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**Phylogenetic conservatism of species range sizes is the combined outcome of phylogeny and environmental stability**

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**Running-head:** Phylogenetic conservatism of range size and environmental stability

**ABSTRACT**

**Aim** To test for the phylogenetic conservatism of geographic range size and to explore the effect of the environment on this potential conservatism.

**Location** The western Tethys Ocean and its surroundings (present-day Europe, the Middle East and North Africa) during the early Pliensbachian (Early Jurassic).

**Methods** Using 104 localities and 1765 occurrences of ammonite species, we estimated geographic range sizes using the extent of occurrence and the latitudinal range. The phylogenetic conservatism of range sizes was tested using Moran's *I* index which measures phylogenetic autocorrelation, and Pagel's  $\lambda$  which indicates whether a phylogeny correctly predicts covariance patterns among taxa on a given trait

27 according to a Brownian evolution model. We conducted these analyses for two neighbouring provinces  
28 with contrasting environmental features (Mediterranean and North West European). We also explored  
29 scale effects by considering the whole western Tethys and two temporal resolutions (chronozone and sub-  
30 stage).

31 **Results** A marked difference in phylogenetic signal is observed between Mediterranean (MED) and  
32 North West European (NWE) species; the range size of MED species is more frequently phylogenetically  
33 conserved than that of NWE species. No phylogenetic conservatism of species range size is observed  
34 during the last chronozone of the early Pliensbachian which is characterized by numerous palaeoclimatic  
35 and palaeoenvironmental changes.

36 **Main conclusions** Species range size may be partly determined by phylogeny, but this phylogenetic  
37 conservatism is modulated by environmental stability. The phylogenetic signal of species range size may  
38 be labile through time within the same lineage and may differ between contemporaneous species of the  
39 same group. This lability stems from the fact that species range size results from a complex interplay of  
40 intrinsic and extrinsic factors. It seems that only some combinations of these factors may lead to range  
41 size conservatism.

42

### 43 **Keywords**

44 **ammonites, Early Jurassic, environment, phylogenetic conservatism, phylogeny, provincialism,**  
45 **species range size**

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48

### 49 **INTRODUCTION**

50 Geographic range size is a fundamental ecological and evolutionary feature of species (Gaston, 2003;  
51 Gaston & Fuller, 2009). Interest in measuring species range sizes and appraising its determinants has  
52 grown over the past decade, along with concern about species extinctions related to climate change and  
53 human activities (Kieffer & Aberhan, 2007; Mace *et al.*, 2008; Joppa *et al.*, 2016). Range size is  
54 postulated to be a good predictor of extinction risk (Jablonski, 1987; Lawton & May, 1995; Rosenzweig,

55 1995; Gaston, 1998; Kiessling & Aberhan, 2007) and as such, it is one of five criteria used by the  
56 International Union for Conservation of Nature to establish the Red List of Threatened Species (IUCN,  
57 2001).

58 Following Rapoport's (1982) work on areography, the definition and measurement of species  
59 geographic ranges have been intensively investigated over the past two decades (Gaston, 1994, 1996,  
60 1998, 2003; Brown & Lomolino, 1998; Gaston & Chown, 1999; Gaston & Fuller, 2009; Tomašových *et*  
61 *al.*, 2015). These studies distinguish two main measurements of species range: the *extent of occurrence*,  
62 i.e. area between the outermost limits to a species occurrence; and the *area of occupancy*, i.e. area over  
63 which the species is actually found. However, as the quantification of species range size depends on the  
64 resolution of available data, it is sometimes estimated using other variables such as the number of  
65 occurrences (e.g. Finnegan *et al.*, 2015; Longrich *et al.*, 2016), maximal latitudinal range (Qian &  
66 Ricklefs, 2004; Powell, 2007; Waldron, 2007), or number of cells/quadrats occupied by a taxon (Webb &  
67 Gaston, 2003; Qian & Ricklefs, 2004; Foote *et al.*, 2008). This diversity of approaches for quantifying  
68 species range size is associated with a lack of consensus about its determinants, especially the role of  
69 phylogeny. Using data from Late Cretaceous molluscs and by comparing the range sizes of sister species  
70 pairs, Jablonski (1987) was among the first authors to suggest the “heritability” of species range size, i.e.  
71 the tendency for closely related species to share similar range sizes. However, his results have been  
72 intensely debated (Webb & Gaston, 2003; Hunt *et al.*, 2005; Waldron, 2007), leading to further  
73 investigations on this issue at the crossroad between macroevolution and macroecology. Several studies  
74 documented phylogenetic conservatism of range size in different clades (Freckleton *et al.*, 2002;  
75 Blackburn *et al.*, 2004; Jones *et al.*, 2005; Freckleton & Jetz, 2009), but other works found that range size  
76 was not a species-level conserved trait (Gaston & Blackburn, 1997; Webb *et al.*, 2001; Freckleton *et al.*,  
77 2002; Böhning-Gaese *et al.*, 2006). Table 1 summarizes these contrasting observations together with the  
78 methods used to assess the phylogenetic signal in range size. Most of these studies focused on  
79 phylogenetic conservatism, but only a few of them considered the role of environmental parameters in  
80 shaping species ranges (Böhning-Gaese *et al.*, 2006; Kiessling & Aberhan, 2007; Mouillot & Gaston,  
81 2009; Abellán & Ribera, 2011). This is all the more surprising as the range size of a species likely results  
82 from a complex interplay of intrinsic and extrinsic factors. Even if it is difficult to analyse their combined

