

# Testing co-evolutionary hypotheses over geological timescales using GIS

Richard J. Butler<sup>1</sup>, Paul M. Barrett<sup>1</sup>, Paul Kenrick<sup>1</sup>, Malcolm G. Penn<sup>2</sup>

<sup>1</sup>Department of Palaeontology, The Natural History Museum, Cromwell Road, London, SW7 5BD  
R.Butler@nhm.ac.uk

<sup>2</sup> Department of Botany, The Natural History Museum

KEYWORDS: Co-evolution, Cretaceous, cycads, dinosaurs, palaeontology

## 1. Introduction

Ecological and behavioural interactions between species are known to exert a strong influence on their evolution (Thompson 1994). Co-evolution occurs when two (or more) species interact with each other in such a way that the evolution of one influences the evolution of the other and *vice versa*. Co-evolutionary processes are commonly divided into ‘tight’ and ‘diffuse’ co-evolution: ‘tight’ co-evolution occurs when there is intimate ecological coupling between pairs of species (e.g. flower/pollinator) and is thought to be important in driving speciation and adaptation, while ‘diffuse’ co-evolution occurs when whole groups of species interact with other groups of species, and is thought to be a key process in shaping the evolution of communities. The significance of co-evolution over ecological timescales is well established; however, it is unclear to what extent it contributes to driving large-scale evolutionary and ecological changes over geological timescales. Many instances of putative co-evolution over geological timescales have been suggested, but few have been evaluated in detail. Here we discuss proposed dinosaur/plant diffuse co-evolution during the Cretaceous period (145-65 million years ago [mya]), focusing in particular on dinosaur/cycad interactions, and the use of GIS as a tool to explore co-evolutionary hypotheses over geological timescales.

### 1.1 Dinosaur/plant co-evolution

Numerous hypotheses of dinosaur/plant co-evolution have been proposed, the best known of which implicates dinosaurs in the origin/radiation of angiosperms (flowering plants) in the Cretaceous (Bakker 1978; Barrett and Willis 2001). Another set of co-evolutionary hypotheses links dinosaurs and cycads (e.g. Watson and Cusack 2005; Mustoe 2007). Cycads are evergreen, insect-pollinated, seed plants with large cones and toxic foliage; in modern ecosystems cycads are of low diversity (10-12 genera) and confined largely to tropical/subtropical regions. Cycads have a long fossil record, extending at least to the Permian (250 mya), and appear to have been more abundant and diverse in the Mesozoic (Triassic, Jurassic and Cretaceous periods) than at present. Co-evolutionary interactions with dinosaurs are proposed to have driven Mesozoic cycad diversification: various groups of herbivorous dinosaurs, particularly the long-necked, large-bodied sauropodomorphs, are suggested as key dispersal agents for cycad seeds. The decline of such dinosaur groups during the Cretaceous is cited as one explanation for cycad decline (Mustoe 2007). Our ongoing work is evaluating hypotheses of dinosaur/cycad interactions using a range of approaches, including GIS.

### 1.2 Use of GIS in palaeontology and co-evolutionary analysis

To date, the palaeontological applications of GIS have been limited; most commonly it has been used to create geospatial databases of fossil localities, but a small number of successful analytical studies have also been published (e.g. Rode and Lieberman 2004; Rayfield et al. 2005). The advantage of using a GIS for palaeontological datasets is that it is possible to rapidly (and easily) integrate palaeobiological, palaeoenvironmental and geological data with a temporal series of maps showing former continental positions (palaeogeographical maps) – this allows identification of spatiotemporal patterns in the distributions of organisms and their environments (e.g. Rayfield et al. 2005). If two taxonomic groups are undergoing diffuse co-evolution their distributions should be closely associated both spatially and temporally; the identification and/or falsification of such spatiotemporal

associations can be carried out by using GIS to compare distributions of two or more taxonomic or palaeoecological groupings.

## 2. Methods

Global occurrences of Cretaceous herbivorous dinosaurs were compiled as a GIS-compatible relational database in Microsoft Access; data was collected from the primary literature, based upon references cited in Weishampel et al. (2004), as well as more recent references and *The Paleobiology Database* ([www.paleodb.org](http://www.paleodb.org)). Faunal information was collected for each locality and combined with data on palaeoecology (e.g. body mass, feeding behaviour), geological age, lithology and palaeoenvironment. For each geological formation yielding herbivorous dinosaur material, we collected information (systematics, physiognomy, palaeoenvironments) on macrofloras and palynofloras from the primary literature. At present, this database contains 9098 fossil occurrences at 1952 localities, representing 407 dinosaur taxa, and over 2300 macrofloral taxa.

