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# Habitat preference of the dinosaurs from the Ibero-Armorican domain (Upper Cretaceous, south-western Europe)

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**Abstract**

Paleoenvironmental preferences for Cretaceous dinosaurs at a regional scale have been mainly assessed in North America. In south-western Europe, the dinosaur-bearing formations ranging the late Campanian to the latest Maastrichtian encompass coastal and lowland environments that produced hundreds of fossil localities with evidence of titanosaurian sauropods, maniraptoran and abelisauroid theropods, and nodosaurid ankylosaurs, together with rhabdodontid and hadrosauroid ornithopods. In order to study environmental associations of dinosaur taxa, we have revised, updated, and expanded upon an existing database that compiles the occurrence and minimum number of individuals for the dinosaur-bearing formations spanning the upper Campanian to the uppermost Maastrichtian of South-Western Europe. Based on this database, the habitat preferences of dinosaur groups in the region were determined by means of statistical tests of independence. All chi-square tests showed positive, mostly moderate-to-strong, and statistically significant associations between the studied groups and the environment they inhabited. The analysis of the residuals indicated that most dinosaur groups preferred lowland environments (including, contrary to previous studies, nodosaurids). The only exception were abelisauroids, which showed no habitat preference. Our results concur with recent works indicating that titanosaur sauropods and hadrosauroids preferred inland environments but clearly disagree with others suggesting that the latter as well as nodosaurid ankylosaurs were positively associated with marine or coastal settings. Considering the changes in occurrence distribution throughout the Maastrichtian turnover in the region, both titanosaurians and nodosaurids probably stablished a feeding strategy-based niche partitioning with ornithopods, although additional data is required to confidently confirm this relationship.

**Keywords** Dinosaur, Habitat, Cretaceous, Sauropoda, Hadrosauroidea

## Introduction

The habitat preferences of the members of a paleocommunity are an important aspect for understanding ancient ecosystems. Such preferences add to the understanding of the life history of a taxon, including its diet, spatial distribution, and the relationships with other coexisting organisms (e.g. such as the presence of niche partitioning among taxa) (Arbour et al., 2016; Fiorillo et al., 2016; Lyson & Longrich, 2011; Mallon, 2019; Mallon et al., 2012; Mannion et al., 2012; Rees et al., 2004).

In the case of extant organisms, the most common approach to ascertain the habitat preference of each clade in a community is to count the taxa present in

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the different habitats of the ecosystem (Chiarenza et al., 2019). These spatial distributions are complemented with the associated environmental conditions, illustrating the distribution of the organism among regional environments. Subsequently, statistically significant habitat-taxon relationships inform on the preferred setting, where organisms would spend more time during a year.

Implementing this procedure to extinct communities, such as those of Late Cretaceous dinosaur-dominated ecosystems is challenging due to the preservation and sampling biases inherent to the incomplete nature of the fossil record (Benson et al., 2013; Butler et al., 2011; Mannion et al., 2013; Moore et al., 2007; Upchurch et al., 2011 and references there in). For example, North America has hitherto the most sampled, accurately dated, and stratigraphically continuous record of Upper Cretaceous dinosaurs. And yet, this region presents latitudinal and longitudinal sampling biases that have not been addressed until recently (Chiarenza et al., 2019). Despite that, North American dinosaur paleocommunities and their habitat preferences have been regarded as representative of global dinosaur populations and even as an indication of their decline during the Late Cretaceous (Butler & Barrett, 2008; Mannion & Upchurch, 2010). This notion, however, has been challenged in light of recent studies that characterised contemporary paleocommunities around the globe (Arbour et al., 2016; Benson et al., 2013; Chiarenza et al., 2019; Vila et al., 2016). During the latest Cretaceous, present-day regions of Portugal, Spain and southern France comprised the emerged territories of what once was Ibero-Armorica, the largest island of the Late Cretaceous European Archipelago. In the last three decades, the knowledge of the dinosaur fossil record in this region has increased significantly and geologic formations ranging from the late Campanian to the latest Maastrichtian yielded hundreds of fossils distributed in various environmental settings. The performance of accurate geologic, stratigraphic and paleontologic studies conducted at the region has provided an enormous amount of information that allows for characterizing changes in the composition of dinosaurian communities during the Maastrichtian (Fondevilla et al., 2019). Although the chronostratigraphy of the vertebrate assemblages in Ibero-Armorica have been studied thoroughly in recent years (e.g. Fondevilla et al., 2016, 2019; Pérez-Pueyo et al., 2021; Puértolas-Pascual et al., 2018), the habitat preferences of dinosaurs have received little attention (Vila et al., 2014).