83 effects due to the lack of adequate datasets, the potential influence of parameters other than phylogeny  
84 should be considered. In addition, except for a few studies on Mesozoic marine organisms and Cenozoic  
85 mammals (Jablonski, 1987; Kiessling & Aberhan, 2007; Carotenuto *et al.*, 2010), most research on  
86 relationships between species range size and phylogeny has focused on extant taxa (Table 1). Since  
87 palaeontological data offer an extensive temporal perspective on biogeographical patterns, climate and  
88 environmental changes, they are pertinent for investigating the relative roles of phylogeny and  
89 environment in determining species range size. For this purpose, an appropriate palaeontological dataset  
90 should be composed of closely related species evolving within at least two contrasting ecoregions.

91 Here we investigate the phylogenetic conservatism of geographic range size for a group of ammonites  
92 (externally-shelled cephalopods) from the early Pliensbachian (Early Jurassic). These ammonites lived in  
93 the western part of the Tethys Ocean which corresponds to present-day Europe, the Middle East and  
94 North Africa (Fig. 1). These species are distributed within two environmentally contrasting provinces  
95 (Smith & Tipper, 1986; Dommergues & El Hariri, 2002; Wignall *et al.*, 2005; Arias, 2007; Dera *et al.*,  
96 2009a, b, 2011; Dommergues *et al.*, 2009). The northern province is characterized by a shallow  
97 epicontinental sea surrounded by continents and punctuated by numerous archipelagos, whereas the  
98 southern province corresponds to a series of deep basins opened on the Tethys Ocean (Fig. 1). The  
99 southern province is known to be more physically stable than the northern province (Hallam, 1972; Smith  
100 & Tipper, 1986; Dera *et al.*, 2011b). Additionally, several important climatic and environmental  
101 disturbances are recorded at the end of the early Pliensbachian (i.e. during the Davoei chronozone) in the  
102 northern province: (i) an increase in sea-surface temperatures (Rosales *et al.*, 2004; Dera *et al.*, 2009a, b;  
103 2011a; Price *et al.*, 2016; Bougeault *et al.*, 2017), (ii) a sea-level increase (Hallam, 2001; Bougeault *et al.*,  
104 in press), (iii) more humid climatic conditions (Dera *et al.*, 2009a; Bougeault *et al.*, in press) and (iv) a  
105 potential incursion of warm water masses from the Tethys Ocean (Dera *et al.*, 2009b, 2015). A  
106 concomitant decline in ammonite species richness is documented (Dommergues *et al.*, 2009; Dera *et al.*,  
107 2010). Based on this environmental context, we address the following questions: (i) is species range size a  
108 phylogenetically conserved trait? (ii) Can the environment affect the phylogenetic signal of range size  
109 conservatism? Since phylogenetic range size conservatism is more likely to occur when species share

110 common environmental conditions (Mouillot & Gaston, 2009), we hypothesize that species range size  
111 will be more phylogenetically conserved when environmental conditions are spatio-temporally stable.

112

113

## 114 MATERIAL AND METHODS

115

### 116 Dataset

117 We used Dommergues *et al.*'s dataset (2009) on early Pliensbachian (Early Jurassic, c.  $191.36 \pm 1$  Ma to  
118  $187.6 \pm 1$  Ma, Gradstein *et al.*, 2012; Ogg *et al.*, 2016; Fig. 1A) ammonites which consists of 214 revised  
119 species distributed among 104 fossil localities in the western Tethys and adjacent areas (Fig. 1B).

120 Palaeocoordinates for each fossil locality were calculated following the procedure described in Appendix  
121 S1 (Supporting Information). The early Pliensbachian is known as a time of marked faunal provincialism  
122 between two provinces: the Mediterranean Tethys (MED) in the south and Northwest Europe (NWE) in  
123 the north (Fig. 1B). These two contrasting provinces have been recognized for ammonites (Neumayr,  
124 1872; Donovan, 1967; Hallam, 1969; Dommergues, 1982; Geczy, 1984; Dommergues & Meister, 1991;  
125 Meister & Stampfli, 2000; Dommergues *et al.*, 2009), brachiopods (Ager, 1973; Vörös, 1977), bivalves  
126 (Hallam, 1977; Liu *et al.*, 1998), ostracods (Lord, 1988; Arias & Whatley, 2005) and belemnites (Doyle,  
127 1987, 1994). In addition to this faunal differentiation, the MED and NWE provinces are characterized by  
128 contrasting palaeogeographies and palaeoenvironments. The NWE province corresponds to an  
129 epicontinental sea not exceeding 200 m in depth, surrounded by continents and punctuated by numerous  
130 archipelagos (Fig. 1B). This singular configuration led to a strong influence of numerous perturbations,  
131 such as freshwater influxes, nutrient inputs, anoxia, incursions of cold and warm waters and changes in  
132 water currents (Rosales *et al.*, 2004; Wignall *et al.*, 2005; Arias, 2007; McArthur *et al.*, 2008; Dera *et al.*,  
133 2009a, b, 2011; Dommergues *et al.*, 2009). Conversely, the MED province corresponds to deep  
134 interconnected basins influenced by warm and nutrient-rich surface waters from the Tethys Ocean and  
135 represents more physically stable open-marine palaeoenvironments (Hallam, 1972; Smith & Tipper,  
136 1986; Dommergues *et al.*, 2009; Dera *et al.*, 2011b).

