1. INTRODUCTION
Dinosaurs are icons of success and failure. According to a long-standing hypothesis (Sloan et al. 1986; Sarjeant & Currie 2001; Sullivan 2006), the group was in decline long before its extinction at the end of the Cretaceous Period, 65 Myr ago. However, new evidence (Fastovsky et al. 2004; Taylor 2006; Wang & Dodson 2006) suggests a major increase in diversification during the Campanian and Maastrichtian, spanning approximately the last 18 Myr of the Cretaceous, a finding that emphasizes the dramatic nature of the apparently sudden extinction of dinosaurs at the end of the Cretaceous. This Late Cretaceous diversification has been seen as evidence that dinosaurs were part of the Cretaceous explosion of terrestrial life (Fastovsky et al. 2004; Weishampel et al. 2004) characterized by, among others, the rise of flowering plants, herbivorous and social insects, squamates, birds and mammals all underwent a rapid expansion. Although an apparent explosion of dinosaur diversity occurred in the mid-Cretaceous, coinciding with the emergence of new groups (e.g. neoceratopsians, ankylosaurid ankylosaurs, hadrosaurids and pachycephalosaurs), results from the first quantitative study of diversification applied to a new supertree of dinosaurs show that this apparent burst in dinosaurian diversity in the last 18 Myr of the Cretaceous is a sampling artefact. Indeed, major diversification shifts occurred largely in the first one-third of the group’s history. Despite the appearance of new clades of medium to large herbivores and carnivores later in dinosaur history, these new originations do not correspond to significant diversification shifts. Instead, the overall geometry of the Cretaceous part of the dinosaur tree does not depart from the null hypothesis of an equal rates model of lineage branching. Furthermore, we conclude that dinosaurs did not experience a progressive decline at the end of the Cretaceous, nor was their evolution driven directly by the KTR.

Keywords: dinosaur; angiosperm; Cretaceous; biodiversity; supertree
as butterflies and moths, all of which diversified rapidly (Grimaldi 1999). Among vertebrates, squamates (lizards and snakes), crocodilians (J. E. Tarver 2008, unpublished data available upon request) and basal groups of placental mammals and modern birds all underwent major diversifications (Hedges et al. 1996; Fountaine et al. 2005; Bininda-Emonds et al. 2007) although the timing of appearance of modern bird orders (Hedges et al. 1996; Dyke 2001) and modern mammal orders (Wible et al. 2007) remains controversial.

Dinosaur evolution was marked by the appearance of truly spectacular new forms. Giant sauropods, the dominant herbivores of the Jurassic, were joined by new kinds of ornithischians at the beginning of the Cretaceous. Subsequent new waves of diversification at the beginning of the Late Cretaceous (some 100 Myr ago) produced a diverse fauna of hadrosaurs, neoceratopsians, ankylosaur ankylosaurs and pachycephalosaurs, among herbivores, as well as new carnivorous groups, including the giant carcharodontosaurines and the smaller troodontids, dromaeosaurs and ornithomimosaurs. Qualitatively then, dinosaurs appear to have been part of the KTR.

As is commonly the case, studies of dinosaur diversity through time have suffered from the lack of a conceptual framework in which ‘diversification’ is defined, detected and quantified. Furthermore, a proper evaluation of sampling biases (e.g. Raup 1972; Benton et al. 2000; Alfroy et al. 2001) has not been carried out on the group. Two key sampling issues are that the fossil record of a group may be truncated (i.e. lacking its youngest and/or oldest members) and that the number of observed taxa depends to some extent on sampling intensity (proxies for this are the number of localities investigated and the number of specimens collected). Here, we address both issues and use analytical protocols to minimize or mitigate their impact.