Here, we ask whether the habitat preferences hypothesised in previous studies (Arbour et al., 2016; Butler & Barrett, 2008; Mannion & Upchurch, 2010) for the main Late Cretaceous dinosaur groups in large continental landmasses are applicable to their representatives from the Ibero-Armorican island, despite differences in scale, the possible effects of insularity, and sample size. In addressing this question, we aim to update the distribution of the Ibero-Armorican dinosaur groups during the Late Cretaceous and statistically test for possible habitat preferences among Ibero-Armorican dinosaurs.

## Materials and methods

### Data collection

We updated and expanded upon the database of Vila et al. (2016) by compiling data from literature used in the original file, together with more recent publications, for each Ibero-Armorican fossil locality. The resulting updated database includes 747 dinosaur occurrences distributed among 505 fossil sites in 215 fossil localities from 28 Iberian and French geological formations. We used the terms “locality” and “site” as defined by Vila et al. (2016). Each entry includes information on the name of the locality, the stratigraphic age, the geologic formation, the type of fossil evidence (osteological, ichnological, and oological), the taxonomy of the remains, and geological setting, together with its paleoenvironmental interpretation (Supplementary Information). Major changes and additions refer to the dating of several localities (especially in French localities) and their paleoenvironmental interpretation, but also to updates in taxonomy and the counts of the minimum number of individuals (MNI). Selected groups consist of the major dinosaur clades present in Ibero-Armorican terrestrial ecosystems during the latest Cretaceous (late Campanian to latest Maastrichtian). Whenever possible, and as in similar paleoecological studies (Arbour et al., 2016; Butler & Barrett, 2008; Mannion & Upchurch, 2010; Vila et al., 2016), taxonomic identifications have been referred to familial and suprafamilial taxonomic ranks: titanosaurian sauropods, hadrosauroid and rhabdodontid ornithopods, nodosaurid ankylosaurs, as well as maniraptoran and abelisauroid theropods. Two different frequency counts were compiled following Vila et al. (2016): (1) occurrences, which count the presence of a taxon or group in a locality for each type of environment; and (2) MNI of a taxon present in each environment (Supplementary Information; Table S1).

Definitions of paleotopographical settings follow Hornung et al. (2023) and environments have been categorised as either coastal (paralic environments with marine influence such as deltas, shallow lagoons, tidal flats, and swamps) or lowland (inland environments with none or sporadic marine influence such as lacustrine lagoons, lower reaches of rivers, and alluvial plains). Additionally, the number of dinosaur occurrences was organised into three types of fossil remains (osteological, oological and icnological) and two time bins (Time Bin 1: late

Campanian-early Maastrichtian; Time Bin 2: late Maastrichtian). Categorising the occurrences in this manner allowed to assess the effects of both the faunal turnover described in the region (Fondevilla et al., 2019; Vila et al., 2016), and how the proportion of counts, as well as the preservational and taphonomical biases of each fossil type informs on the interpretation and determination of habitat preferences. To evaluate the possible effects of the Maastrichtian turnover on dinosaur habitat preferences, we performed chi-square tests without time-bins (late Campanian-late Maastrichtian, henceforth Time Bin 1 + 2) and two time-binned tests (late Campanian-early Maastrichtian and late Maastrichtian, henceforth Time Bin 1 and Time Bin 2, respectively).

Although skewed, both the ichnological and oological records add their own nuances to the interpretation of the habitat preference. Compared to the osteological record (bones and teeth), the usually lower and/or and taxonomically biased sample size of footprints and eggs hinders the possibility to perform time-binned analyses. Instead, tests performed on these two record types included the osteological record occurrences together with either the oological or the ichnological record, so sample size would be enough for the result to be statistically significant while keeping the differences of each record type recognisable. Tests were conducted separately for each record type, as well as considering all three as a whole using the number of occurrences (Table 1).

## Statistical analysis

We performed chi-square ($\chi^2$-test) and Fisher's exact tests implemented in the R statistical framework (v. 4.3.0) (Supplementary Information), with a significance level of 0.05 (confidence interval of 95%), to quantitatively infer the existence of any environmental association for each group, using the occurrence and MNI data. The null hypothesis is that no relationship existed between the categorical (and independent) variables.