137 Dommergues *et al.* (2009) thoroughly revised the taxonomy of early Pliensbachian ammonites. Hardy  
138 *et al.* (2012) built upon this work by further introducing a species-level phylogenetic hypothesis (Fig. 2)  
139 that they used to demonstrate phylogenetic clustering of species extinctions during this interval. Here we  
140 use this phylogeny to investigate whether closely related species exhibit more similar range sizes than  
141 expected by chance and whether environmental stability can alter this phylogenetic signal. Species  
142 occurrences are documented for the three successive chronozones of the early Pliensbachian, i.e.  
143 Jamesoni, Ibex and Davoei (Page, 2003; Fig. 1A).

144

### 145 **Range size phylogenetic conservatism**

146 We tested the phylogenetic conservatism of species range size using Moran's index of spatial  
147 autocorrelation  $I$  (Moran, 1950; Gittleman & Kot, 1990), as implemented in the *gearymoran* function in  
148 the *ade4* package (Chessel *et al.*, 2004; Dray *et al.*, 2007) in R (v.3.0.2; R Development Core Team,  
149 2010). We chose this index because (i) it is frequently used to test for phylogenetic autocorrelation (e.g.  
150 Gittleman & Kot, 1990; Gittleman *et al.*, 1998; Jones *et al.*, 2005; Hardy *et al.*, 2012), (ii) it applies to  
151 whole phylogenies rather than species-pairs (Harmon & Glor, 2010; Abellán & Ribera, 2011), (iii) it does  
152 not imply an evolutionary model (Münkemüller *et al.*, 2012), (iv) it is broadly insensitive to tree size and  
153 tree balance (Lockwood *et al.*, 2002) and polytomies have very small effects on it (Münkemüller *et al.*,  
154 2012) and (v) it is non-parametric as implemented in *gearymoran*. As this index is not based on a  
155 Brownian model of trait evolution, its values cannot be directly compared across studies (Münkemüller *et al.*  
156 *et al.*, 2012). The null hypothesis of no phylogenetic signal was tested for significance using 1000 random  
157 permutations of range size values across the tips of the phylogenetic tree. Moran's  $I$  varies from -1 to +1,  
158 with positive values indicating that the trait of interest is more similar than expected by chance and  
159 negative values indicating an absence of correlation between the trait and inter-species phylogenetic  
160 distance (Paradis, 2012; p. 210). We also assessed the phylogenetic signal of range size conservatism  
161 using Pagel's  $\lambda$  (Pagel, 1999; Freckleton *et al.*, 2002), as implemented in the *phylosig* function in the  
162 *phytools* package (Revell, 2012). This index indicates whether the phylogeny correctly predicts  
163 covariance patterns among species on a given trait according to a Brownian model of character evolution  
164 (Felsenstein, 1985; Harvey & Pagel, 1991). A value of  $\lambda = 0$  indicates a trait evolution that is independent

165 of phylogeny, whereas a value of  $\lambda = 1$  indicates a trait evolving according to a Brownian motion along  
166 the phylogeny. Intermediate values of  $\lambda$  correspond to traits that have evolved according to a process in  
167 which the effect of phylogeny is weaker than in the Brownian model (Freckleton *et al.*, 2002). Compared  
168 to Moran's  $I$ , Pagel's  $\lambda$  is less adapted to our data because (i) it implies a model of trait evolution that may  
169 not correspond to the evolution of ammonite traits and (ii) it requires a normal distribution of the variable  
170 tested (see following sections).

171 The use of these two indices requires quantification of inter-species phylogenetic distances. In the  
172 absence of branch length information, all species are positioned at the same distance from the root,  
173 making the early Pliensbachian ammonite phylogenetic tree ultrametric (Fig. 2). Inter-species  
174 phylogenetic distances were obtained after slicing the phylogeny at regular nodal depths, with the most  
175 closely-related species being at a distance of two units (see Corey & Waite, 2008 and Hardy *et al.*, 2012  
176 for similar approaches).