At the heart of our analysis is a new supertree of dinosaurs, which represents a development and expansion of an earlier study (Pisani et al. 2002), consisting of 440 species (some 70% of the total number of valid species, based on Weishampel et al. 2004) and an additional 15 undescribed or indeterminate forms. The tree was constructed using a variety of techniques to ensure that it represents the best possible summary of current knowledge. It is highly resolved (99.2% compared to a fully bifurcating tree) and its nodes are mostly well supported (see the electronic supplementary material), making the tree amenable to diversity analyses. Use of large trees in diversification analyses is commonly twopronged. Previous workers have used them to fill implied gaps in the fossil record and estimate species richness accordingly (Weishampel & Jianu 2000; Upchurch & Barrett 2005), though never for the whole of Dinosauria. A completely different approach is to use tree shape to search for and date perturbations in diversification patterns that diverge from a simple birth–death model (e.g. Forest et al. 2007; Ruta et al. 2007). Here we use both approaches to test whether dinosaurs responded to the KTR, by comparing the magnitude and rates of their diversification in the Cretaceous with their diversification patterns in the Triassic and Jurassic.

As with the previous studies (listed above), the focus of this contribution is the non-avian dinosaurs and throughout ‘dinosaurs’ should be read as meaning non-avian dinosaurs.

2. MATERIAL AND METHODS

(a) Supertree construction

We expanded significantly upon a previous list of source trees of dinosaur interrelationships (Pisani et al. 2002) with publications up to the end of 2006. This list was then shortened by removing those trees that have not been built through a formal cladistic analysis (i.e. a matrix and character list must be available either as a part of the publication itself, as an electronic appendix, or obtainable from the senior author). Retention of this information allowed us to determine redundant source trees (Bininda-Emonds et al. 2004), reinsert out-group(s) discarded in published figures and rerun analyses where the source publication did not provide a standardized (strict) consensus tree. Not all trees could be considered novel and hence independent (Bininda-Emonds et al. 2004). When one analysis clearly superseded an earlier work, we retained the later tree and discarded the original. When multiple later works had equal claim, we included them all, but weighted them in tree searches so that their net contribution was equal to one independent tree. Overall, these filters led to a strong skew in the data towards more recent analyses (figure 1), greatly enhancing the chances of recovering a tree that represents current consensus.

Unlike the previous genus-level effort (Pisani et al. 2002), we chose to produce a species-level supertree. This decision was bolstered by an authoritative recent compilation of valid names (Weishampel et al. 2004) that served as our primary reference for nonina dubia, which were purged, and junior synonyms, which were replaced with their senior counterpart. Birds more derived than Archaeopteryx and non-dinosaurian taxa were also purged from the source trees. Supraspecific taxa were replaced with all species that could be unequivocally assigned to that higher taxon based on the labelled nodes of source trees (Page 2004), with the exception of genera, which were replaced by their most completely known species. Each source tree was processed in this way and both a tree (Page 1996) and an XML file were produced (these are available for download from http://www.graemetlloyd.com). The latter contains metadata about the source publication, taxa and characters, ensuring a consistent standard of data collection and audit trail for future updates. Standard (Baum 1992) and Purvis (Purvis 1995) MRP matrices were then produced using a modified version of SuperMRPplus (Bininda-Emonds et al. 2005), RadCon (Thorley & Page 2000) and CLANN (Creevey & McInerney 2005).

Tree searches were performed following an established protocol (Pisani et al. 2002, 2007). First, 5000 heuristic searches were performed in PAUP v. 4b10 (Swoford 2003) with the MultTree option turned off. Trees obtained from these searches were saved and swapped using the tree bisection reconnection algorithm and the MultTree option on (to retain multiple equally optimal trees). The Parsimony Ratchet (Nixon 1999) could not find a better tree. The splitfit supertree (Wilkinson et al. 2005a) was built analysing the standard MRP matrix using Mix, which is part of the PHYLIP package (Felsenstein 2000). To enforce Mix to run a compatibility analysis, the threshold parsimony option was set to 2. One hundred heuristic searches were performed, and characters were weighted (as described above) using a specifically generated weight file (Felsenstein 2000).