The chi-square ($\chi^2$) test determines if there is a statistically significant association among clades and their paleoenvironment. It determines whether these groups were equally distributed between both environments or whether they were overrepresented in one environment over the other; Butler and Barrett (2008). A positive or negative significant association between a clade and an environment indicates that its occurrences in that environment are significantly greater or fewer, respectively, than expected if all clades are spread evenly across both environments. Alternatively, the lack of a significant association indicates that the number of occurrences in that environment do not differ significantly from those predicted by simple probability models, indicating no preference for any particular habitat). Considering that it is better optimised for small samples, the Fisher's Exact test was used whenever the sample size for a chi-square test was too small to obtain a statistically significant result. However, Arbour et al. (2016) indicated that chi-square tests are better suited for similar paleoecological analyses than Fisher's exact test because the latter assumes that both the row and column marginals (or total values) of the table are fixed and predetermined, which is not the case for our contingency tables. The results of these correlation tests are reported in the Supplementary Information.

The Bonferroni-Holm and Cramer's V post-hoc correction tests were also applied to the chi-square tests. As in the chi-square test to which is applied, the Bonferroni-Holm correction (Holm, 1979) performs pairwise comparisons, albeit using a lower significance level. This is because the correction divides the original significance p-value of 0.05 by the total number of analyses, reducing the probability of incorrectly attributing significance

**Table 1** Results of the Chi-square ($\chi^2$-test) and Fisher's exact tests

| Number | Time period | TEST | C | F | B | V (DF = 5–3) | Effect size | Result |
|---|---|---|---|---|---|---|---|---|
| 1 | Time Bin 1 + 2 | Total MNI | 0.0064 | 0.0085 | 0.006 | 0.18 | Moderate | Support for a preferent group-environment relationship |
| 2 | | Total occurrences | 0.0047 | 0.0020 | 0.005 | 0.14 | Moderate (0.15) | |
| 3 | | Type of Fossil: Osteological and ichnological record | 9.71E−09 | 0.0004998 | 9.71E−09 | 0.33 | Strong | |
| 4 | | Type of Fossil: Osteological and oological record | 3.04E−03 | 0.002999 | 3.04E−03 | 0.15 | Moderate | |
| 5 | Time Bin 1 | Total occurrences | 3.29E−03 | 0.001499 | 3.29E−03 | 0.17 | Moderate | |
| 6 | Time Bin 1 + 2 | Type of Fossil: Osteological record | 1.05E−01 | 0.1259 | 1.05E−01 | 0.16 | Moderate | Support for group-environment independence |
| 7 | Time Bin 2 | Total occcurrences | 3.41E−01 | 0.2664 | 3.41E−01 | 0.13 | Weak (DF = 3, < 0.17) | |

B: Bonferroni-Holm adjusted p-value; C: Chi-square p-value; DG: degrees of freedom; F: Fisher's Exact Test result; MNI: Minimum number of individuals; V: Cramer's V statistic to our pairwise comparisons (Mannion & Upchurch, 2010). Meanwhile, the Cramer's V correction test is a statistic that evaluates the strength of a chi-square significant association (contingency tables must be larger than 2 × 2) by transforming the chi-square statistic into a value between 0 and 1 (no association and perfect association, respectively) (Kim, 2017; Kumar et al., 2014). Because the contingency tables used for statistical analysis were larger than 2 × 2, Cramer's V may be affected by the larger number of marginals and, as explained by Sharpe (2015), underestimate the size effect in the chi-square tests and therefore the strength of the significant associations. However, based on the degrees of freedom (DF) of the contingency tables used for chi-square testing and the effect size interpretation of Cramer's V from Kim (2017), when the latter statistic is higher than 0.22 (considering that our tests have at most five degrees of freedom), the association is considered strong.

In cases where a chi-square test supported an association clade-environment, but the occurrences (or MNI) were similarly distributed between both settings, the analysis of calculated residuals (Haberman, 1973; Shan & Gerstenberger, 2017) was used to evaluate whether the observed frequencies of a group were skewed towards an environment. Thus, whereas the chi-square test determines whether is there an association between clade and environment, the analysis of the residuals specifies whether the association is with a lowland or coastal setting. This in turn indicates the preferred habitat where a group would spend significantly more time during the year. Frequencies similarly distributed between settings are indicative of an ambivalent presence of a group in both environments (Haberman, 1973). The raw residuals were calculated by subtracting the expected values from the observed occurrences for each clade-environment combination. Following Sharpe (2015), we then obtained the standard deviation and both the standardised and the adjusted standardised residuals (see Supplementary Information). Considering that the latter are more statistically reliable than the former (Shan & Gerstenberger, 2017), we used the values of the adjusted standardised residuals for our interpretations. According to Haberman (Haberman, 1973), the residuals determine how much a cell of the tested contingency tables (in our case, a clade-environment pair) contributed to the chi-square results. Thus, when the residuals are close to zero, the observed frequency of that cell was close to the expected frequency (no significant relationship of a clade with that environment). Positive residuals indicate a higher observed frequency than expected. This means that the clade is overrepresented in that environment (preferred habitat). Negative residuals indicate a lower frequency than expected, meaning that the clade was underrepresented in that environment (unfavourable conditions, less time spent there). Residuals with values greater than two are usually considered to be significantly deviated from the expected frequencies (Haberman, 1973; Sharpe, 2015).