177 For both extant and extinct species, the actual geographic range size is a hardly accessible feature as  
178 its estimation depends on the sampling effort (e.g. De Silva & Medellín, 2008; Fritz *et al.*, 2013; Yang *et al.*,  
179 2013). However, ammonites are among the most frequently preserved fossil organisms because of  
180 their relatively thick shell and their very high abundance in Mesozoic seas. Furthermore, our dataset is  
181 one of the most highly resolved among available fossil datasets, both in terms of space and time  
182 (Dommergues *et al.*, 2009). Consequently, we estimated species range sizes using two variables, the  
183 extent of occurrence (i.e. minimum convex polygon for species with at least three occurrences; Gaston,  
184 2003) and the latitudinal range (for species with at least two occurrences). These two variables  
185 correspond to “maximal” species range sizes as they are calculated based on the sum of species  
186 occurrences for the early Pliensbachian and for each chronozone. Thus, they do not represent  
187 instantaneous ranges but rather the whole range explored by a species during its lifetime or during a  
188 specific time interval. The extent of occurrence was calculated using the *ahull* function in the *alphahull*  
189 package (Pateiro-López & Rodríguez-Casal, 2010) in R (v.3.0.2; R Development Core Team, 2010). For  
190 species range size calculations at the chronozone scale, we only consider occurrences observed in the  
191 chronozone of interest (Appendix S2). We also evaluated the robustness of range size phylogenetic  
192 conservatism by removing a given percentage of species occurrences 1000 times and by comparing



193 Moran's  $I$  values for the degraded datasets with those of the original dataset. Overall, our conclusions  
194 remain unchanged (see Appendix S2).

195 While conducting the analyses, we tested whether these two variables yielded consistent signals of  
196 phylogenetic conservatism. The frequency distribution of geographic range sizes tends to be strongly  
197 right-skewed for extant and fossil marine species (Jablonski, 1987; Jablonski & Valentine, 1990;  
198 McAllister *et al.*, 1994; Kiessling & Aberhan, 2007; Powell, 2007; Foote *et al.*, 2008; Myers *et al.*, 2013),  
199 as for most terrestrial assemblages (Blackburn & Gaston, 1996; Gaston & Blackburn, 1997; Gaston,  
200 1998, 2003). Our dataset is no exception (Fig. 3).

201 We conducted analyses at the province scale. Only species occurring exclusively in one province  
202 (hereafter referred as "MED species" and "NWE species") were taken into account. In addition, we  
203 explored the phylogenetic conservatism of species range size at the scale of western Tethys. In this case,  
204 the dataset is composed of MED species, NWE species and trans-province species (i.e. species that occur  
205 in both provinces). Analyses were conducted for the entire early Pliensbachian and for each of the three  
206 chronozones considered independently. The scale of the chronozone presents three advantages: (i) it  
207 represents the best compromise between a high spatio-temporal resolution and a large sample size (Zacai  
208 *et al.*, 2016), (ii) biostratigraphic correlation (i.e. correlation among sedimentary layers based on their  
209 fossil content) between the NWE and MED provinces are robust at this scale (Dommergues & Meister,  
210 1991; Page, 2003; Zacai *et al.*, 2016), and (iii) this finer resolution allows us to track potential changes in  
211 the phylogenetic conservatism of species range size through successive time intervals. For analyses on  
212 chronozone subdatasets, inter-species phylogenetic distances were calculated on subtrees containing only  
213 species occurring in the chronozone and/or area of interest (Appendix S1). They are therefore different  
214 from those calculated on the complete early Pliensbachian phylogenetic tree (Fig. 2). Similar analyses  
215 were also conducted by using subtrees directly extracted from the complete tree, without recalculating  
216 inter-species phylogenetic distances in order to estimate the influence of uncertainties on phylogenetic  
217 branch lengths (Appendix S1).

218 Geography can be a confounding factor when investigating phylogenetic autocorrelation (Legendre,  
219 1993; Qian & Ricklefs, 2004; Purvis, 2008; Hardy *et al.*, 2012). Spatial autocorrelation is a common  
220 property of ecological data that can reduce the power of statistical tests because it violates the assumption

221 of sample independence (Legendre, 1993). To control for potential spatial autocorrelation of ammonite  
222 range sizes, we calculated the geographic range midpoint of each species for each subdataset of interest,  
223 and then used these midpoints to calculate triangular matrices of great-circle (i.e. orthodromic) distances  
224 between each species pair. We found non-significant Moran's  $I$  values for each subdataset analysed  
225 (Appendix S3), which means that ammonite species range sizes are not spatially autocorrelated.

226

227

## 228 **RESULTS**

229 At the scale of the early Pliensbachian, species latitudinal range size is phylogenetically conserved in both  
230 provinces and for the western Tethys Ocean (Moran's  $I > 0$ ;  $p < 0.05$ ; Table 2). The extent of occurrence  
231 is phylogenetically conserved for MED and western Tethys species, but not for NWE species (Moran's  
232  $I < 0$ ;  $p > 0.05$ ; Table 2).

