



# Diversity and faunal changes in the latest Cretaceous dinosaur communities of southwestern Europe



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## ABSTRACT

Characterization of macroecological patterns for latest Cretaceous dinosaur communities is essential to understand how those faunas were changing during the run-up to the Cretaceous–Paleogene extinction event, and thus the cause of the extinction. Outside of the well-studied latest Cretaceous dinosaurs of North America, southwestern Europe (France, Spain and Portugal) preserves one of the richest end-Cretaceous dinosaur fossil records, as it has produced hundreds of dinosaur fossil localities. We compiled a comprehensive database of all dinosaur fossil occurrences from the uppermost Cretaceous of the Ibero-Armorican region and analyze it statistically, providing the first numerical study of the ecological and taxonomic diversities of these communities. Our study corroborates previous work that has identified a major faunal change in the latest Cretaceous terrestrial vertebrate assemblages, and places this event around the C31r–C31n reversal, in the early late Maastrichtian (c. 69 Ma). Significant differences in ecological diversity metrics (dominance, Shannon and Simpson) characterize the pre- and post-turnover assemblages. The turnover event, therefore, did not only lead to a taxonomic replacement but also important reorganizations in the structure of dinosaur communities. Herbivorous dinosaurs suffered the most dramatic alterations across the turnover, in terms of relative dominances, by shifting their contributions within the communities (hadrosauroids replacing titanosaurs as the dominant taxon in the medium-to large-bodied herbivore niche) or even disappearing (rhabdodontids and nodosaurids). The carnivores apparently maintained similar relative abundances before and after the turnover, and the relative proportions between carnivorous and herbivorous taxa remained static through time. Further improvement of the present database might allow for the identification of new ecological patterns, and higher-resolution comparison with the North American records.

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## 1. Introduction

One of the central goals of ecology is to understand patterns of diversity and faunal abundance (Brown, 1995), not only in extant ecosystems but also in extinct ones. Research in this area often relies on the analysis of macroecological patterns that describe aspects of community structure. The relative abundance of organisms provides keystone information into the commonness and rarity of taxa within a community, and patterns of biodiversity through time and space. Information on community composition, and ecological and taxonomic diversity, can be provided from

multi-taxon assemblages of fossils. In some cases, such fossil assemblages can give critical insight into how communities changed during mass extinction events, which has relevance to understanding how modern ecosystems may be affected by climate and environmental changes.

In this regard, the extensive vertebrate fossil record of the Late Cretaceous formations of southwestern Europe, with hundreds of localities and specimens collected (Csiki-Sava, Buffetaut, Ósisi, Pereda-Suberbiola, & Brusatte, 2015; Weishampel et al., 2004), offers a unique opportunity to assess ecological patterns in dinosaur communities before the Cretaceous–Paleogene extinction event. The so-called Ibero-Armorican domain, the biggest island of the European archipelago in Late Cretaceous times, was the paleogeographical setting where these dinosaur faunas evolved from the late Campanian to the latest Maastrichtian. What is

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particularly important about the Ibero-Armorican dinosaur assemblage is that it is one of the few good records of how dinosaurs changed during the latest Cretaceous, outside of the classically studied Campanian-Maastrichtian sequences of western North America. Therefore, it provides a valuable test of whether ecological and extinction patterns recorded in North America are a global (not merely local) phenomenon, and offers insight into how latest Cretaceous dinosaurs living in the unusual island environment of Europe dealt with the global changes around the Cretaceous–Paleogene boundary.

Several studies have focused on characterizing dinosaur assemblages during the last ten millions of years of the Cretaceous in the Ibero-Armorican region of Europe (Buffetaut & Le Loeuff, 1991; Company, Pereda-Suberbiola, & Ruiz-Omeñaca, 2009; Csiki-Sava et al., 2015; Laurent, 2003; Le Loeuff, Buffetaut, & Martin, 1994; López-Martínez, 2003; Pereda-Suberbiola, Company, & Ruiz-Omeñaca, 2004; Pereda-Suberbiola et al., 1999; Riera, Oms, Gaete, & Galobart, 2009; among others). Most of them have noted the apparent dominance of some taxonomic groups of dinosaurs relative to others, which changed over time. For example, Le Loeuff et al. (1994) stated that “an early Maastrichtian fauna dominated by titanosaurid sauropods was replaced by a late Maastrichtian assemblage dominated by hadrosaurs”. This faunal turnover hypothesis was based on analysis of the fossil record from restricted areas of the Ibero-Armorican domain, mainly from the French Pyrenees. Later works from other regions supported this hypothesis but pointed out that titanosaurid sauropods persisted until the end of the Maastrichtian alongside an abundant population of hadrosauroids (Canudo, 2001; Laurent, Bilotte, & Le Loeuff, 2002; López-Martínez et al., 2001; Riera et al., 2009; Vila et al., 2012, 2013). Apart from the clear patterns characterizing these two major groups of herbivorous dinosaurs, the turnover pattern seems to be more complex since it involves two additional herbivore groups (nodosaurid ankylosaurs and rhabdodontids or ornithomimids) as well as a distinct fauna of carnivorous theropods (mainly abelisaurid and dromaeosaurid taxa) which is still poorly known (Canudo & Ruiz-Omeñaca, 2003; Csiki-Sava et al., 2015; Riera et al., 2009; Sellés, Vila, & Galobart, 2014a; Torices, Currie, Canudo, & Pereda-Suberbiola, in press; Tortosa et al., 2014). Nevertheless, these previous studies on faunal composition and abundance have been based only on analysis of apparent frequency and occurrence of taxa in a particular time interval or geographic region, but no numerical data have been provided so far for the whole Ibero-Armorican dinosaur record, nor has such data been analyzed statistically to quantify macro evolutionary and ecological patterns.