Then, by calculating the absolute value of the difference between the residuals produced by coastal/lowland environments for a given clade, the cell with a greater difference (thus indicating a greater frequency of occurrences) points towards its habitat preference. These values were obtained for all the time bins to observe changes throughout the Late Cretaceous (Supplementary information; Table S1).

## Results

Nearly all chi-square tests based on number of occurrences and MNI counts supported a positive and statistically significant association between dinosaur groups and the environment they inhabited (Table 1). Exceptions were those tests based on the smallest sample sizes (test 6 and 7). By splitting the sample into stage-level time bins or type of fossil record, both tests showed that a reduced sample size influences the statistical reliability of our results. Additionally, test 6 (osteological occurrences) was regarded as an osteological evidence-only reference or control test; its results comparable to those of the tests that combine osteological evidence with a second type of fossil record (e.g. osteological and oological, test 4) in order to increase sample size, and thus statistical reliability. Therefore, the acceptance of the null hypothesis for both tests was derived from insufficient sample size, especially considering the statistical strength of the results in similar tests. For the sake of simplicity, this pair of tests were not considered in the remainder of the results section.

All other tests showed a statistically significant relationship ($p < 0.05$) between dinosaur groups and environments, with p-values ranging from 9.71E−09 (test 3) to 0.0064 (test 1). Significant associations ($p < 0.05$) were also obtained when the Fisher's exact test was performed onto all datasets in case sample sizes were too small for the correct estimation of chi-square tests, as in test 6.

All the statistically significant chi-square results remained as such after applying the Bonferroni-Holm correction (Holm, 1979). The Cramer's V statistic shows that the strength of these positive associations between dinosaur groups and environment varies among tests, from mostly moderate to strong statistical significance (Kim, 2017), being test 3 the one with the strongest association ($0.33 > 0.22$ or limit for strong associations with $DF = 5$) and test 7 the one with the weakest ($0.13 < 0.17$ or limit for moderate associations with $DF = 3$).

The analysis of the adjusted standard residuals (Supplementary Information, Table S1) for all chi-square tests also indicates significant positive associations between dinosaur groups and environments. Specifically, all the tested groups showed a moderate-to-strong statistical overrepresentation in at least one environment indicative of habitat preference. However, abelisauroids did not show a preference for either setting in all the tests where the clade was evaluated by itself. All other Ibero-Armorican dinosaur groups showed a habitat preference skewed towards inland environments for all tests. The only exceptions were the preference of titanosaurians for coastal settings in test 1 (MNI-based counts) and the lack of preference for nodosaurids in test 7 (Time Bin 1 + 2).

Based on the counting of raw occurrences in our database we can analyse the distribution of the Ibero-Armorican dinosaur groups. When considering the most inclusive test (test 2, total occurrences in Time Bin 1), all groups are present in both environments, with rhabdodontids and titanosaurians showing a similar, lowland-preferent distribution (1:4). Hadrosauroids displayed a similar lowland-preferent distribution, although they were slightly more present in coastal environments than rhabdodontids (3:7). Nodosaurids were mostly restricted to lowland habitats (1:9). Theropods were widespread between both environments (1:1), with maniraptorans more skewed towards inland settings (2:3). When residuals in a cell were found to be negative (meaning that the group is underrepresented in that environment) or close to zero (indicating no preference for that environment), those cells were adjacent to cells with large residuals (> 2) corresponding to associations with another setting, and therefore representing a clear preference for one environment over the other (Table S1). If the difference between residuals was close to zero (< 1), then the clade showed preference for neither environment.