233 These signals are not maintained through time as shown by analyses at the chronozone scale (Table 2).  
234 MED species show a phylogenetic conservatism of both latitudinal range and extent of occurrence during  
235 the Jamesoni and Ibex chronozones but not during the Davoei chronozone. NWE species never show this  
236 phylogenetic conservatism, which highly contrasts with the results for MED species. Western Tethys  
237 species show phylogenetic conservatism of both latitudinal range and extent of occurrence during the  
238 Jamesoni chronozone, extent of occurrence during the Ibex chronozone, and no phylogenetic  
239 conservatism during the Davoei chronozone. Therefore, regardless of the spatial scale of analysis, species  
240 range size is not phylogenetically conserved during the Davoei chronozone.

241 Analyses conducted after keeping the same inter-species phylogenetic distances as those of the  
242 complete tree show few differences with analyses conducted by recalculating branch lengths: the signal  
243 contrast between MED and NWE species is less pronounced and range size is less often conserved in the  
244 western Tethys (see Table 2 and Table S3 in Appendix S3). This suggests that potential uncertainties in  
245 branch length estimates have little effect on the observed signal of range size conservatism.

246 Results obtained with Pagel's  $\lambda$  are similar to those obtained with Moran's  $I$  (Table 2). The only  
247 significant signal of range size conservatism detected for NWE species with Moran's  $I$  (i.e. latitudinal  
248 range at the scale of the early Pliensbachian) is no longer significant with Pagel's  $k$  (Table 2). This

249 underlines the contrast of phylogenetic signal in range size conservatism between the two provinces. The  
250 extent of occurrence is no longer phylogenetically conserved for western Tethys species during the early  
251 Pliensbachian and the Ibex chronozone, and for the MED species during the Ibex chronozone when using  
252 Pagel's  $\lambda$  (Table 2).

253 In summary: first, both provinces show a marked contrast in the phylogenetic signal, MED species  
254 range sizes are more frequently phylogenetically conserved than those of NWE species. Second, species  
255 range size is not phylogenetically conserved during the Davoei chronozone.

256

257

## 258 **DISCUSSION**

### 259 **Methodological aspects**

260 Early Pliensbachian ammonites of the western Tethys are characterized by phylogenetic conservatism of  
261 their range size. This signal is found with two different indices (Moran's  $I$  and Pagel's  $\lambda$ ) and with two  
262 different methods for calculating phylogenetic branch lengths. The absence of phylogenetic conservatism  
263 for NWE species at the chronozone scale may partly result from small sample sizes in the subdatasets  
264 (Table 2). NWE species richness is half that of the MED province and this difference does not result from  
265 a bias in sampling effort (Dommergues *et al.*, 2009). However, analyses conducted without recalculating  
266 branch lengths for subtrees show that Moran's  $I$  can be significant and positive even for small sample  
267 sizes (e.g. latitudinal range for NWE species during the Ibex chronozone; Table S3, Appendix S3). As  
268 such, the reduced species richness of the NWE province cannot entirely account for the absence of  
269 phylogenetic conservatism of range size in this province.

270 Gaston (1998) proposed different temporal dynamics models of species range size. According to  
271 Carotenuto *et al.* (2010), most species biogeographic ranges apparently show a maximum range occurring  
272 halfway through their duration. In this work, we only deal with maximum species range sizes, *i.e.* the sum  
273 of their occurrences for their entire duration. This might be considered as a source of noise, especially at  
274 the chronozone level. However, 74% of the studied early Pliensbachian ammonites have a geological  
275 duration of a single chronozone, meaning that most of the "maximal" range sizes used in our analyses are  
276 not truncated. This percentage falls to 21% and 6% for a duration of two and three chronozones,

277 respectively. As such, we consider that the use of “maximal” species range sizes is not a source of bias in  
278 this work.

279

### 280 **Phylogenetic conservatism of species range size**

281 Species range size is a trait defined by a complex interplay of biological and environmental factors  
282 including species’ dispersal ability, ecological tolerance, inter-specific competition, environmental  
283 features and physical barriers (e.g. Brown & Lomolino, 1998; Gaston, 2003; Böhning-Gaese *et al.*, 2006).  
284 As such, phylogenetic conservatism of this macroecological trait probably involves more complex  
285 processes than a simple transmission of biological characters from ancestors to descendants. Thus, species  
286 range size will be best conserved in a lineage if the transmission of biological characters is associated  
287 with a spatio-temporal stability of environmental conditions. This may specifically apply to organisms  
288 whose dispersal is largely controlled by the environment, such as ammonites which are supposed to  
289 achieve their long-distance dispersal essentially through passive planktonic drift during early juvenile,  
290 post-hatching stages (Westermann, 1996; Brayard *et al.*, 2006, 2009; De Baets *et al.*, 2012; Ritterbush *et*  
291 *al.*, 2014; Naglik *et al.*, 2015; Zacaï *et al.*, 2016). Mouillot & Gaston (2009) raised this point for extant  
292 species by suggesting that phylogenetic conservatism of geographic range size is more likely to occur  
293 when closely related species share common environmental conditions. Our findings are consistent with  
294 this statement. Spatially, species range size conservatism is more pronounced in the MED province which  
295 is characterized by physically stable open-marine palaeoenvironments during the early Pliensbachian  
296 (Hallam, 1972; Smith & Tipper, 1986; Dera *et al.*, 2011b). Conversely, the weak phylogenetic signal in  
297 the NWE province (Table 2) probably results from the spatio-temporal instability of its  
298 palaeoenvironments. The singular configuration of this province led to a strong influence of numerous  
299 perturbations such as freshwater influxes, nutrient inputs, incursions of cold Boreal and warm Tethyan  
300 waters, changes in current dynamics, and anoxia (Hallam, 1972; Smith & Tipper, 1986; Rosales *et al.*,  
301 2004; Wignall *et al.*, 2005; Arias, 2007; McArthur *et al.*, 2008; Dera *et al.*, 2009a, b, 2011b;  
302 Dommergues *et al.*, 2009), all susceptible to modifying ammonite dispersal and ranges.

