.* 1987; Smith *et al.* 1994; Miller *et al.* 2005) or our sampling proxy. Given that many studies of the highly abundant record of marine invertebrates suggest a correlation between sampling and sea-level (see above), its absence from our data is an issue that requires further investigation. Purported ‘eustatic’ sea-level estimates such as those presented by Miller *et al.* (2005) have been criticized as they may be strongly influenced by localized mantle flow induced topographic changes (Moucha *et al.* 2008). Detailed macrostratigraphic data have only been compiled for North America (Peters 2006b, 2008; Peters & Heim 2010), but their assembly over wider geographical areas presents one avenue by which more accurate estimates of fossil sampling and continental flooding might be quantified.

Implications for the ‘common cause’ hypothesis

The concept of fossil sampling as a direct explanation of observed palaeodiversity has been challenged on the grounds that both may instead be driven by a common, external driving mechanism (Sepkoski 1976; Peters 2005, 2006a; Benton & Emerson 2007; Smith 2007). The most commonly cited mechanism is sea-level, which drives continental flooding and has been proposed for both the marine (e.g. Sepkoski 1976; Peters 2005, 2006a) and terrestrial (Benton & Emerson 2007; Benton 2009) settings. In the marine

setting, increased submerged continental shelf area may result in increased deposition of fossiliferous rock, as well as an increased habitable area for shallow marine organisms, thus inflating estimates of correlation between sampling proxies and observed palaeodiversity. This principle is termed the ‘common cause’ hypothesis.

The strong relationship between taxic diversity of shallow marine tetrapods and continental flooding recovered in our study is congruent with the results of studies of the Phanerozoic fossil record (Sepkoski 1976; Peters 2005, 2006a), the majority of which comprises shallow marine invertebrates. These studies have yielded the strongest evidence in support of continental flooding as the driver of ‘common cause’. However, because a strong relationship with continental flooding is absent (or very weak), the relationship between taxic diversity of open ocean tetrapods and fossil sampling cannot be explained by the ‘common cause’ hypothesis. Instead, our data support a direct, causal relationship between observed taxic diversity of open ocean tetrapods and temporal heterogeneity in fossil sampling. This contrasts with results recovered by Marx (2008) and Marx & Uhen (2010), which suggest that sampling is not an important determinant of the observed palaeodiversity of open ocean mammals (cetaceans; which would be classified as open ocean taxa using our approach).

Diversification and extinctions of Mesozoic marine tetrapods

Our previous analysis of total taxic diversity of marine tetrapods suggested a link between diversity and sampling, obscured by pronounced Lagerstätten effects (Benson *et al.* 2010). This allowed the construction of a ‘sampling corrected’ curve of residual diversity remaining after subtraction of the value of diversity expected given measured sampling within each geological stage. The present study shows a more complex picture in which the diversity of shallow marine taxa is more strongly tied to flooding of the continental shelves (a similar pattern was observed by Hagdorn & Rieppel (1999) in a detailed study of marine tetrapods from the Triassic sediments of the Germanic Basin). This hypothesis was reviewed and discussed in detail by Hallam & Cohen (1989) and Smith (2007). Both studies proposed that factors other than the literal extent of habitable area (e.g. ocean bottom anoxia, perturbation of primary productivity) might be important. In our study, high values in taxic diversity of shallow marine tetrapods span the Anisian–Carnian (Triassic: basal sauropterygians, non-parvipelvic ichthyosaurs, thalattosaurs), Bathonian–Tithonian (Jurassic: thalattosuchian crocodyliforms) and