## Discussion

Nearly all chi-square tests support the existence of clade-environment associations, although such relationship was weakest for test 2 (Table 1). This is not surprising, considering that the corresponding contingency table included the total number of occurrences for all dinosaur groups in the late Campanian-late Maastrichtian time bin (Time Bin 1 + 2) and for all types of fossil record (osteological, ichnological, and oological). Despite being one of the weakest, the strength of the association based on this highly generalistic test is considered as weak-to-moderate, given that its Cramer's V statistic (0.14) is near the lower threshold (0.15) for moderate-strength associations when the tested contingency tables have DF = 4. Additionally, it is worth mentioning that, when counting the frequency of a taxon or group in an environment, the MNI-based counting tends to overestimate it in comparison with counting the total number of osteological occurrences (MNI > osteological occurrence), since the MNI counts each representative of a group in a single locality (counts ≥ 1), while occurrence-based counts consider that a group is only either present (count = 1) or absent (count = 0) in a locality. Therefore, when MNI was used as a proxy for the osteological record instead of total osteological occurrences, sample size was not perfectly translatable between them. From a statistical standpoint, each of these frequency counts has its benefits and disadvantages (Mannion & Upchurch, 2010). Considering the results of the analysis of the residuals, the raw distribution of Ibero-Armorican dinosaur groups has been characterised by obtaining the percentage of fossil findings for each group per environment.

### Titanosaurian sauropods

Ibero-Armorica is one of the few regions in the world where the titanosaurian record includes a comprehensive spectrum of fossil evidence, from direct evidence (bones) to indirect evidence (eggs and tracks) in both coastal and lowland environments. Although the group was present in both environments (almost one coastal occurrence per every four inland) we found statistical support for titanosaurians preferring lowland habitats (Fig. 1), in agreement with Butler and Barrett (2008), Mannion and Upchurch (2010), Fricke et al. (2011), Vila et al. (2014), and Hornung et al. (2023).

Due to the inclusion of 50 individuals from the paralic locality of Fumanya, the aforementioned overestimation of osteological occurrences derived from the use of the MNI tipped the balance towards a coastal preference for titanosaurs in test 1, while the count based on total occurrences (osteological evidence, oological and ichnological evidence) points towards a preference for lowland settings, as do all other test. The observed overrepresentation suggests that titanosaurians spent longer periods of time in the lowlands, a preference that is strongly supported by the occurrence of numerous nesting localitys and some tracks found lowland, in fluvial environments (Castanera et al., 2014; Cojan et al., 2003; Garcia & Vianey-Liaud, 2001; Sellés & Vila, 2015; Sellés et al., 2013; Vila et al., 2011, 2010a, 2010b), with a few exceptions in coastal plain (Sanz et al., 1995; Díaz-Molina et al., 2007; but see Sander et al., 1998) and lagoonal settings (López-Martínez et al., 2000; Vila et al., 2010b). Thus, we speculate that the denser vegetation and more secluded spaces of fluvial lowlands (Marmi et al., 2016a, 2016b) may have facilitated access to food, water and hiding spots for precocial hatchlings. Some of the tracks found in these lowland environments suggest a muddy terrain (Vila et al., 2013) that would have facilitated excavation for construction of nests (Vila, et al., 2010a) and would have hindered the mobility of predators, particularly that of

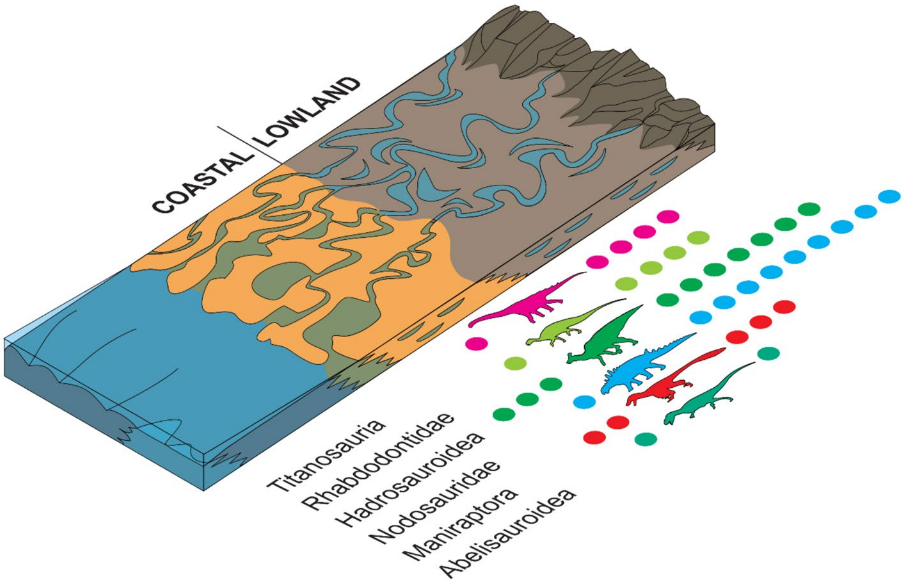

**Fig. 1** Graphical representation of the habitat preference and distribution of the Ibero-Armorican dinosaur groups during the late Campanian-late Maastrichtian (Time Bin 1 + 2). Dots represent the proportion of lowland occurrences of each group per coastal occurrence. Modified from Vila et al. (2014) and Oms et al. (2007)