We imported our database into ArcGIS 9.1, plotting the data onto palaeogeographical maps, shapefiles for which are available for six different Cretaceous timeslices (Scotese 2001). Modern day latitude–longitude coordinates for database localities were converted to palaeolatitude–longitude coordinates at intervals corresponding to the available palaeogeographical maps using PointTracker software (Scotese 2004). For each of the twelve Cretaceous temporal subdivisions (‘stages’) we used attribute selection to create new data layers (on appropriate palaeogeographical maps) displaying occurrences from that temporal stage of: a) cycads; b) ‘cycadophytes’ (cycads and cycad-like fossil groups); c) various groups of dinosaurs including Sauropodomorpha, Ankylosauria, Ornithomimidae, and Ceratopsia. Overlaying occurrence data allows visual comparison of the spatial distributions of two groups within a time-slice. In areas in which sampling of the fossil record was good we digitised a polygon to create a minimum palaeobiogeographic range that included all occurrences of that taxonomic/paleoecological grouping – construction of minimum range polygons for two or more groups allows comparison of the degree of range overlap between two groups. The absence of range overlap between two groups proposed to be co-evolving falsifies that co-evolutionary hypothesis on the basis of available fossil data; conversely, repeated and extensive range overlap is consistent with a co-evolutionary hypothesis.

## 3. Results and Directions

Preliminary analyses and results highlight two major problems in assessing dinosaur/cycad co-evolutionary hypotheses: 1) the Cretaceous plant fossil record is relatively incomplete spatially and temporally, with the northern hemisphere being notably better represented than the southern hemisphere; as a result, cycad ranges can only be assessed for a relatively small number of stages and geographic areas (notably the Late Cretaceous of North America); 2) true cycad foliage is difficult to distinguish from ‘cycadophytes’, which include specimens probably assignable to the extinct plant group Bennettitales, thus complicating attempts to determine ranges. Cycads have a near global distribution during the Cretaceous, and are most abundant during the early part of the Cretaceous (Berriasian-Hauterivian; 145-130 mya). Co-evolution is therefore not supported for dinosaur groups which are temporally and/or geographically restricted (e.g. Pachycephalosauria, Late Cretaceous of East Asia/North America). One of the most interesting results concerns the latest Cretaceous (Campanian-Maastrichtian; 83-65 mya) of North America; in this timeslice both plant and dinosaur records are well sampled geographically. Sauropodomorphs are geographically restricted in this timeslice to the SW of the United States, and do not range into the northern United States or Canada; by contrast, records of cycads from this timeslice are largely limited to the northern United States or Canada, and the ranges of sauropodomorphs and cycads do not appear to extensively overlap. This is inconsistent with the hypothesis of sauropodomorph/cycad co-evolution, whereby sauropodomorphs were the major dispersers of cycad seeds (Mustoe 2007).

Other analytical approaches also yield results inconsistent with co-evolutionary hypotheses: for example, diversity analyses indicate a major extinction of sauropodomorphs at the Jurassic/Cretaceous boundary (145 mya), but this extinction event preceded the beginnings of cycad decline by around 10 million years, and cycad decline actually begins just as sauropodomorphs (and

other groups potentially capable of dispersing cycad seeds, such as primitive birds) are beginning to recover, radiate and diversify. These results suggest that although dinosaurs *may* have acted as dispersal agents for cycad seeds, there is little evidence at present that cycad diversity was reliant on dinosaur diversity and *vice versa*. Ongoing work will continue to use GIS to explore patterns of spatiotemporal diversity in cycads and dinosaurs, as well as exploring other co-evolutionary hypotheses, such as those relating to angiosperm origins. For instance, we plan to use indicator kriging to interpolate from available data, and subsequently carry out statistical tests of correlation between dinosaur/cycad distributions, using approaches that attempt to account statistically for spatial autocorrelation (e.g. Rangel et al. 2006).

#### 4. References

- Bakker RT (1978) Dinosaur feeding behaviour and the origin of flowering plants *Nature* **274** pp661-663
- Barrett PM and Willis KJ (2001) Did dinosaurs invent flowers? Dinosaur-angiosperm coevolution revisited *Biological Reviews* **76** pp411-447
- Mustoe GE (2007) Coevolution of cycads and dinosaurs *The Cycad Newsletter* **30** pp6-9
- Rangel TFLVB, Diniz-Filho JAF and Bini LM (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography *Global Ecology and Biogeography* **15** pp321-327
- Rayfield EJ, Barrett PM, McDonnell RA and Willis KJ (2005) A Geographical Information System (GIS) study of Triassic vertebrate biochronology *Geological Magazine* **142** pp327-354
- Rode AL and Lieberman BS (2004) Using GIS to unlock the interactions between biogeography, environment, and evolution in Middle and Late Devonian brachiopods and bivalves *Palaeogeography, Palaeoclimatology, Palaeoecology* **211** pp345-359
- Scotese CR (2001) *Earth System History Geographic Information System v. 02b*. PALEOMAP Project, Arlington, Texas.
- Scotese CR (2004) *PointTracker v. 04c*. PALEOMAP Project, Arlington, Texas.
- Thompson JN (1994) *The Coevolutionary Process*. Chicago University Press, Chicago.
- Watson J and Cusack HA (2005) Cycadales of the English Wealden *Palaeontographical Society Monographs* **622** pp1-189
- Weishampel DB, Dodson P and Osmólska H (2004) *The Dinosauria, 2nd Edition*. University of California Press, Berkeley.

#### Biography

*Dr Richard Butler is a postdoctoral researcher funded by the award of a NERC Standard Grant (NE/C002865/1) to PMB, PK and MP. His PhD was carried out at the University of Cambridge, and his research focuses on dinosaur evolution and the testing of macroevolutionary hypotheses using quantitative analytical techniques, including GIS.*