In order to obtain a well-resolved tree, we undertook some post hoc taxon pruning where poorly constrained species, producing unacceptably high numbers (more than 5000) of equally probable supertrees, were removed. Choosing a tree
Figure 1. The year of publication of source trees shows a strong skew among included trees towards more recent analyses. Excluded trees include those that were uncorroborated; solid grey line (lacked an accompanying matrix and character list) or redundant; dashed grey line (trees that have been superseded by a later, more comprehensive study). Included trees are either independent; solid black line (are characterized by a unique combination of characters and taxa) or dependent; dashed black line (trees derived from a shared character list, but have differing and non-redundant taxon sets). The latter were down-weighted in the supertree searches so that their summed contribution was equal to that of one independent tree. The three major peaks (1990, 1999 and 2004) correspond to the publication of The Dinosauria first edition (Weishampel et al. 1990), a Science review paper (Sereno 1999) and The Dinosauria second edition (Weishampel et al. 2004), respectively.

for diversity analyses was based on overall supertree support. Here we used the V1 index (Wilkinson et al. 2005b), which indicated that support was highest for the standard MRP supertree.

(b) Diversification metrics
We calculated the percentage change, per million years, of global species richness among 12 successive time bins of approximately equal duration created by grouping geological stages for three different datasets: (i) a recent database of the known dinosaur record (Weishampel et al. 2004), (ii) the same dataset but with some species’ first appearances extended back in time as implied by a sister group relationship with an older taxon (Norell 1992) in the supertree, and (iii) a subsampled dataset.

This latter dataset was created using a subsampling method similar to rarefaction. Rarefaction methods have played an important role in ecology (Gotelli & Colwell 2001) and palaeoecology (Raup 1975; Tipper 1979), as they offer the opportunity to examine the effects of taxonomic sampling on measures of species richness. Here we measure sample size as the total number of species occurrences by locality for each of our 12 time bins. Methodologically, our approach is equivalent to setting the global quality of the record as equal to that of the worst part of it. In this case, the worst bin was bin 5 (Pliensbachian–Aalenian), with only 39 occurrences, and this set the number to be subsampled in each case. In order to calculate the mean and 95% error bars, subsampling was performed 10 000 times and the number of species observed in 39 randomly drawn occurrences from each bin was recorded. Subsampling was performed using custom-built code (available for download from http://www.graemelloyd.com) in the freely available statistical programming language ‘R’ (http://cran.r-project.org/). Note that, in all cases, diversification rates were calculated for each time bin, except the first, as there are no unequivocal dinosaurian fossils, and second, as there is no previous richness value; diversification is infinite.

An alternative approach to quantifying diversification patterns relies on phylogenetic tree shape. Phylogeny is determined by the available taxa and the inferred pattern of relationships, and phylogenetic tree shape reflects large-scale variations in speciation and extinction rates (Mooers & Heard 1997). Topological methods (Bininda-Emonds et al. 1999; Katzourakis et al. 2001; Chan & Moore 2005; Jones et al. 2005) may be used to identify diversification rate shifts in phylogenetic trees, based on comparison between the observed tree and one expected under an equal rates Markov (ERM) model. A diversification shift is simply a change in net speciation rate (i.e. rate of splitting of evolutionary lineages). In the ERM model, such rates are constant, resulting in a constant splitting of lineages. The ERM model is best seen as a standard reference model for measuring significant changes in lineage splitting (Nee 2006). Simply put, given two groups subtended by a node, if one group is significantly more speciose than the other, a diversification rate shift is inferred to have taken place, i.e. a significant departure from an ERM model of clade growth has occurred.

Phylogenetic shifts in diversification were detected using SYMMTREE v. 1.0 (Chan & Moore 2005). Analyses of tree shape are biased when a group is paraphyletic, as a particularly speciose clade (in this case, birds) is represented by a single terminal (Archaeopteryx). A modification was thus required in order to account for the absence of birds. Although it was not feasible in the present contribution to include all birds, a hand-drawn phylogeny of the better-known Mesozoic taxa (72 species in total) was inserted at the node subtending Archaeopteryx + Jinfengopteryx, effectively making the tree a Mesozoic time slice. (This placement of Jinfengopteryx is based on the original description (Ji et al. 2005), but more recent analyses, e.g. Turner et al. (2007), have placed it within Troodontidae.) Polytomies were treated as soft, with the size-sensitive ERM algorithm set to perform 10 000 random resolutions per individual node and 1 000 000 random resolutions for the entire tree. Internal branches within the phylogeny on which diversification shifts are inferred to have occurred were identified using the Δs shift statistic. This process was repeated for time slices of the whole tree as described in Ruta et al. (2007) to avoid violating the ERM model.

