

# Testing coevolutionary hypotheses over geological timescales: interactions between Cretaceous dinosaurs and plants

RICHARD J. BUTLER<sup>1\*</sup>, PAUL M. BARRETT<sup>FLS<sup>1</sup></sup>, MALCOLM G. PENN<sup>2</sup> and PAUL KENRICK<sup>FLS<sup>1</sup></sup>

<sup>1</sup>*Department of Palaeontology, The Natural History Museum, London SW7 5BD, UK*

<sup>2</sup>*Department of Botany, The Natural History Museum, London SW7 5BD, UK*

*Received 8 July 2009; accepted for publication 25 November 2009*

Testing coevolutionary scenarios over extended geological timescales is fraught with difficulties. Most tests rely on comparisons of temporal variations in taxonomic diversity for the groups of interest: however, this approach typically excludes spatiotemporal data. Here, we apply a quantitative method that incorporates the spatiotemporal distributions of the proposed coevolving groups using a Geographical Information System. Distributional data for Cretaceous dinosaur and plant groups were mapped onto palaeogeographical reconstructions in a series of time-slices. Within each time-slice, palaeocontinental surfaces were divided into a series of grids, each of which was scored as present, absent or inapplicable (unsampled) for each group. Distributions were compared statistically to determine whether the putative coevolving groups co-occurred within grid squares more or less frequently than expected by chance. Pairwise comparisons were made between herbivorous dinosaur clades and major plant groups (e.g. cycads, angiosperms) on a global scale. Only three nonrepeated associations of marginal significance were recovered, demonstrating that, in general, current knowledge of the spatiotemporal distributions of these groups provides little support for coevolutionary hypotheses. The Geographical Information System methods used are readily applicable to many other questions whose answers are reliant on a detailed knowledge of organismal distributions in time and space. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, **100**, 1–15.

**ADDITIONAL KEYWORDS:** angiosperms – coevolution – cycads – Dinosauria – Geographical Information System.

## INTRODUCTION

Coevolutionary interactions play a key role in the promotion and maintenance of biological diversity (e.g. Thompson, 1994; Brooks & McLennan, 2002). As this process is important over ecological timescales, it is unsurprising that evolutionary biologists have assumed that it would have been equally important in the past. Consequently, numerous coevolutionary scenarios have been proposed to unfold over extended geological timescales (e.g. Janzen & Martin, 1981; Stebbins, 1981; Bakker, 1983; Stanley, Van

Valkenburgh & Steneck, 1983; Vermeij, 1983, 1987; Collinson & Hooker, 1991; Scott, Stephenson & Chaloner, 1992; Zavada & Mentis, 1992; Labandeira *et al.*, 1994; Labandeira, 1997, 2002; Wilf *et al.*, 2000; Labandeira, Johnson & Wilf, 2002; Becerra, 2003; Gandolfo, Nixon & Crepet, 2004; Rønsted *et al.*, 2005; Strömberg, 2006). These include hypotheses of ‘tight’ and ‘diffuse’ coevolution (cf. Janzen, 1980). Both categories involve reciprocal interactions between different organisms, but ‘tight’ interactions are specific (e.g. host-specialized pollination associations: Rønsted *et al.*, 2005; Terry *et al.*, 2007; host–parasite system: Ronquist & Liljeblad, 2001), whereas ‘diffuse’ interactions may occur between multiple groups of

\*Corresponding author. E-mail: butler.richard.j@gmail.com

organisms exerting both direct and indirect selection pressures on each other.

'Tight' coevolutionary scenarios can be recognized in the fossil record by the identification of species-specific anatomical or behavioural characters that demonstrate close functional linkage between a pair of coevolving organisms (e.g. matching foliar damage to insect-feeding behaviours: Wilf *et al.*, 2000). Alternatively, these hypotheses can be evaluated by comparing timings of divergence events within the phylogenies of the proposed coevolving species. For example, Rønsted *et al.* (2005) provided strong evidence for fig-wasp codivergence events over a 60 million year timescale. By contrast, 'diffuse' patterns are harder to test as they rely on more generalized pattern recognition. For example, plants might develop varied mechanical (e.g. thorns, phytoliths) or chemical (toxins, e.g. Farrell, Dussourd & Mitter, 1991) defences to deter not one, but many herbivorous mammal species; this, in turn, might promote counter-adaptations in grazers, including changes to digestive physiology or improved masticatory abilities that might appear in response to selection for more than one food plant (e.g. Coughenour, 1985; Danell & Bergström, 2002). Unfortunately, palaeontological data are generally insufficient to disentangle such complex ecological relationships. Diffuse coevolutionary patterns (such as the possible impact of grass evolution on grazer biology) might only be detectable over extended taxonomic, spatial and temporal scales (Herrera, 1985; Strömberg, 2006); their identification and testing will be strongly affected by the completeness and quality of the fossil record.

One approach used to test deep time coevolutionary hypotheses has been to compare temporal variations in lineage or ecomorphotypic diversity for the proposed coevolving groups at either global or local scales. For example, Labandeira & Sepkoski (1993) and Labandeira *et al.* (1994) demonstrated that many lepidopteran insect lineages appeared prior to the main angiosperm radiation, suggesting that the latter did not have an impact on the diversification of numerous lepidopteran groups, thereby falsifying this potential coevolutionary scenario. Similarly, Collinson & Hooker (1991) noted that changes in Tertiary mammal diversity coincided with various floral events, including an apparent relationship between primate diversity and the availability of fleshy fruits. Coevolutionary scenarios can also be tested with abundance data: Strömberg (2006) and Strömberg *et al.* (2007) demonstrated that grasses became important components of the flora in Asia Minor and the Great Plains of North America prior to the arrival of horses with hypsodont dentitions, suggesting that the rise of grasses was not necessarily closely linked with the appearance of these herbivores.

Diversity, abundance-based and codivergence approaches are informative, but usually exclude information on the spatial distributions of the taxa in question [see Strömberg (2006) for an example that incorporates geographical data]. An alternative approach for testing whether available fossil data are consistent with a given diffuse coevolutionary hypothesis is to assess the degree of spatial association (e.g. similarity of palaeogeographical ranges) between the taxonomic (or ecomorphotypic) groups that are proposed to have coevolved. If reciprocal coevolutionary interactions are occurring between groups of organisms, these groups should exhibit similar spatial distributions for the duration of the period in which coevolution is thought to have occurred – the absence of a recognizable spatial association between the groups indicates either that a coevolutionary relationship did not exist or that the fossil record is insufficiently complete (at least at present) to provide robust support for the existence of such a relationship. Moreover, we would also expect that, if the distribution of a group changes through time, the distribution of any coevolving groups will change in concert, and that the overall geographical ranges of the groups would remain comparable (Thompson, 1994). However, although the absence of a spatial association can be used to falsify coevolutionary hypotheses, the presence of a spatial association needs to be combined with evidence of a mechanism facilitating coevolutionary interactions before coevolution can be considered to be well supported.