303 Temporally, range size is phylogenetically conserved for MED and western Tethys species during the  
304 Jamesoni and Ibex chronozones but not during the Davoei chronozone (Table 2). While the first two

305 chronozones do not record any noticeable environmental and climatic changes, the Davoei chronozone is  
306 characterized by an increase in sea-surface temperatures of about 4°C in the studied area (Rosales *et al.*,  
307 2004; Dera *et al.*, 2009a, b; 2011a; Price *et al.*, 2016), a sea-level increase (Hallam, 2001), more humid  
308 climatic conditions (Dera *et al.*, 2009a) and a potential incursion of warm water masses from the Tethys  
309 Ocean into the NWE province (Dera *et al.*, 2009b, 2015). In addition to these climatic and environmental  
310 changes, another possible explanation for the absence of a phylogenetic signal in range size conservatism  
311 during the Davoei chronozone is the low species richness that characterizes it (Table 2). This genuine  
312 decline could be related to an increase in sea water temperature (Rosales *et al.*, 2004; Dera *et al.*, 2009a,  
313 b; 2011a; Dommergues *et al.*, 2009; Price *et al.*, 2016) and to low origination rates (Dera *et al.*, 2010).

314 Overall, this suggests that species range size may be partly determined by phylogeny (i.e.  
315 biological/physiological heritable characters), but that phylogenetic conservatism is probably modulated  
316 by environmental stability through space and time. Our results echo the concept of *potential range* (i.e.  
317 area within which a species would be found if all dispersal limitations were overcome) vs. *realized range*  
318 (i.e. smaller area within which a species does occur; Udvardy & Papp, 1969; Gaston, 1994, 2003). Given  
319 the results of species range size conservatism, we can hypothesize that MED species may have expressed  
320 their potential range more fully than NWE species, resulting in a more frequent significant phylogenetic  
321 signal for the former. This hypothesis is supported by the fact that MED species range sizes are larger  
322 than the ones of NWE species in average (Fig. 3).

323  
324 Over the last decade, the question of phylogenetic conservatism of species range size has been  
325 addressed for a variety of clades. However, evidence for species range size conservatism is mixed and for  
326 the moment, no consistent conclusion has been reached (e.g. Mouillot & Gaston, 2009; Morin &  
327 Lechowicz, 2013). Here we show that phylogenetic conservatism may differ between contemporaneous  
328 species of the same group and that it may be labile through time within a same lineage. The lability of this  
329 macroecological trait can explain the conflicting results of previous studies on phylogenetic conservatism  
330 of species range size (Table 1). It should be mentioned that only a multi-scale approach can identify this  
331 lability. Our conclusions on range size phylogenetic conservatism would have been different if we had  
332 focused our analyses on one geographical area and one chronozone only. The instability of the

333 phylogenetic signal through time and space suggests that range size conservatism may be scale-dependent  
334 and emerges only for certain given combinations of extrinsic and intrinsic factors. Future studies should  
335 thus investigate environmental conditions that may favour species range size conservatism.

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## 347 **REFERENCES**

- 348 Abellán, P. & Ribera, I. (2011) Geographic location and phylogeny are the main determinants of the size  
349 of the geographical range in aquatic beetles. *BMC evolutionary biology*, **11**, 1. Ager, D.V. (1973)  
350 Mesozoic brachiopoda. *Atlas of Palaeobiogeography* (ed. by A. Hallam), pp. 431–436. Elsevier,  
351 Amsterdam.
- 352 Arias, C. (2007) Pliensbachian-Toarcian ostracod biogeography in NW Europe: evidence for water mass  
353 structure evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **251**, 398–421.
- 354 Arias, C. & Whatley, R. (2005) Palaeozoogeography of Western European Lower Jurassic (Pliensbachian  
355 and Toarcian) Ostracoda. *Geobios*, **38**, 697–724. Benton, M. J., Wills, M. A. & Hitchin, R. (2000)  
356 Quality of the fossil record through time. *Nature*, **403**, 534–537.
- 357 Benton, M. J., Dunhill, A. M., Lloyd, G. T. & Marx, F. G. (2011) Assessing the quality of the fossil  
358 record: insights from vertebrates. *Geological Society London Special Publications*, **358**, 63–94.