3. RESULTS
(a) Ghost ranges account for some irregularities in the diversity curves
The supertree of dinosaur species is plotted on a geological time scale (Gradstein et al. 2004; figure 2a; electronic supplementary material) subdivided into 12 approximately equal-length time bins to assess the extent of ghost ranges (Norell 1992). Ghost ranges, minimal basal stratigraphic range extensions implied by the geometry of the phylogenetic tree, indicate missing fossil data, and allow us to correct diversity profiles for the group through the Mesozoic and to compare diversification rates, the proportional change in observed species
from the Middle Jurassic onwards. When the mean remaining two-thirds of their history, i.e. the 120 Myr ago occurred early, whereas very little is detected in the significant and 7 substantial shifts in the Jurassic; 2 significant and 2 substantial shifts in the Triassic; 11 substantial diversification shifts are distributed as follows: Campanian (1; Ceratopsidae). The 15 significant and 11 losauria, Eumaniraptora), Turonian (1; Euhadrosauria) and the Aalenian (1; Neosauropoda), Kimmeridgian (2; Anky-

Later statistically significant diversification shifts occur in Maniraptoriformes, Maniraptora and Oviraptorosauria). The robustness of these results was tested further by ‘time slicing’ our tree to avoid issues surrounding violation of the ERM model’s assumptions (Ruta et al. 2007). This involved creating 11 separate trees, one for each of our time bins, which included only the taxa that existed, or are posited to have existed (through range extensions), at that time. Results based upon time-sliced trees strongly support our whole-tree analysis, with 11 out of the 15 significant shifts also occurring in the time-sliced trees. Only one novel significant shift was discovered in the time-sliced trees, coincident with the origin of the sauropod clade Lithostrotia in the Valanginian (140 Myr ago). Again, the highest mean $\Delta_2$ shift statistic (0.69) was found in bin 4, with a general decrease in diversification shift likelihood in later time bins. Similarly, over half of the significant pairwise comparisons between $\Delta_2$ values show time bins 4 and 5 to have had higher likelihoods of a diversification shift. All results are robust even if the controversial taxon *Eshanosaurus* (Xu et al. 2001), which is here placed as a therizinosaur and is responsible for pinpointing the date of four of the significant shifts (Tetanurae, Coelurosauria, Maniraptoriformes and Maniraptora), is removed.

(c) Diversification shifts are concentrated in the lower (earlier) half of the dinosaur tree

Analysis of diversification rates in our dinosaur supertree using the software SYMMETREE (see §2) shows that statistically significant ($p<0.05$) and substantial (0.05 < $p < 0.1$) diversification shifts (i.e. multiplications of evolutionary lineages) were heavily concentrated in the first one-third of dinosaurian history (figure 2a; electronic supplementary material). The majority occur near the base of the group, in the Late Triassic to Early Jurassic (230–175 Myr ago), and are closely, although not always exactly, associated with the origin of major clades (10 significant shifts: Genosauria, Eurypod, Cerapoda, Saoapodo-
morpha, Neotheropoda, Tetanurae, Coelurosauria, Maniraptoriformes, Maniraptora and Oviraptorosaurus). Later statistically significant diversification shifts occur in the Aalenian (1; Neosauropoda), Kimmeridgian (2; Anky-
losauria, Eumaniraptora), Turonian (1; Euhadrosauria) and Campanian (1; Ceratopsid). The 15 significant and 11 substantial diversification shifts are distributed as follows: 2 significant and 2 substantial shifts in the Triassic; 11 significant and 7 substantial shifts in the Jurassic; 2 significant and 2 substantial shifts in the Cretaceous. Our results confirm that most of the diversification among dinosaurs occurred early, whereas very little is detected in the remaining two-thirds of their history, i.e. the 120 Myr ago from the Middle Jurassic onwards. When the mean $\Delta_2$ shift statistic, which represents the likelihood that a shift occurred, is plotted against time (figure 2c), there is a peak value of 0.58 during the Rhaetian–Sinemurian (Bin 4; 205–190 Myr ago) followed by an overall decrease towards the present. Two-thirds of significant pairwise comparisons between $\Delta_2$ values (Kruskal–Wallis test; $p<0.05$) show bins 4 and 5 (Rhaetian–Aalenian; 205–170 Myr ago) to have higher likelihoods of a diversification shift than all other bins.