In this article, we propose a novel approach for testing coevolutionary hypotheses over geological timescales using a Geographical Information System (GIS). A GIS is a computer-based mapping system for storing, visualizing, modelling and analysing spatially referenced data and associated attributes (e.g. Longley *et al.*, 2001). Such tools are increasingly being used in evolutionary studies on extant organisms, including the analysis of geographical variation in body size, hybrid zones, phylogeography, phenotypic character evolution and speciation (e.g. Rodríguez, López-Sañudo & Hawkins, 2006; Kozak, Graham & Wiens, 2008; Swenson, 2008). Few studies have used GIS to examine evolutionary questions in 'deep time'. Examples include work on Devonian invertebrate biogeography (Rode & Lieberman, 2004, 2005; Stigall & Lieberman, 2006), the diversity and biogeography of North American Miocene mammals (e.g. Barnosky, Carrasco & Davis, 2005) and Triassic vertebrate biochronology (Rayfield *et al.*, 2005). In this article, we demonstrate that a GIS-based approach to coevolution has the potential to dynamically integrate palaeobiological and palaeoenvironmental data with a temporal series (series of time-slices) of palaeogeographical

maps, allowing visual inspection and comparison of temporal changes in distributional patterns. Moreover, we propose a technique whereby the spatial distributions of taxonomic/palaeoecological groups can be compared statistically within a given time-slice (or series of time-slices), allowing quantitative identification of spatiotemporal associations. This GIS approach is widely applicable over a broad range of temporal and spatial scales, with potential applications to numerous macroevolutionary problems in which time-sliced spatial data are important, such as hypotheses of competitive replacement, faunal responses to climatic change, and the temporal and geographical context of mass extinctions. The GIS framework allows much more explicit consideration of spatial data from the fossil record than previously possible.

GIS approaches are most effective when the temporal and geographical distributions of putative coevolving groups are well documented. With this caveat, we focus on the coevolution of terrestrial vertebrates and plants (angiosperms, cycadophytes) during the Cretaceous period, a time when fossil distributions are comparatively well understood. Angiosperms dominate modern floras, and their Cretaceous origin and radiation are key events in the evolution of terrestrial biotas (e.g. Crane, 1987; Crane, Friis & Pedersen, 1995; Wing & Boucher, 1998; Frohlich & Chase, 2007). Coevolutionary hypotheses have been proposed that link this radiation to changes in contemporaneous dinosaur faunas: specifically, a change from a high-browsing Jurassic herbivore fauna to a low-browsing Cretaceous fauna is suggested to have created disturbed ground conditions that favoured r-selected early angiosperms (Bakker, 1978, 1986). The subsequent radiation of angiosperms during the middle to Late Cretaceous is proposed to have driven the diversification of several dinosaur clades, including iguanodontians and ceratopsians, and the evolution of complex jaw mechanisms (e.g. Coe *et al.*, 1987; Wing & Tiffney, 1987a, b; Weishampel & Norman, 1989; Tiffney, 1992, 2004). These hypotheses predict that Early Cretaceous angiosperms should show positive spatial associations with low-browsing dinosaur clades (e.g. Ornithopoda, Ceratopsia) and negative spatial associations with high-browsing clades (e.g. Sauropoda). In the Late Cretaceous, these hypotheses predict continued positive spatial associations between angiosperms and diversifying clades, such as Ornithopoda and Ceratopsia; some hypotheses also predict a positive spatial association between angiosperms and sauropods in the Late Cretaceous (Coria & Salgado, 2005).

Cycads have also been implicated in dinosaur evolution. These insect-pollinated gymnosperms bear

large cones and toxic foliage. In modern ecosystems, cycads are of low diversity and confined largely to tropical/subtropical regions (e.g. Norstog & Nicholls, 1997; Jones, 2002), but during the late Mesozoic they formed an important component of global floras (Niklas, Tiffney & Knoll, 1985; Crane, 1987; Lidgard & Crane, 1990). Herbivorous dinosaurs, particularly sauropods and stegosaurs, have been proposed as key cycad seed dispersers (Burbidge & Whelan, 1982; Van der Pijl, 1982; Weishampel, 1984; Tiffney, 1986, 1992, 1997, 2004; Watson & Cusack, 2005; Mustoe, 2007), and a coevolutionary relationship has been suggested linking a significant cycad decline during the Early Cretaceous with falling abundance and species' richness of these herbivores (see Mustoe, 2007). These hypotheses predict positive spatial associations between cycads and the proposed dispersers: sauropods and stegosaurs.

Sereno (1997), Weishampel & Jianu (2000), Barrett & Willis (2001) and Butler *et al.* (2009a) questioned these hypotheses, and demonstrated that the diversifications of many herbivorous dinosaur clades either pre- or post-dated the appearance of angiosperms in the earliest Cretaceous, potentially removing the temporal correlations necessary to support diffuse coevolutionary interactions. Similarly, Butler *et al.* (2009b) identified only one correlation between the diversity of dinosaurs and cycads: an apparent coincidence between falling stegosaur diversity and falling cycad diversity during the Lower Cretaceous. However, although these studies included a discussion of ecological parameters and taxonomic diversity patterns (e.g. relative abundance of organisms through time, changes in dinosaur feeding mechanisms, evolution of plant characteristics), none included detailed considerations of palaeobiogeographical distributions. This is a significant omission: as diffuse coevolutionary relationships might develop over extended timescales (Herrera, 1985; Strömberg, 2006), this has the potential to create apparent evolutionary lags in the fossil record that could confound attempts to test coevolutionary hypotheses using temporal data alone. Comparisons of spatial distributions through time can be used as an auxiliary criterion to help investigate these questions in more detail (e.g. Strömberg, 2006).

We aim to test two sets of coevolutionary hypotheses relating to: (1) the influence of herbivorous dinosaurs on the early radiation of angiosperms and (2) the interactions between dinosaurs and cycads. In particular, did the geographical ranges of dinosaurs and angiosperms or dinosaurs and cycads overlap to an extent that long-term interactions between the groups were feasible? Were changes in their geographical ranges through time correlated? Were these geographical associations more frequent than would be expected by chance?