359 Bernardo, J., Ossola, R.J., Spotila, J. & Crandall, K.A. (2007) Interspecies physiological variation as a  
360 tool for cross-species assessments of global warming-induced endangerment: validation of an intrinsic  
361 determinant of macroecological and phylogeographic structure. *Biology Letters*, **3**, 695–699.

362 Blackburn, T.M. & Gaston, K.J. (1996) Spatial patterns in the geographic range sizes of bird species in  
363 the New World. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*,  
364 **351**, 897–912.

365 Blackburn, T.M., Jones, K.E., Cassey, P. & Losin, N. (2004) The influence of spatial resolution on  
366 macroecological patterns of range size variation: a case study using parrots (Aves: Psittaciformes) of  
367 the world: range size resolution in parrots. *Journal of Biogeography*, **31**, 285–293.

368 Böhning-Gaese, K., Caprano, T., Ewijk, K. van, Veith, M., Chown, A.E.S.L. & Losos, E.J.B. (2006)  
369 Range size: disentangling current traits and phylogenetic and biogeographic factors. *The American*  
370 *Naturalist*, **167**, 555–567.

371 Bougeault, C., Pellenard, P., Deconinck, J. F., Hesselbo, S. P., Dommergues, J. L., Bruneau, L.,  
372 Cocquerez, T., Laffont, R., Huret, E. & Thibault, N. (2017) Climatic and palaeoceanographic changes  
373 during the Pliensbachian (Early Jurassic) inferred from clay mineralogy and stable isotope (CO)  
374 geochemistry (NW Europe). *Global and Planetary Change*, **149**, 139–152.

375 Brayard, A., Brühwiler, T., Bucher, H. & Jenks, J. (2009) *Guodunites*, a low-palaeolatitude and trans-  
376 Panthalassic Smithian (Early Triassic) ammonoid genus. *Palaeontology*, **52**, 471–481. Brayard, A.,  
377 Bucher, H., Escarguel, G., Fluteau, F., Bourquin, S. & Galfetti, T. (2006) The Early Triassic  
378 ammonoid recovery: paleoclimatic significance of diversity gradients. *Palaeogeography*,  
379 *Palaeoclimatology, Palaeoecology*, **239**, 374–395.

380 Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*. Sinauer Associates, Sunderland, Massachusetts.

381 Calosi, P., Bilton, D.T., Spicer, J.I. & Atfield, A. (2007) Thermal tolerance and geographical range size in  
382 the *Agabus brunneus* group of European diving beetles (Coleoptera: Dytiscidae). *Journal of*  
383 *Biogeography*, **35**, 295–305.

384 Calosi, P., Bilton, D.T., Spicer, J.I., Votier, S.C. & Atfield, A. (2010) What determines a species’  
385 geographical range? Thermal biology and latitudinal range size relationships in European diving  
386 beetles (Coleoptera: Dytiscidae). *Journal of Animal Ecology*, **79**, 194–204.

387 Carotenuto, F., Barbera, C. & Raia, P. (2010) Occupancy, range size, and phylogeny in Eurasian Pliocene  
388 to Recent large mammals. *Paleobiology*, **36**, 399–414.

389 Chessel, D., Dufour, A.B. & Thioulouse, J. (2004) The ade4 package-I-One-table methods. *R news*, **4**, 5–  
390 10.

391 De Baets, K., Klug, C., Korn, D. & Landman, N.H. (2012) Early evolutionary trends in ammonoid  
392 embryonic development: evolutionary trends in ammonoid embryos. *Evolution*, **66**, 1788–1806.

393 Dera, G., Neige, P., Dommergues, J.-L. & Brayard, A. (2011b) Ammonite paleobiogeography during the  
394 Pliensbachian–Toarcian crisis (Early Jurassic) reflecting paleoclimate, eustasy, and extinctions. *Global  
395 and Planetary Change*, **78**, 92–105.

396 Dera, G., Neige, P., Dommergues, J. L., Fara, E., Laffont, R. & Pellenard, P. (2010) High-resolution  
397 dynamics of Early Jurassic marine extinctions: the case of Pliensbachian-Toarcian ammonites  
398 (Cephalopoda). *Journal of the Geological Society*, **167**, 21–33.

399 Dera, G., Pellenard, P., Neige, P., Deconinck, J.-F., Pucéat, E. & Dommergues, J.-L. (2009a) Distribution  
400 of clay minerals in Early Jurassic Peritethyan seas: palaeoclimatic significance inferred from  
401 multiproxy comparisons. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **271**, 39–51.

402 Dera, G., Pucéat, E., Pellenard, P., Neige, P., Delsate, D., Joachimski, M.M., Reisberg, L. & Martinez, M.  
403 (2009b) Water mass exchange and variations in seawater temperature in the NW Tethys during the  
404 Early Jurassic: evidence from neodymium and oxygen isotopes of fish teeth and belemnites. *Earth and  
405 Planetary Science Letters*, **286**, 198–207.