Cenomanian–Maastrichtian (Cretaceous: dyrosaurid crocodyliforms and marine squamates, including mosasauroids). These high values approximately correspond to sea-level high-stands and are separated by major regression events in the Late Triassic–Early Jurassic and earliest Cretaceous (Fig. 2; Hallam 1978; Haq *et al.* 1987; Miller *et al.* 2005). During these regressions, taxic diversity of shallow marine tetrapods declined to low or zero observed values, and higher clades of shallow marine taxa became extinct. The Late Triassic regression, potentially representing the minimum extent of Mesozoic continental flooding (Smith *et al.* 1994), had a catastrophic effect on shallow marine taxa: thalattosaurs, non-plesiosaurian sauropterygians (Storrs 1993a; Hagdorn & Rieppel 1999; Rieppel 2000) and non-parvipelvian ichthyosaurs (Motani 2005) became extinct (see also Bardet 1992, 1994). The earliest Cretaceous regression corresponds to a drop in thalattosuchian diversity, and morphological disparity (Pierce *et al.* 2009a; Young *et al.* 2010) that may have occurred later in the southern hemisphere than it did in the northern hemisphere (Hallam 1986; Bardet 1994; Pierce *et al.* 2009a). Finally, a dramatic drop in sea-level, and corresponding reduction in the extent of continental flooding at the Cretaceous–Palaeogene boundary may have contributed to the extinction of abundant shallow marine squamates, including mosasauroids. Note, however, that the plesiopodal dyrosaurid crocodyliforms (Hill *et al.* 2008; Jouve *et al.* 2008) were not strongly affected by this event, and may have taken refuge in terrestrial freshwater ecosystems (Buffetaut 1990). Note also that numerous other factors have been invoked to explain this catastrophic extinction event that affected a wide range of terrestrial and marine organisms (e.g. Bardet 1994; Archibald *et al.* 2010; Schulte *et al.* 2010). Our previous results suggested declining diversity during the terminal stages of the Cretaceous based on sampling-corrected diversity estimates (Benson *et al.* 2010). However, the present study suggests that these estimates are not appropriate for shallow marine tetrapods, which may therefore have been undergoing a major diversification right up until the end of the Cretaceous, as suggested by Bardet (1992, 1994) and Ross (2009; for mosasauroids). This is especially likely given a slight decrease in fossil sampling, coincident with an increase in observed palaeodiversity in the final stage of the Cretaceous (Maastrichtian). One remaining question regarding shallow marine-tetrapod diversity is the presence or absence of end-Cenomanian crash in diversity. This was suggested by Bardet (1992, 1994) based on observation of taxic diversity and origination and extinction rates among marine tetrapods. However, Benson *et al.* (2010) suggested that it coincided with

substantially low sampling of Turonian/Coniacian marine fossils (Fig. 3). Although temporal heterogeneity in fossil sampling has been shown not to have a strong influence on observed palaeodiversity of shallow marine tetrapods for most stages of the Mesozoic, the magnitude of the post-Cenomanian sampling low is such that it is difficult to dismiss as a possible explanation.

The relationship between open ocean tetrapod diversity and continental flooding is weak or absent. Thus, the evolution of highly pelagic forms among ichthyosaurs and plesiosaurians, which occurred by the Late Triassic (Storrs 1994; Motani 2005), released these animals from dependence on shallow marine habitats. This may explain their ‘escape’ from extinction events driven by marine regressions such as that in the Late Triassic. Thus, plesiosaurians and ichthyosaurs were diverse in the earliest Jurassic (Fig. 3; e.g. McGowan & Motani 2003; Ketchum & Benson 2010), and are represented by high levels of residual diversity after regression against our sampling proxy and a variable coding the presence or absence of Lagerstätten (Fig. 3c). The effect of the Jurassic–Cretaceous extinction on open ocean tetrapods is difficult to determine as this boundary also marks a transition out of the Lagerstätten-dominated Jurassic sampling regime. However, Bakker (1993) suggested that Jurassic plesiosaur lineages were truncated at this boundary. Unfortunately, the problem of deep water Lagerstätten is pervasive in the Jurassic. Extreme cases were identified, in which a single or small number of formations have yielded a high proportion of fossil discoveries (Benson *et al.* 2010). However, other, less extreme cases were not identified or accounted for in our analyses and it is difficult to interpret the meaning of our residual diversity plot confidently (Fig. 3c). We do not advocate a literal interpretation of high frequency oscillations in residual diversity observed in the Jurassic: the Jurassic record of marine tetrapods has been sampled by palaeontologists in an extremely heterogeneous fashion and this presents a fundamental obstacle to interpreting patterns in diversity. In contrast, the Cretaceous record is more evenly sampled (Fig. 3). This may allow a more confident interpretation of patterns in diversity. Residual diversity of open ocean tetrapods shows a similar pattern to that of total marine tetrapod diversity recovered by Benson *et al.* (2010): a progressive increase in diversity from the Early Cretaceous to a Santonian (middle Late Cretaceous) peak. This is interrupted by a local peak in the Barremian. An extended period of low ichthyosaur diversity preceded their final disappearance after the Cenomanian (e.g. Sander 2000; McGowan & Motani 2003), which does not coincide with reduced diversity of other clades and thus did