larger theropods (García-Ramos et al., 2022). Therefore, our results provide quantitative support and concur with other evidence relating the nesting behaviour of titanosaurs and lowland environments in other regions of the globe (Cojan et al., 2003; Garrido et al., 2010; Leuzinger et al., 2021).

However, most of the titanosaurian ichnological record is found in paralic environments (López-Martínez et al., 1997; Marmi et al., 2014; Schulp & Brokx, 1999; Vila et al., 2008, 2013) where more nutritious foodstuffs (Gee, 2011; Howell et al., 2023; Marmi et al., 2016a, 2016b) and more open spaces such as vast muddy plains ( Oms et al., 2016; Vila et al., 2008) would presumably had been more suitable for the roaming of these animals (Castanera et al., 2014). Nonetheless, it must be pointed out that there is a great preservational bias for ichnological evidence between coastal and lowland environments, given that tracks are less likely to be preserved in the latter due to paedogenic activity and flooding events (Castanera et al., 2014; Jackson et al., 2009; Vila et al., 2013).

Thus, despite their preference for lowland settings, the ichnological and oological records support that titanosaurians dwelled in both environments when they roamed and therefore produced their tracks (more abundant in paralic substrates due to preservational bias) or laid their eggs (complete nests mostly found in fluvial settings). We are just beginning to understand whether this environmental distribution is related to a migratory behaviour due to climatic seasonality, but studies establishing the paleoclimate in the Ibero-Armorican domain during the Maastrichtian indicate a subtropical climate, with a mild seasonality and periods of extreme drought, despite the accentuated global cooling during the end of the period (Cojan et al., 2003; Domingo et al., 2015; Martín-Chivelet et al., 2019; Martínez De Espronceda et al., 2024; Riera et al., 2013), thus suggesting that climatic conditions were similar across both habitats.

## Ornithopods

Contrary to Butler and Barrett (2008), the evidence presented here indicates that Ibero-Armorican hadrosauroids, preferred the riparian environments of the lowlands (with some seasonal marine influence; Díez-Canseco et al., 2014). This also represents a shift from the deltaic (coastal) plain preference proposed by Fiorillo et al. (2016). Similarly, rhabdodontid ornithopods also showed a significant association with lowland environments (Fig. 1). Both groups displayed a similar distribution between paralic and inland settings (around 1:4, respectively), although rhabdodontids could have been slightly more restricted to such environments than hadrosauroids (3:7). It may be speculated that a reduced habitat range could have been one of the factors leading to the eventual replacement of rhabdodontids by hadrosauroids during the Maastrichtian faunal turnover in Ibero-Armorica 69–70 Ma ago (Fondevilla et al., 2019; Sellés et al., 2017; Vila et al., 2016). Indeed, rhabdodontids are absent from the post-turnover upper Maastrichtian strata of the Ibero-Armorican domain while there is an increase in hadrosauroid occurrences during this lapse. Additionally, some evidence shows that the first Ibero-Armorican hadrosauroids appear to be slightly more abundant than rhabdodontids in coastal environments of the late-early Maastrichtian (Conti et al., 2020; Fondevilla et al., 2019), which could reflect an early preference for this setting, as proposed by Butler and Barrett (2008) and Fiorillo et al. (2016). However, their distribution during the Maastrichtian becomes significantly more skewed inland (3:7 to 1:4, see Supplementary Information). This suggests that hadrosauroids could have arrived in Ibero-Armorica preferring paralic environments, eventually taking over the same niche of the comparatively more environmentally restricted rhabdodontids until the latter were forced out of their habitat or became extinct. Regardless, the rare presence of both groups in shared localities supports that the differences observed in their distribution are the result of genuine habitat preferences, minimally affected by sampling bias (Mannion & Upchurch, 2010). Only four Ibero-Armorican localities yielded both rhabdodontids and hadrosauroids throughout the entire time bins analysed (Time Bin 1 + 2). Therefore, the observed frequencies of both competing groups are due to genuine ecological signals (instead of sampling artifacts), which translates to the presence of a spatial niche-partitioning between them (either by actively avoiding one another or having different lowland sub-habitat preferences). Furthermore, there is a lower proportion of rhabdodontids in relation to hadrosauroids in all shared localities, which can be speculated as a sign of the increasing competition with hadrosauroids, eventually culminating in the absence of rhabdodontids in Ibero-Armorica during the late Maastrichtian.