4. DISCUSSION

(a) Diversification shifts are not always concentrated in the lower half of a tree

Geometric arguments might suggest that it is inevitable to find the majority of diversification shifts low in a phylogenetic tree. To an extent, of course, one can expect statistically significant diversification shifts to occur at the base of the tree, as founding taxa within the clade split and major branches become established. Bats, for example, show a similar early diversification pattern (Jones et al. 2005), but ants do not (Forest et al. 2007). The reason is that clades do not stop diversifying once they have become established. Studies of the distribution of clade shapes (Gould et al. 1977; Valentine 1990; Uhen 1996; Nee 2006) show all possible shapes (after paraphyly has been accounted for), ranging from bottom-heavy to top-heavy, tall and thin, short and broad and even spindle-shaped, e.g. when a clade has been hit hard by an extinction event or other bottlenecks crisis and has then recovered. In the case of dinosaurs, this clade continues to expand up to the end of the Cretaceous and yet, statistically speaking, the Cretaceous expansion cannot be distinguished from an undriven ERM.

(b) Sampling must be taken into account

The fossil record of continental vertebrates is clearly patchy, with large temporal gaps between sampling horizons. The seriousness of sampling bias is debated, with opinion ranging from assumptions that the fossil record offers more of a geological than a biological signal (Raup 1972; Alroy et al. 2001; Peters & Foote 2002) to acceptance that sampling error does not much modify the apparent macroevolu-
tionary patterns (Sepkoski et al. 1981; Benton 1998). Comparisons of cladograms with the fossil record show good congruence in most cases (Norell & Novacek 1992;
Benton et al. (2000), thus suggesting that the biological signal is probably adequately represented when assessed at the correct scale. Current efforts (Smith 2007) focus on methods to quantify sampling bias and to determine parts of the fossil record signal that stand out after sampling has been evaluated.
In this paper, we have used the number of dinosaur localities in each time bin as a crude measure of sampling. Other measures could have been area of rock exposure, volume of rock deposited per unit time, total number of geological formations (whether fossiliferous or not) or intensity of worker effort (e.g. measured as the number of palaeontologists working on a specific group). The relative merit of all these measures is the subject of much current debate; we note that the use of any sampling measure to correct diversity figures may be sufficiently heavy-handed that any biological signal may be swamped (Peters & Foote 2002; Smith 2007). For example, there is doubtless a species-area effect (Smith 2001), in which rock area or volume, or number of formations, is linked with the diversity of life. For example, during the times of high sea level, continental margins flood and species on the continental shelf increase in abundance and diversity. Corrections of those diversity figures, obtained by dividing them by shelf area or rock volume, could potentially remove the whole of the biological signal.

Our solution, to offer both the raw data and the sampling-modified data (figure 2b), allows comparison of the data without making an assumption that either version is correct, and points to the need for further examination of each of the undoubted biases in our understanding of this fossil record. Before applying a correction factor, we need evidence of how collecting intensity (i.e. number of palaeontologists; number of field days), rock availability and other sampling factors affect the results. The relationship is almost certainly not linear, and that in itself speaks against crude application of sampling corrections. For example, discovery curves for dinosaurs and other fossil taxa, when calibrated against worker effort, show a variety of shapes: that for trilobites is more or less a straight line (Tarver et al. 2007), whereas the more intensively studied dinosaurs show a classic logistic shape, where huge efforts at present do not necessarily yield huge numbers of new fossils, after many decades of collection (Benton in press).

(c) Dinosaurs and the KTR

There are two issues to be considered in associating dinosaur diversification with the KTR: the timing of that diversification and evidence that dinosaurs did, or did not, benefit from the diversification of angiosperms.