## METHODS

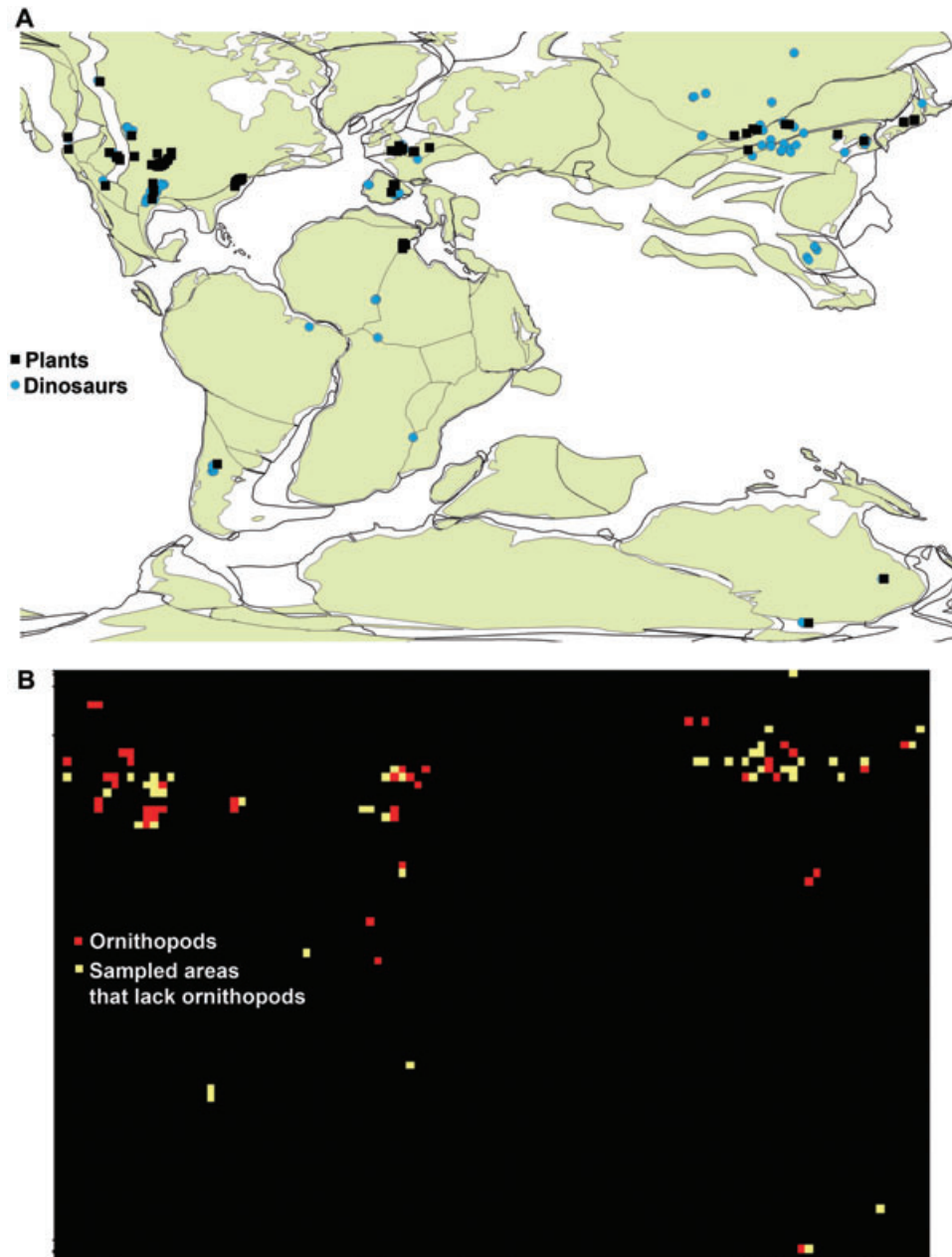
Most hypotheses of plant–dinosaur coevolution have been formulated at coarse taxonomic levels, involving comparisons of species' richness and/or abundance between major clades/grades of organisms (e.g. Bakker, 1978; Coe *et al.*, 1987; Weishampel & Norman, 1989; Mustoe, 2007). It is these diffuse coevolutionary scenarios that we aim to test herein. However, it should be noted that such taxonomically coarse analyses potentially mask genuine coevolutionary processes operating at other taxonomic levels or between more specialized ecomorphotypes. For example, it may be that a particular sauropod clade (e.g. diplodocids) exhibited a coevolutionary relationship with a specific plant clade (e.g. araucariacean conifers), but this relationship may not be supported by broader comparisons (e.g. sauropods vs. conifers). Nevertheless, few authors have proposed hypotheses that focus on interactions between less inclusive dinosaur or plant clades. Even where such finer scale hypotheses have been proposed (it has been suggested, for example, that titanosaurian sauropods may have coevolved with angiosperms in the Late Cretaceous: Coria & Salgado, 2005), the clades under consideration are speciose (> 40 genera in the case of titanosaurs) and may incorporate wide phenotypic variety. This combination of factors might still obscure the identification of tighter coevolutionary interactions. Moreover, in the case of dinosaurs and Mesozoic plants, testing tight coevolutionary scenarios (e.g. between dinosaur and plant species) is hampered by the lack of sufficiently large sample sizes to allow meaningful statistical comparisons. As diffuse coevolution has been proposed as an important process in moulding the evolutionary histories of dinosaurs and plants, it is necessary and meaningful to test these macroevolutionary hypotheses, even if the relatively coarse level at which these analyses have to be undertaken might obscure some genuine instances of tight coevolutionary interactions.

Our dataset contains information on the global distributions of nonavian herbivorous dinosaurs and plants during the Cretaceous period (65.5–145.5 Mya). Occurrences of herbivorous dinosaurs were compiled in a GIS-compatible relational database using Microsoft Access. Distributional data were based on references in Weishampel *et al.* (2004a) and more recently published works. All Cretaceous ornithischians and sauropodomorphs, and several theropod clades (Therizinosauroidea, Oviraptorosauria, Ornithomimosauria), are considered to be herbivorous (cf. Weishampel & Norman, 1989; Barrett, 2005). Taxonomic assignments follow Weishampel *et al.* (2004a, b), except where more recent information is available. Faunal information was collected for each