not occur during a catastrophic episode of mass extinction. One possible explanation is the rise of fast-swimming actinopterygian fish as prey and marcopredaceous sharks as competitors (Lingham-Soliar 2003). The terminal stages of the Cretaceous, the Campanian and Maastrichtian, show a slight decrease in diversity, suggesting a gradual decline prior to the Cretaceous–Palaeogene mass extinction event (Fig. 3c). Highly pelagic chelonoid turtles (and continental, freshwater turtles; Hutchison & Archibald 1986) were largely unaffected by the terminal Cretaceous extinction event, but plesiosaurs and open ocean mosasauroids like *Plotosaurus* became extinct. This is congruent with observed high levels of selectivity in terminal Cretaceous extinctions (e.g. Buffetaut 1990). One possibility is that because turtles are oviparous with zero parental care, they survived the acme of highly-stressed terminal Cretaceous environments as eggs (which is also possible for crocodyliformes). Other marine tetrapods were likely viviparous (Caldwell & Lee 2001; Cheng *et al.* 2004). This is analogous to the situation among open ocean planktonic organisms, among which diatoms suffered proportionally little extinction (e.g. Thierstein 1982). This is hypothesized to result from a meroplanktic life cycle, incorporating a dormant resting cyst phase (Kitchell *et al.* 1986).

Timing of the 'Late Triassic' marine tetrapod extinction

Extinction of shallow marine tetrapod lineages in the early Late Triassic is demonstrated here and by previous studies (Bardet 1992, 1994; Rieppel 2000). The last appearances of many higher clades occur early in the Late Triassic (Benson *et al.* 2010), although the basal sauropterygian placodonts (Pinna & Mazin 1993; Storrs 1994) and some non-parvipelvian ichthyosaurs (Motani 2005) are represented in the latest Triassic (Rhaetian). It is possible that all, or most, of these extinctions coincide with a wider, but controversial, global extinction event at the end of the Triassic, affecting terrestrial tetrapods, plants and marine invertebrates (e.g. Benton 1995; Tanner *et al.* 2004). However, this is not currently consistent with the last appearance data of most marine tetrapod clades, or our results. If extinction among shallow marine tetrapods was driven by reduction in flooded continental area then it should precede the end of the Triassic as the sea-level minimum may have occurred as early as the Norian (Haq *et al.* 1987; Miller *et al.* 2005). Unfortunately, this time interval is poorly resolved in the non-marine area estimates of Smith *et al.* (1994) (Fig. 2a).

Conclusions

Vertebrates offer unique insights into the relationships between observed palaeodiversity, sampling of the fossil record, and continental flooding, because they are well-studied and occupy a range of habitats indicated by clearly established ecomorphotypes. During the Mesozoic, shallow marine tetrapod diversity was strongly tied to the extent of flooded continental area. Decreases in diversity in the Late Triassic, earliest Cretaceous and latest Cretaceous coincide with major regressions and may have been driven by a reduction in habitable shallow marine area, or concurrent effects such as a break in primary productivity or ocean bottom anoxia. In contrast, open ocean marine tetrapod diversity shows a weak or absent relationship with shallow marine habitat area. Instead, open ocean palaeodiversity has a stronger relationship with temporal heterogeneity in fossil sampling.

Tetrapods gave rise to multiple independent radiations adapted for shallow marine life. Representatives of these radiations were vulnerable to major regressions, which drove extinction events. Invasion of the open ocean by parvipelvian ichthyosaurs, plesiosaurs and chelonoid turtles freed these lineages from their dependence on shallow marine environments and made them less vulnerable to extinction driven by regression. The existence of different diversification trajectories among shallow marine and open ocean tetrapods suggests that diversity curves predominantly based on shallow marine invertebrates should not be generalized across all animals.

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