### Nodosaurids

Unlike Butler and Barrett (2008) and Arbour et al. (2016), our data shows that nodosaurids, like in all taxonomic groups analysed, clearly preferred lowland habitats (Fig. 1) despite having one of the lowest sample sizes. However, such small sample size implies that both sampling and preservation bias could have influenced the results, as exemplified by the apparent lack of preference for any environment in nodosaurids during the late Maastrichtian (resulting from insufficient sample size in test 7). Testing these results will require a larger sample size by inclusion of more European nodosaurids and regions. For example, beyond Ibero-Armorica, the nodosaurid record extends to the lower Campanian paralic localities of Muthmannsdorf in Austria and the early Maastrichtian Vurpăr locality in Romania (Codrea et al., 2010; Csiki-Sava et al., 2015; Ősi et al., 2014; Pereda-Suberbiola & Galton, 2001), as well as the fluvial environments of the Santonian Iharkút and Maastrichtian Sânpetru localities from Hungary and Romania, respectively (Csiki-Sava et al., 2015; Ősi et al., 2014). Nevertheless, and in agreement with Mallon et al. (2012) and Mallon (2019), the preference of nodosaurids for lowland environments have been observed in almost all tests, including those with the strongest associations (test 3), which suggests that this association is statistically robust.

The coexistence of the three lowland-preferent groups of herbivorous dinosaurs discussed above is consistent with different diets and feeding heights in relation to niche partitioning among them (Arbour et al., 2016; Mallon, 2019; Mallon et al., 2013; Mannion & Upchurch, 2010). Such niche partitioning probably may have persisted in Ibero-armorica through the Maastrichtian faunal turnover (Fondevilla et al., 2019; Sellés et al., 2014; Vila et al., 2016). The latter is mainly evidenced in this work by the replacement of rhabdodontids by hadrosauroids. Based on the frequency distribution for all three groups, both titanosaurians and hadrosauroids had a similar presence in post-turnover Ibero-Armorican ecosystems (1:4). Nodosaurids appear to be more present in coastal environments (1:9 to 3:7). However, this probably does not reflect a genuine distribution given the extremely low sample size available for Late Maastrichtian nodosaurids. Regardless, the fact that both titanosaurian and nodosaurids are present in similar proportions during the Late Maastrichtian suggests that ecological competition with hadrosaurids was not as intense as with rhabdodontids. It is also likely that niche partitioning of inland environments was in effect between the groups. Therefore, we hypothesise that titanosaurians, rhabdodontids, and nodosaurids had a similar ecological dynamic and niche partitioning in pre-turnover paleocommunities and titanosaurians, hadrosauroids, and nodosaurids had in post-turnover times. Still, stage-level analysis and a larger sample size for these groups are necessary to further investigate this.

### Theropods

Theropods as a whole showed a preference for lowland environments despite being widespread in the ecosystems of Ibero-Armorica. Particularly, maniraptorans were skewed towards lowland settings in all tests where they could be analysed separately from Abelisauroidea; the latter did not show any habitat preference. This is probably why, unlike abelisauroids, the larger sample size of maniraptoran occurrences skewed habitat preference towards lowland settings. Eggs and eggshells (e.g. Garcia et al., 2000; Sellés et al., 2014; Vianey-Liaud & Garcia, 2000; Vianey-Liaud & López-Martínez, 1997) have also been found in both types of environments, although the only theropod nests found (those of *Sankofa pirenaica*, López-Martínez & Vicens, 2012), appeared in a coastal setting. As with titanosaurians, this could mean that there was a preference for nesting environments, but the discovery of more nests is needed to determine if that is the case. However, fewer nests and specimens is something to be expected, not only because their carnivore niche would have made theropod populations less abundant than those of phytophagous dinosaurs (Cho & Lee, 2013; Erickson et al., 2009), but, more importantly, because of a preservational bias. Contrary to other dinosaur groups such as sauropods and ornithopods that bury or cover their nests, theropods constructed open nests. The exposure of these nests, together with thinner and more fragile eggs (Paik et al., 2004; Varricchio et al., 2015) hindered their preservation. Despite the lack of fossil remains, our database shows that several species of carnivores had been distributed throughout Ibero-Armorica, being maniraptoran clades like dromaeosaurids and troodontids more abundant than abelisauroids (Buffetaut et al., 2021; Isasmendi et al., 2022; Marmi et al., 2016a, 2016b; Torices et al., 2013).