locality and linked to separate data tables containing information on palaeoecology (e.g. body mass, jaw mechanisms), geological age, lithology and depositional environment. For each geological formation yielding herbivorous dinosaur material, we collected information on macrofloras from the primary literature (systematics, physiognomy, palaeoenvironments, etc.). Our database therefore comprises a subset of global floral diversity, namely the flora of dinosaur-bearing formations. In acquiring plant data, we critically reviewed taxonomic assignments by consulting recent reviews and correcting identifications from the older literature. We focus on angiosperms, cycads (Cycadales) and non-bennettitalean cycadophytes, as explicit coevolutionary hypotheses involving dinosaurs have been formulated for these groups. Cycad foliage strongly resembles that of the extinct Bennettitales, but the two groups are not closely related (e.g. Watson & Sincock, 1992; Watson & Cusack, 2005; Hilton & Bateman, 2006). The term 'cycadophyte' is used for foliage that cannot be placed with confidence in either Cycadales or Bennettitales. We also consider the category non-bennettitalean cycadophytes – a group that includes all cycad occurrences as well as occurrences of cycadophytes that cannot be identified as referable to either Cycadales or Bennettitales (i.e. all occurrences that might potentially represent cycads). We keep these two categories separate in our analyses and discussion. The database contains 6549 dinosaur and macroplant occurrences at 1952 localities, representing 407 dinosaur taxa and > 2300 macrofloral taxa. Many of the macrofloral taxa are form taxa, and thus the number of whole plant taxa might be considerably less (although it is not possible to accurately estimate the probable true number on the basis of available taxonomic information). The database is available on the website of *Biological Reviews* as online supplementary material to Butler *et al.* (2009b).

The Cretaceous dinosaur–plant database was imported into the GIS applications ArcGIS 9.1 and DIVA-GIS 5.2 (<http://www.diva-gis.org>). Distributional data were plotted onto PALEOMAP Project palaeogeographical reconstructions (Scotese, 2001), which are available for six Cretaceous time-slices (see below; see Fig. 1A). Prior to importing these data, modern day latitude/longitude coordinates for database localities were converted to palaeolatitude/palaeolongitude coordinates at intervals corresponding to the available palaeogeographical reconstructions using PointTracker software (Scotese, 2004). Selections of dinosaur and plant occurrences can be made rapidly within either GIS application on the basis of specified combinations of attributes (e.g. clade, body size, temporal occurrence), allowing the creation of new data layers; for example, it is possible





**Figure 1.** A, Palaeogeographical map for 120 Mya from Scotese (2001). Dinosaur and plant localities of Aptian age have been plotted onto this palaeogeographical reconstruction using ArcGIS 9.1 and PointTracker (Scotese, 2004). Note the major sampling biases, particularly towards the Northern Hemisphere. B, Gridded distributional surface (generated at a two square decimal degree scale) for Aptian ornithopods produced using DIVA-GIS (<http://www.diva-gis.org>). The grid is generated to cover the maximum global extent over which dinosaur and plant localities occur. Areas coloured black are unsampled (and are excluded from statistical comparisons). This grid surface can be exported as a data array allowing Aptian ornithopod distribution to be compared with the distribution of other dinosaur–plant groups.

to rapidly select and visualize all occurrences of North American sauropodomorphs from the Maastrichtian stage of the Late Cretaceous (Fig. 3). For each of the 12 Standard European Stages comprising the Cretaceous, we used this attribute selection procedure to

create data layers (on appropriate palaeogeographical reconstructions) displaying occurrences from that time-slice of major dinosaur and plant groups. Data layers do not reflect instantaneous surfaces of time, but are time-averaged, with all occurrences within a

stage plotted on a single layer. The palaeogeographical reconstructions used were: 140 Mya (Berriasian–Hauterivian); 120 Mya (Barremian–Aptian); 100 Mya (Albian–Cenomanian); 90 Mya (Turonian–Coniacian); 80 Mya (Santonian–Campanian); and 70 Mya (Maastrichtian). Overlaying occurrence data allows a visual comparison of the spatial distributions of two groups within a time-slice.

In addition to visual comparisons of distributions (see above), statistical comparisons were carried out using a grid approach, analogous to the use of quadrats in ecological sampling (e.g. Waite, 2000; Barnosky *et al.*, 2001). Point distributions on each map were converted to grids using DIVA-GIS (see Fig. 1B). For each taxonomic group of interest and for seven of the 12 stage-level time-slices (the plant record is too poorly sampled during the Valanginian–Hauterivian and Turonian–Santonian for these stages to be considered – each of these stages has < 10 grid squares with plant–dinosaur co-occurrences), grids were generated to cover the entire global area over which plant–dinosaur fossil data are present in the database: grids were generated at a scale of two square decimal degrees. Within the grid, each individual square is scored as present, absent or inapplicable for each relevant taxonomic grouping (Fig. 1B) – inapplicable refers to areas in which either or both plant and dinosaur fossil data are absent (i.e. areas that have not been sampled). These grids were then exported from the GIS software as text files that could be imported into Microsoft Excel, allowing statistical comparisons between the distributions of different plant and dinosaur groups. Inapplicable grid squares were discarded, as were those that yielded only dinosaur or plant fossils, so that comparisons were only made across areas that contained both dinosaur and plant fossils. A nonparametric statistical test of association (Fisher's exact test; Waite, 2000) was used to assess whether or not pairs of plant and dinosaur taxa co-occurred in squares within the grid significantly more or less often than would be expected if they occurred independently of one another. Fisher's exact test (two-tailed) was used because, in most cases, sample sizes were too small for chi-squared tests to be applicable (Waite, 2000). Small sample sizes result from incompleteness of the terrestrial fossil record; more rigorous statistical approaches could be employed with larger sample sizes (e.g. fossil marine invertebrates, Quaternary ecosystems). Significant positive associations between particular plant and dinosaur taxa identified in multiple time-slices would be consistent with (although not necessarily indicative of) a coevolutionary relationship, especially if supported by other lines of evidence (e.g. diversity analyses, ecomorphological characterization, e.g. Barrett & Willis, 2001; Butler *et al.*, 2009a, b). By

contrast, repeated significant negative associations or an absence of significant correlations would either falsify the coevolutionary hypothesis or indicate that the fossil record is insufficiently complete (at least at present) to support the coevolutionary hypothesis.