The main goals of the present study are to provide a more accurate timing for the latest Cretaceous Ibero-Armorican dinosaur turnover and the first numerical characterization of the latest Cretaceous dinosaur communities of southwestern Europe in terms of ecological and taxonomic diversity. This quantitative assessment will focus on the faunal communities existing before and after the turnover, and will give insight into the ecological dynamics of the dinosaur communities before the Cretaceous–Paleogene extinction event. This will provide information on how dinosaurs reached the extinction event in the largest paleogeographic region of Europe, far away from where the asteroid hit in Central America and from western North America, where latest Cretaceous dinosaurs have been studied in the most detail.

## 2. Methodology

We gathered information from the literature and first hand observations to construct a comprehensive database containing all dinosaur fossil occurrences in the upper Campanian–Maastrichtian

from three main sampling areas in southwestern Europe (Pyrenees, Iberia and Provence). Information on each fossil occurrence includes the name of the site, the stratigraphic age, the geologic formation, the type of evidence (skeletal, eggs, tracks), and the taxonomy of the remains. We used “locality” to refer a discrete area or stratigraphic section where fossils occur and which may or may not include various sites. A “site” refers to a discrete fossil-bearing level within a locality. When possible, all the taxonomic identifications have been ascribed to what are commonly held to be familial (Titanosauridae, Nodosauridae, Rhabdodontidae) or suprafamilial (Hadrosauroidea) ranks, except for the theropods, which have been pooled into two general categories: “large theropods” and “small theropods” categories. The current record of theropods is limited and it is difficult to ascribe the known fossils to higher-level clades, hence our conservative grouping of theropods into two general size-related categories. We hope that future work will reveal a larger sample of easier-to-classify theropods. Up to 126 sites have been ruled out from the database due to the lack of information on some of these criteria. The complete dataset used herein is available in the supplementary material.

The minimum number of individuals (MNI) of each group was estimated for different temporal and geographic bins. Calculation of the MNI was performed on the basis of reports and descriptions of skeletal evidence (bones and teeth) in the literature. For bones, MNI is calculated on (a) counts of a single occurrence at a particular site, (b) counts of the most abundant, non-replicated element present from one side of the body or (c) counts “determined by joint consideration of the skeletal parts represented” in terms of size or age characteristics (Badgley, 1986). This is, more than one individual is considered at a single site only if an element is replicated or if a significant size variation exists between the elements of the fossil association. Estimates of MNI by using teeth are highly problematic but for theropods (where most of the evidence corresponds to isolated shed teeth) it is the only way to estimate their relative abundance. Thus, we assumed that each distinguishable quantitative morphotype occurring in a certain site corresponds at least to a single individual, irrespective of the number of specimens collected. We recognize that this procedure will almost certainly underestimate MNI in this clade, because while most sites provided a few number of isolated teeth some other sites yielded a richer sample (e.g. Laño quarry), which probably indicates a larger number of individuals represented. The issue with theropods is probably a more general concern: the fragmentary and usually disarticulated nature of most of the specimens in the Ibero-Armorican record means that the actual number of individuals in the sample is probably underestimated (Badgley, 1986). Finally, we ruled out the use of tracks or eggs for MNI counts because a single individual could have produced several of these remains. Regarding counts of sites, we counted each site only once, irrespective of the number of occurrences or individuals present.

Diversity differences between time bins and geographic regions were analyzed statistically in PAST v3 (Hammer, Harper, & Ryan, 2001). Three sets of comparisons were made: 1) overall dinosaur diversity in the Ibero-Armorican domain between the “pre-turnover” and the “post-turnover” time intervals; 2) geographic diversity between the Pyrenees, Iberia, and Provence sub-regions during the “pre-turnover” time interval (cf. late Campanian–early Maastrichtian interval); 3) geographic diversity between the same sub-regions during the “post-turnover” time interval (cf. late Maastrichtian). The “pre-turnover” and “post-turnover” bins refer to the times intervals before and after the turnover event that occurred sometime around, but not strictly in, the early Maastrichtian–late Maastrichtian boundary (see below). Because there clearly was a turnover in latest Cretaceous European faunas, we feel that this scheme is a more useful way of binning taxa to

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