### Sampling bias vs. habitat preference

Mannion and Upchurch (2010) discussed how statistical analyses of dinosaur distributions may not provide evidence of genuine habitat preferences. This is because of the many factors that may influence data, such as sampling bias or long-term trends in taxon abundance and diversity, leading to equally statistically significant skewed distributions towards an environment. When time-binning the data, finding an association that persists at geochronological stage-level would make our results more reliable, even if that association differs from the general trend of habitat preference for that group. However, sample size was too small for tests in which the Late Cretaceous was partitioned into stage-level time bins. On top of that, the strength of the association clade-environment in those tests was amongst the lowest. Therefore, the effects of the Maastrichtian faunal turnover on dinosaur habitat preferences could not be reliably tested.

Mannion and Upchurch (2010) also reinterpreted the results of Butler and Barrett (2008) into two hypotheses. On one hand, the "weak hypothesis", posits that occurrences are an accurate representation of dinosaur distributions. Thus, the habitat preference of each group would reflect subtle differences among them, such as the time spent in one environment relative to the other or their relative abundance.

On the other hand, the "strong hypothesis plus noise" assumes that the habitat preferences of a group are completely skewed to one environment, but noise reduces the signal. The authors indicate that this noise can be introduced by sampling and preservation bias of the studied material, osteological occurrences in an environment due to post-mortem transportation, the error generated by the choice of groups and their taxonomic level, the choice of time-bins (if any) and the number and type of environments (Mannion & Upchurch, 2010). The data presented here supports elements from both hypotheses. Therefore, the studied groups spent a significantly longer time in a preferred environment but were present in both coastal and lowland settings, albeit to different degrees. However, the noise present in the occurrence database may have somewhat reduced the genuinely ecological signal. Despite that, a clear preference for each studied group has been determined.

## Conclusions

The present study determines the most likely habitat preference of the major clades of Ibero-Armorican dinosaurs through the review, update, and statistical analysis of their fossil occurrences. The statistical tests of independence (chi-square test, Fisher's exact test) showed preference for lowland environments for all dinosaur groups, except abelisauroids, during the late Campanian-late Maastrichtian. Furthermore, quantitative support for a preference towards lowland habitats for nesting in titanosaurians was also found, given the diverse fossil evidence of this group in Ibero-Armorica. It was also hypothesised that the disappearance of the lowland-exclusive rhabdodontids from Ibero-Armorica beyond the Maastrichtian faunal turnover in the region might have been related to their habitat being progressively restricted by the appearance of the hadrosauroids during the early Maastrichtian. Unlike previous studies that posited a coastal preference for nodosaurid ankylosaurs, the present analyses indicated that these animals preferred instead a lowland environment. Together with titanosaurians, nodosaurids may have occupied different ecological niches than ornithopod dinosaurs because they do not appear to be affected by the Maastrichtian arrival of hadrosauroids. Collectively, theropod dinosaurs showed a lowland-skewed habitat preference. It is also suggested that Abelisauroids were widespread between lowland and coastal environments (albeit sample size is too small to confirm), whereas maniraptorans preferred more lowland settings.

## Supplementary Information

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Supplementary Material 1.

Supplementary Material 2.

Supplementary Material 3.

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**Author contributions**

B. J. V. wrote the main manuscript text, the updated occurrence database and Table S1 (both in Supplementary Information), and prepared Fig. 1. B. J. V. performed and interpreted the statistical analyses and the analysis of the residuals. B. V. reviewed the statistical results. B. V. and A. S. created the basis for the database used in Supplementary Information and the manuscript text. A. P. M. reviewed the manuscript to ensure its quality and clarity in English. B. V., A. P. M., and A. S. were major contributors to the interpretation of the results. All authors reviewed the manuscript, figures, and Supplementary Information. All authors have approved the submitted version of the manuscript and have agreed both to be personally accountable for the author's own contributions and to ensure that questions related to the accuracy or integrity of any part of the work, even ones in which the author was not personally involved, are appropriately investigated, resolved, and the resolution documented in the literature.

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**Availability of data and materials**

All data generated or analysed during this study are included in this published article and its supplementary information files. The database supporting the conclusions of this article is included within the article (and its additional files).

## Declarations

**Ethics approval and consent to participate**

Not applicable.

**Competing interests**

The authors declare no competing interests.

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