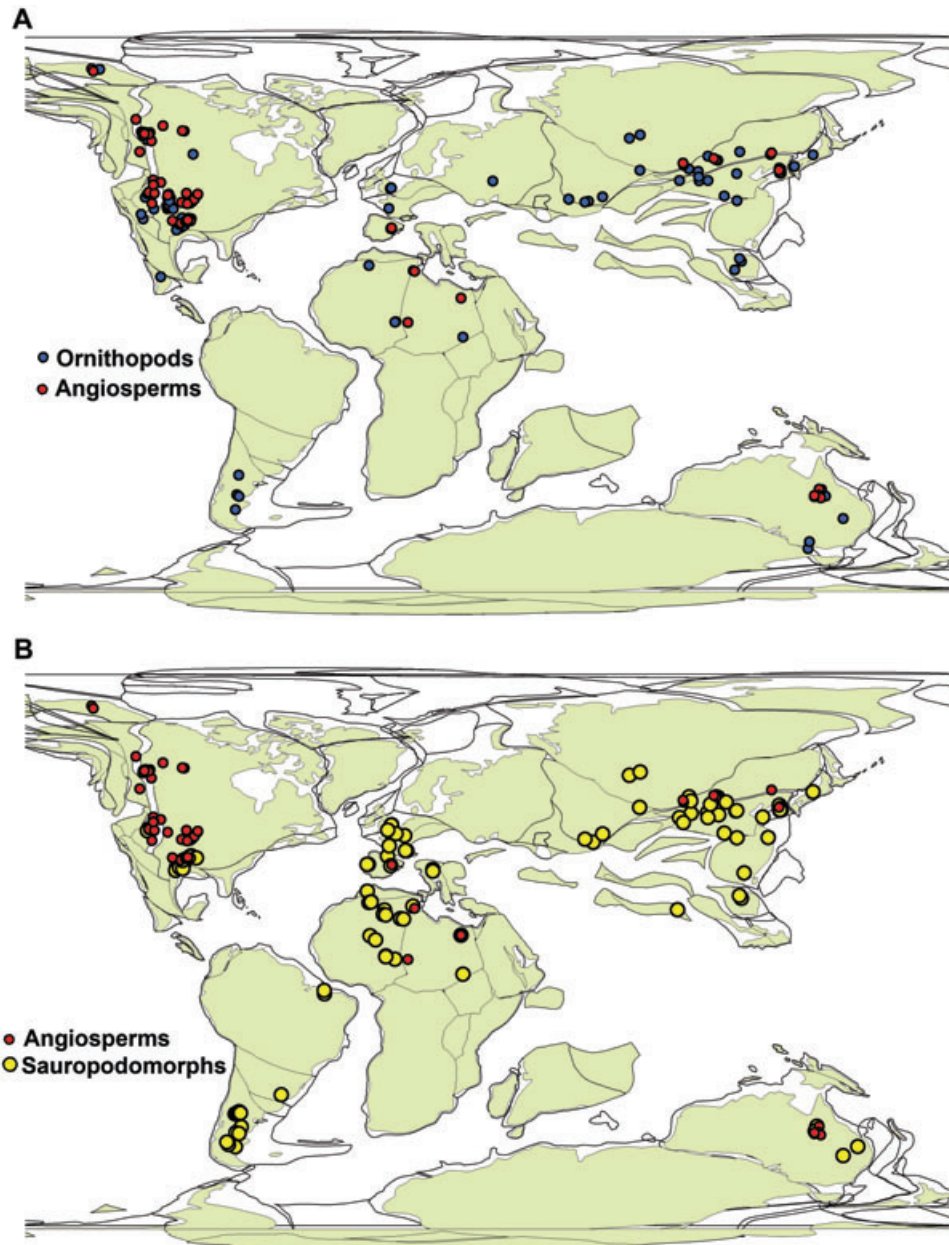
In order to test the validity of the quadrat approach, we applied this methodology to a subset of the data that were expected to provide significant positive and negative associations between particular dinosaur clades. Maastrichtian dinosaur faunas are well known for their provinciality (e.g. Holtz, Chapman & Lamanna, 2004). Most notable is the abundance of sauropods and the scarcity of ornithischians on Gondwanan continents – this contrasts with the abundance of ornithischians and scarcity of sauropods in Laurasia. This faunal provinciality suggests that sauropods should show negative associations with most ornithischian clades, as a result of their disparate distribution, whereas the ornithischian clades should show positive associations with one another. We tested these predictions using the aforementioned approach: the larger sample sizes allowed the use of nonparametric chi-squared tests, in addition to Fisher's exact tests.

## RESULTS

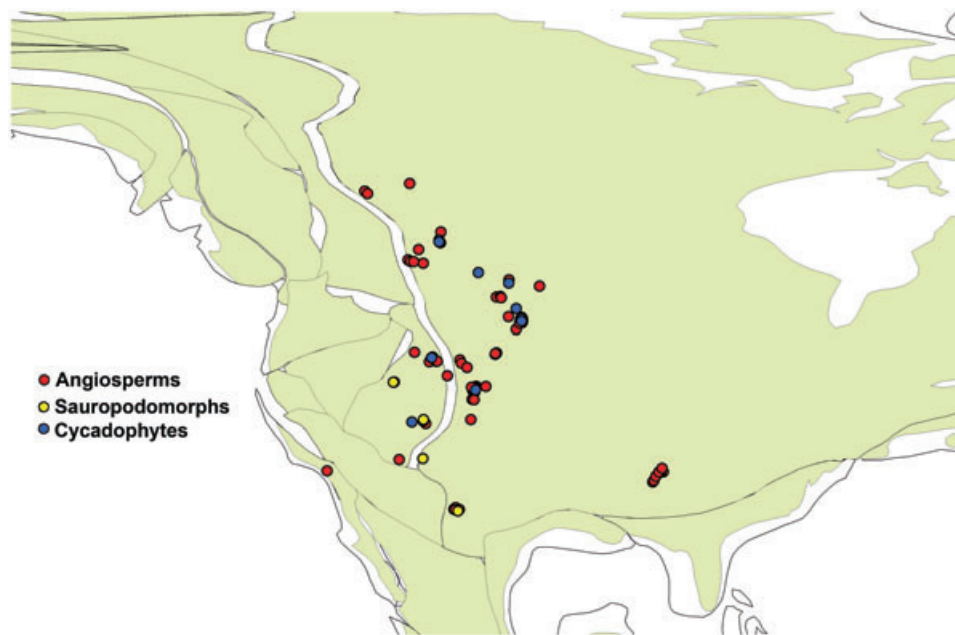
### VISUAL COMPARISON OF DISTRIBUTIONS

Simple visual comparisons can identify distributional patterns inconsistent with coevolutionary hypotheses: GIS greatly facilitates this procedure. Although an overview of dinosaur and plant distribution throughout the Cretaceous is beyond the scope of this article, we outline some key results that demonstrate the utility of this approach.