Whereas the raw data show that dinosaurs diversified substantially during the Cretaceous, and especially in the last 18 Myr of the period (Fastovsky et al. 2004; Taylor 2006; Wang & Dodson 2006), and we confirm this, we have shown that appearances are deceptive. As we show, and as noted before (Fastovsky et al. 2004), much or all of the Campanian and Maastrichtian boost in diversity in the last phases of the Mesozoic is probably an artefact of abundant preservation and intense sampling. Our diversification shift tests indicate that only two significant diversifications happened in the Late Cretaceous, corresponding to the initial diversifications of the euhadrosaurs and the ceratopsids. We therefore do not find evidence for a steadily increasing rate of diversification throughout dinosaurian evolution, nor do we see evidence for the continuing appearance of innovations driving an increasing variety of behavioural strategies, as had been posited (Fastovsky et al. 2004).

Previous studies have been equivocal about whether dinosaurs fed on angiosperms. The Late Cretaceous expansion of dinosaurian diversity, found especially on the diversification of herbivorous dinosaurs such as hadrosaurs, ceratopsians, and ankylosaurs, might have suggested that these groups, all of which either arose or diversified substantially only after the origin of angiosperms in the mid-Cretaceous, specialized on an angiosperm diet. Bakker (1978), for example, argued that the ornithopods of the Early Cretaceous fed close to the ground, and so favoured gymnosperms in their diet. Owing to their intense low-level feeding, the only plants that could survive the onslaught were the earliest angiosperms that held their reproductive organs close to the ground. And so, in his words, dinosaurs invented flowers.

This view is disputed (Wedel et al. 2000) and there is actually only limited evidence to demonstrate that Cretaceous dinosaurs fed on angiosperms (Barrett & Willis 2001). The patterns of rises and falls in the diversity of Cretaceous dinosaurs and Cretaceous plants, as well as their palaeogeographic distributions, do not suggest any correlation. Coprolites, fossil faeces, are rare and often cannot be attributed to their producer; Cretaceous examples include some with traces of the angiosperm biomarkers oleananes (a group of chemicals with suppressing effects on insect pests), whereas others contain exclusively gymnosperm material. An Early Cretaceous ankylosaur, Minmi, has been reported (Molnar & Clifford 2000) with remnants of angiosperm fruits in its gut, and some remarkable coprolites from India show that some dinosaurs ate early grasses (Prasad et al. 2005). Fossil occurrences and studies of the teeth and postulated jaw functions of herbivorous dinosaurs suggest that angiosperms were a part of the diet of many dinosaurs, but that gymnosperms were still the major constituent in most cases (Chin & Gill 1996; Barrett & Willis 2001; Ghosh et al. 2003). Plant-eating insects and mammals very likely benefited more from the new sources of plant food.

Detailed studies of dinosaurian herbivory and plant evolution (Barrett & Willis 2001) had already suggested there was limited evidence that angiosperm diversification drove the Cretaceous diversification of dinosaurs. Our new evidence confirms that the KTR was a key in the origination of modern continental ecosystems, but that the dinosaurs were not a part of it. Hadrosaurs and ceratopsians showed late diversifications, but not enough to save the dinosaur dynasty from its fate.

Computationally intense analyses were performed using the computer cluster of NUI Maynooth High Performance Computing Centre. Subsampling was performed using modified code taught to G.T.L. by John Alroy as part of the Paleobiology Database Intensive Summer Course in Analytical Paleobiology (http://paleodb.org). We thank Sarda Sahney for help with the figures and discussions concerning subsampling methods and Nicholas Minter for pointing us towards the Genise et al. (2005) paper. This manuscript was improved following comments on an earlier draft by Michael P. Taylor and an anonymous reviewer. G.T.L., K.E.D. and J.E.T. acknowledge receipt of NERC studentships NER/S/A/2004/12222, NER/S/A/2003/11241 and NER/S/A/2003/11198A, respectively. M.J.B. and M.R. acknowledge receipt of NERC grant NE/C518973/1. D.W.E.H. is supported by DFG grant RA 1012/-3 as part of Unit 533.