The earliest unquestionable angiosperm macrofossils are rare occurrences from the Barremian–Aptian of China, Europe and the USA between palaeolatitudes of 30 and 45°. Sauropods, ornithopods and ankylosaurs are widely distributed in Barremian–Aptian faunas, and have been found in close proximity to all early angiosperm occurrences. By contrast, stegosaurs and ceratopsians are geographically restricted in these time-slices, and are absent or scarce in several areas yielding early angiosperms (e.g. both clades are absent from the Barremian–Aptian of North America). The major radiation of angiosperms occurs from the Albian–Cenomanian onwards (Crane, 1987; Wing & Boucher, 1998: Fig. 2). The Albian–Cenomanian is the first point at which a notable discontinuity occurs between the distributions of angiosperms and sauropods (Fig. 2B). Within North America, sauropods in these time-slices are limited to the south-west USA and do not occur above



**Figure 2.** A, Palaeogeographical map for 100 Mya from Scotese (2001). Angiosperm and ornithopod occurrences of Albian–Cenomanian age have been plotted onto this palaeogeographical reconstruction using ArcGIS 9.1 and Point-Tracker (Scotese, 2004). Note that ornithopods are globally distributed and that there is no noticeable discontinuity between ornithopod and angiosperm distribution (note that, in North America and north Africa, there are several regions in which angiosperms are present but ornithopods appear to be absent – ornithopods are indeed present in these areas, but the relevant data points are obscured at this scale by overlying angiosperm data points). B, Palaeogeographical map for 100 Mya. Angiosperm and sauropodomorph occurrences of Albian–Cenomanian age have been plotted onto this palaeogeographical reconstruction. Note that sauropodomorph occurrences are abundant and globally distributed; however, a notable discontinuity occurs between sauropodomorph and angiosperm distributions within North America. Within North America, sauropodomorphs are scarce and limited to the south-west of the continent; angiosperms extend over a much broader area, reaching as far north as present-day Alaska.



**Figure 3.** North American palaeogeographical map for 70 Mya from Scotese (2001). Angiosperm, cycadophyte and sauropodomorph occurrences of Maastrichtian age have been plotted onto this palaeogeographical reconstruction. Note that, although sauropodomorphs are palaeogeographically limited to the south-west of the continent, angiosperms and cycadophytes extend over a much broader area, reaching considerably further north.

palaeolatitudes of 40°. Sauropods are unknown from the Turonian–Santonian of North America, but are restricted to the south-west USA and Mexico during the Campanian–Maastrichtian interval (Fig. 3). By contrast, Albian–Maastrichtian angiosperms have been reported from much higher palaeolatitudes, extending into British Columbia and Alaska. However, on other continents, angiosperms are found in close proximity to sauropod occurrences throughout this time period, and sauropod occurrences remain common, particularly in Gondwana.

Throughout the middle to Late Cretaceous, ornithopods are globally distributed (although they are generally scarcer in Gondwana than in Laurasia), and there is no clear discontinuity between angiosperm and ornithopod distributions (Fig. 2A). The same is true of ankylosaurs, although they are only rare components of Gondwanan faunas. Pachycephalosaurs and ceratopsians are limited to Laurasia (with the exception of two controversial ceratopsians from the Southern Hemisphere), although, within Laurasia, they are generally found in close proximity to angiosperms.

In the earliest Cretaceous (Berriasian–Barremian), occurrences of cycads are sparse, but have a global distribution: in all cases, they are found in close proximity to stegosaurs, sauropods and some other groups (e.g. ornithopods). Stegosaurs decline (in terms of both occurrences and taxonomic diversity)

from the Barremian onwards, and this coincides with cycad decline. The first incongruence between the distribution of sauropods and cycads/non-bennettitalean cycadophytes occurs in the Cenomanian–Maastrichtian (Fig. 3). As discussed above, sauropods are geographically restricted in these time-slices to the south-west USA and do not range into the northern USA or Canada (Fig. 3). Given the relatively well-sampled Late Cretaceous record for North America (particularly in the Campanian and Maastrichtian), it seems likely that this palaeogeographical restriction is genuine. By contrast, Late Cretaceous cycads and non-bennettitalean cycadophytes occur over a much broader geographical range, including the northern USA, Alaska and Canada. Therefore, cycads inhabited a broad geographical range in which sauropods were apparently absent.

#### STATISTICAL COMPARISON OF RAW DISTRIBUTIONS USING A QUADRAT APPROACH

An overwhelming majority (98%) of our pairwise comparisons detected no significant spatial associations between dinosaur and plant groups in any of the time-slices sampled (Tables 1–7). Three comparisons yielded positive associations of marginal significance: ankylosaurs and non-bennettitalean cycadophytes during the Albian ( $P = 0.03$ ) (Table 4); iguanodontians



**Table 1.** Berriasian, statistical comparisons of dinosaur–plant distributions using Fisher’s exact test (two-tailed). Number of grid squares with co-occurrences = 10

	Cycadophytes	Cycadales	Angiosperms
Sauropods	$P = 0.52$	$P = 0.17$	N/A
Ankylosaurs	$P = 1.0$	$P = 1.0$	N/A
Stegosaurs	$P = 0.47$	$P = 0.07$	N/A
Ornithopods	$P = 0.47$	$P = 1.0$	N/A
Iguanodontians	$P = 0.2$	$P = 1.0$	N/A

**Table 2.** Barremian, statistical comparisons of dinosaur–plant distributions using Fisher’s exact test (two-tailed). Number of grid squares with co-occurrences = 17

	Cycadophytes	Cycadales	Angiosperms
Sauropods	$P = 0.64$	$P = 0.64$	$P = 0.23$
Ankylosaurs	$P = 0.62$	$P = 1.0$	$P = 1.0$
Stegosaurs	$P = 0.47$	$P = 0.51$	$P = 1.0$
Ornithopods	$P = 1.0$	$P = 1.0$	$P = 0.12$
Iguanodontians	$P = 0.35$	$P = 1.0$	$P = 0.58$
Ceratopsians	$P = 1.0$	$P = 1.0$	$P = 0.33$
Theropoda	$P = 0.62$	$P = 0.28$	$P = 1.0$

**Table 3.** Aptian, statistical comparisons of dinosaur–plant distributions using Fisher’s exact test (two-tailed). Number of grid squares with co-occurrences = 31

	Cycadophytes	Cycadales	Angiosperms
Sauropods	$P = 0.7$	$P = 0.63$	$P = 1.0$
Ankylosaurs	$P = 1.0$	$P = 0.63$	$P = 0.41$
Ornithopods	$P = 1.0$	$P = 0.61$	$P = 1.0$
Iguanodontians	$P = 0.25$	$P = 1.0$	$P = 1.0$
Ceratopsians	$P = 1.0$	$P = 0.17$	$P = 0.58$
Theropoda	$P = 1.0$	$P = 0.17$	$P = 0.09$

**Table 4.** Albian, statistical comparisons of dinosaur–plant distributions using Fisher’s exact test (two-tailed). Number of grid squares with co-occurrences = 27

	Cycadophytes	Cycadales	Angiosperms
Sauropods	$P = 1.0$	$P = 1.0$	$P = 0.25$
Ankylosaurs	$P = 0.03^*$	$P = 0.33$	$P = 0.45$
Ornithopods	$P = 0.58$	$P = 1.0$	$P = 1.0$
Iguanodontians	$P = 0.19$	$P = 0.03^*$	$P = 0.25$
Ceratopsians	$P = 0.29$	$P = 0.55$	$P = 1.0$

\*Indicates  $P < 0.05$ .

and cycads during the Albian ( $P = 0.03$ ) (Table 4); and iguanodontians and angiosperms during the Campanian ( $P = 0.04$ ) (Table 6).

Comparisons of the Maastrichtian distributions of the major dinosaur groups with one another

show multiple significant associations (Tables 8, 9). Notably, sauropods show significant negative spatial associations with hadrosaurs ( $P = 0.001$ ) and ceratopsians ( $P = 0.001$ ), and weakly significant positive spatial associations are found between hadrosaurs

**Table 5.** Cenomanian, statistical comparisons of dinosaur–plant distributions using Fisher’s exact test (two-tailed). Number of grid squares with co-occurrences = 17

	Cycadophytes	Cycadales	Angiosperms
Sauropods	$P = 0.49$	N/A	$P = 0.14$
Ankylosaurs	$P = 0.47$	N/A	$P = 1.0$
Ornithopods	$P = 0.51$	N/A	$P = 1.0$
Iguanodontians	$P = 1.0$	N/A	$P = 0.58$
Hadrosaurs	$P = 1.0$	N/A	$P = 1.0$
Ceratopsians	$P = 1.0$	N/A	$P = 1.0$

**Table 6.** Campanian, statistical comparisons of dinosaur–plant distributions using Fisher’s exact test (two-tailed). Number of grid squares with co-occurrences = 28

	Cycadophytes	Cycadales	Angiosperms
Sauropods	$P = 1.0$	$P = 1.0$	$P = 0.31$
Ankylosaurs	$P = 0.61$	$P = 0.61$	$P = 1.0$
Ornithopods	$P = 0.48$	$P = 0.48$	$P = 0.06$
Iguanodontians	$P = 1.0$	$P = 1.0$	$P = 0.04^*$
Hadrosaurs	$P = 0.25$	$P = 0.25$	$P = 0.14$
Ceratopsians	$P = 0.31$	$P = 0.31$	$P = 0.41$
Ceratopsidae	$P = 0.6$	$P = 0.6$	$P = 0.22$
Pachycephalosaurs	$P = 0.27$	$P = 0.27$	$P = 1.0$
Theropoda	$P = 0.29$	$P = 0.29$	$P = 0.37$

\*Indicates  $P < 0.05$ .

**Table 7.** Maastrichtian, statistical comparisons of dinosaur–plant distributions using Fisher’s exact test (two-tailed). Number of grid squares with co-occurrences = 34

	Cycadophytes	Cycadales	Angiosperms
Sauropods	$P = 1.0$	$P = 0.31$	$P = 1.0$
Ankylosaurs	$P = 0.71$	$P = 0.34$	$P = 1.0$
Ornithopods	$P = 0.69$	$P = 0.29$	$P = 0.1$
Iguanodontians	$P = 0.44$	$P = 0.15$	$P = 0.3$
Hadrosaurs	$P = 0.44$	$P = 0.15$	$P = 0.3$
Ceratopsians	$P = 0.47$	$P = 0.38$	$P = 0.63$
Ceratopsidae	$P = 0.47$	$P = 0.38$	$P = 0.63$
Pachycephalosaurs	$P = 0.19$	$P = 0.57$	$P = 1.0$
Theropoda	$P = 1.0$	$P = 1.0$	$P = 0.56$

and ceratopsids ( $P = 0.02$ ) and hadrosaurs and pachycephalosaurs ( $P = 0.03$ ).

## DISCUSSION

Statistical comparisons between the distributions of major Maastrichtian dinosaur clades reveal multiple significant results, both positive and negative. These results match those predicted on the basis of an a priori knowledge of the Late Cretaceous dinosaur record (e.g. Holtz *et al.*, 2004), namely they reflect

faunal provinciality, with Gondwanan faunas dominated by sauropods and Laurasian faunas dominated by ornithischians. These results validate the GIS-based quadrat methodology as a way of identifying quantitatively spatial associations in the fossil record.

The visualization of Cretaceous dinosaur and plant distribution highlights one of the major problems in testing dinosaur–plant coevolutionary hypotheses using spatiotemporal data: the plant groups of interest are widespread and have a global distribution, as do some of the dinosaur groups (e.g. sauropods,

**Table 8.** Maastrichtian, statistical comparisons of the distributions of major dinosaur clades with one another using Fisher's exact test (two-tailed)

	Sauropods	Ankylosaurs	Ornithopods	Iguanodonts	Hadrosaurs	Ceratopsians	Ceratopsidae	Pachyceph.	Theropoda
Sauropods	N/A	$P = 0.247$	$P = 0.00053^*$	$P = 0.00136^*$	$P = 0.00136^*$	$P = 0.0012^*$	$P = 0.0075^*$	$P = 0.196$	$P = 0.119$
Ankylosaurs	N/A	N/A	$P = 0.7$	$P = 0.443$	$P = 0.443$	$P = 0.062$	$P = 0.183$	$P = 0.001^*$	$P = 0.343$
Ornithopods	N/A	N/A	N/A	N/A	N/A	$P = 0.428$	$P = 0.077$	$P = 0.196$	$P = 0.119$
Iguanodonts	N/A	N/A	N/A	N/A	N/A	$P = 0.322$	$P = 0.029^*$	$P = 0.054$	$P = 0.031^*$
Hadrosaurs	N/A	N/A	N/A	N/A	N/A	$P = 0.165$	$P = 0.015^*$	$P = 0.028^*$	$P = 0.015^*$
Ceratopsians	N/A	N/A	N/A	N/A	N/A	N/A	N/A	$P < 0.0001^*$	$P = 0.001^*$
Ceratopsidae	N/A	N/A	N/A	N/A	N/A	N/A	N/A	$P = 0.0004^*$	$P = 0.007^*$
Pachyceph.	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	$P = 0.0015^*$
Theropoda	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

\*Indicates  $P < 0.05$ .**Table 9.** Maastrichtian, statistical comparisons of the distributions of major dinosaur clades with one another using chi-squared tests of association

	Sauropods	Ankylosaurs	Ornithopods	Iguanodontians	Hadrosaurs	Ceratopsians	Ceratopsidae	Pachyceph.	Theropoda
Sauropods	N/A	1.458	13.064*	10.925*	10.925*	10.567*	7.923*	N/A	N/A
Ankylosaurs	N/A	N/A	0.18	0.775	0.821	4.008*	1.88	N/A	N/A
Ornithopods	(neg, * $P = 0.0003$ )	N/A	N/A	N/A	N/A	0.686	3.74	N/A	N/A
Iguanodontians	(neg, * $P = 0.001$ )	N/A	N/A	N/A	N/A	1.301	5.119*	4.53*	5.356*
Hadrosaurs	(neg, * $P = 0.001$ )	N/A	N/A	N/A	N/A	2.29	13.154*	5.179*	6.245*
Ceratopsians	(neg, * $P = 0.001$ )	(pos, * $P = 0.045$ )	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Ceratopsidae	(neg, * $P = 0.005$ )	N/A	N/A	(pos, * $P = 0.024$ )	(pos, * $P = 0.01$ )	N/A	N/A	N/A	N/A
Pachyceph.	N/A	N/A	N/A	(pos, * $P = 0.033$ )	(pos, * $P = 0.023$ )	N/A	N/A	N/A	N/A
Theropoda	N/A	N/A	N/A	(pos, * $P = 0.021$ )	(pos, * $P = 0.012$ )	N/A	N/A	N/A	N/A

\*Indicates  $P < 0.05$ .

ornithopods), at least for part of the geological record. The ubiquitous occurrences of these groups complicate attempts to identify spatiotemporal correlations. However, this is unsurprising given the low taxonomic level at which these analyses have to be conducted. Nevertheless, visualization does provide some informative results. For example, the coevolutionary hypothesis of Bakker (1978, 1986) predicts that early angiosperms should generally be found in close spatial association with ornithopods, but not with sauropods. This hypothesis was based largely on the North American record and, for much of the Cretaceous (Albian–Maastrichtian), there is indeed incongruity between the distributions of angiosperms and sauropods, with sauropods absent from much of the area over which angiosperms occur, but not between angiosperms and ornithopods. However, this signal is clearly limited to North America as, on other continents, sauropods remain widespread and are repeatedly found in close proximity to angiosperms, as are ornithopods.

When visualized at a global level, Cretaceous distributional patterns provide little evidence in support of angiosperm–dinosaur diffuse coevolutionary hypotheses. Statistical comparisons of the distributions of angiosperms and major dinosaur groups found just one significant result: iguanodontian ornithopods and angiosperms are found in close geographical proximity more often during the Campanian than expected if they were distributed independently of one another. This result is consistent with the hypotheses of coevolution between ornithopods and angiosperms during the Late Cretaceous (e.g. Weishampel & Norman, 1989), but statistical support is marginal ( $P = 0.04$ ), is not repeated in any other time-slices and is based on small sample sizes. This result should therefore be interpreted with caution, and not considered as strong supporting evidence for coevolution at this stage.

Cycads also have a global distribution for most of the Cretaceous, and are generally found in close proximity to occurrences of their proposed dispersers, sauropods and stegosaurs, as well as to other widespread dinosaur groups (e.g. ornithopods). There are no verified records of stegosaurs from the Late Cretaceous, although occurrences of cycads and other non-bennettitalean cycadophytes are known. As discussed above, the apparent limitation of sauropods to southwest North America during the middle to Late Cretaceous provides the only clear example of an incongruity between the distribution of cycads and non-bennettitalean cycadophytes and proposed dispersers: cycads/non-bennettitalean cycadophytes occur over a wide area from which the proposed dispersers (sauropods, stegosaurs) are absent. Such a result is inconsistent with a diffuse coevolutionary

hypothesis. Nearly all statistical comparisons of cycad and dinosaur distribution are insignificant: significant spatial associations do occur between ankylosaurs and non-bennettitalean cycadophytes and between iguanodontians and cycads during the Albian. Our results are therefore potentially consistent with diffuse coevolutionary relationships between ankylosaurs, iguanodontians and cycads during the Albian (mid-Cretaceous), but the statistical support is again marginal ( $P = 0.02–0.03$ ) and not repeated in any other time-slice, and sample sizes are small. For these reasons, such results should be interpreted with caution and not considered as strong supporting evidence for coevolution at this stage.

Positive spatiotemporal correlations between dinosaur and plant groups can be cited as a basis for recognizing the potential for diffuse coevolutionary interactions (see above). By contrast, the lack of any positive correlation (i.e. the recovery of significant negative correlations or the absence of any statistically significant correlation) does not necessarily allow the rejection of coevolutionary hypotheses. The absence of spatiotemporal correlations might reflect genuine disjunctions between the distributions of the groups in question, but may also indicate that the fossil record is either too poor or too coarsely sampled to allow the recognition of positive correlations. The majority of the analyses presented herein failed to find any significant relationship between plant and dinosaur groups (Tables 1–7). As a result, diffuse coevolutionary scenarios are poorly justified on the basis of current data.

## CONCLUSIONS

This study demonstrates the utility of GIS techniques in testing macroevolutionary patterns over extended spatiotemporal scales, and represents a novel application of this methodology to evolutionary biology. Our analysis of spatiotemporal associations among major dinosaur groups demonstrates multiple statistically significant associations during the Maastrichtian, which are clearly interpretable in terms of faunal provincialism. Similar comparisons between major groups of herbivorous dinosaurs and plants (angiosperms, cycads, non-bennettitalean cycadophytes) at a global level found only three nonrepeated associations of marginal significance. We therefore conclude that there is little support from the spatiotemporal distributions of plant and dinosaur fossils for the proposed hypotheses of diffuse coevolution. Indeed, the fossil record of these two groups does not represent an adequate foundation for rigorous coevolutionary hypotheses at present. The GIS methods used here are readily applicable to a vast array of other questions whose answers are reliant on a



detailed knowledge of organismal distributions in time and space.

## ACKNOWLEDGEMENTS

This research was funded by an NERC Standard Grant (NE/C002865/1) awarded to PMB, MGP and PK. We thank three anonymous referees and Conrad Labandeira for their thoughtful comments on previous versions of the manuscript.

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