406 Dera, G., Brigaud, B., Monna, F., Laffont, R., Pucéat, E., Deconinck, J. F., Pellenard, P., Joachimski,  
407 M.M. & Durlet, C. (2011a) Climatic ups and downs in a disturbed Jurassic world. *Geology*, **39**, 215–  
408 218.

409 Dera, G., Prunier, J., Smith, P. L., Haggart, J. W., Popov, E., Guzhov, A., Rogov, M., Delsate, D., Thies,  
410 D., Cuny, G., Pucéat, E., Charbonnier, G. & Bayon, G. (2015) Nd isotope constraints on ocean  
411 circulation, paleoclimate, and continental drainage during the Jurassic breakup of Pangea. *Gondwana  
412 Research*, **27**, 1599–1615.

413 De Silva, H. G., & Medellín, R. A. (2001) Evaluating completeness of species lists for conservation and  
414 macroecology: a case study of Mexican land birds. *Conservation Biology*, **15**, 1384–1395.



415 Dommergues, J.-L. (1982) Le provincialisme des ammonites nord-ouest européennes au Lias moyen. Une  
416 crise faunique sous contrôle paléogéographique. *Bulletin de la Société géologique de France*, **24**,  
417 1047–1051.

418 Dommergues, J.-L. & El Hariri, K. (2002) Endemism as a palaeobiogeographic parameter of basin history  
419 illustrated by early- and mid-Liassic peri-Tethyan ammonite faunas. *Palaeogeography*,  
420 *Palaeoclimatology, Palaeoecology*, **184**, 407–418.

421 Dommergues, J.-L. & Meister, C. (1991) Area of mixed marine faunas between two major  
422 paleogeographical realms, exemplified by the Early Jurassic (Late Sinemurian and Pliensbachian)  
423 ammonites in the Alps. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **86**, 265–282.

424 Dommergues, J.-L., Fara, E. & Meister, C. (2009) Ammonite diversity and its palaeobiogeographical  
425 structure during the early Pliensbachian (Jurassic) in the western Tethys and adjacent areas.  
426 *Palaeogeography, Palaeoclimatology, Palaeoecology*, **280**, 64–77.

427 Donovan, D.T. (1967) The geographical distribution of Lower Jurassic ammonites in Europe and adjacent  
428 areas. *Aspects of Tethyan Biogeography*, **7**, 111–134.

429 Doyle, P. (1987) Lower Jurassic-Lower Cretaceous belemnite biogeography and the development of the  
430 Mesozoic Boreal Realm. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **61**, 237–254.

431 Doyle, P. (1994) Aspects of the distribution of Early Jurassic belemnites. *Palaeopelagos Special*  
432 *Publication*, **1**, 109–120.

433 Dray, S., Dufour, A.B. & Chessel, D. (2007) The ade4 package-II: Two-table and K-table methods. *R*  
434 *news*, **7**, 47–52.

435 Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist*, **125**, 1–15.

436 Finnegan, S., Anderson, S.C., Harnik, P.G., Simpson, C., Tittensor, D.P., Byrnes, J.E., Finkel, Z.V.,  
437 Lindberg, D.R., Liow, L.H., Lockwood, R., Lotze, H.K., McClain, C.R., McGuire, J.L., O’Dea, A. &  
438 Pandolfi, J.M. (2015) Paleontological baselines for evaluating extinction risk in the modern oceans.  
439 *Science*, **348**, 567–570.

440 Foote, M., Crampton, J.S., Beu, A.G. & Cooper, R.A. (2008) On the bidirectional relationship between  
441 geographic range and taxonomic duration. *Journal Information*, **34**, 421–433.

442 Freckleton, R.P., Harvey, P.H., Pagel, M. & Losos, A.E.J.B. (2002) Phylogenetic analysis and  
443 comparative data: a test and review of evidence. *The American Naturalist*, **160**, 712–726.

444 Fritz, S. A., Schnitzler, J., Eronen, J. T., Hof, C., Böhning-Gaese, K. & Graham, C. H. (2013) Diversity in  
445 time and space: wanted dead and alive. *Trends in ecology & evolution*, **28**, 509–516.

446 Gaston, K.J. (1994) *Rarity*, Springer Netherlands, Dordrecht.

447 Gaston, K.J. (1996) Species-range-size distributions: patterns, mechanisms and implications. *Trends in*  
448 *Ecology & Evolution*, **11**, 197–201.

449 Gaston, K.J. (1998) Species-range size distributions: products of speciation, extinction and  
450 transformation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **353**, 219–230.

451 Gaston, K.J. (2003) *The Structure and Dynamics of Geographic Ranges*, Oxford University Press,  
452 Oxford.

453 Gaston, K.J. (2009) Geographic range limits of species. *Proceedings of the Royal Society B: Biological*  
454 *Sciences*, **276**, 1391–1393.

455 Gaston, K.J. & Blackburn, T.M. (1997) Age, area and avian diversification. *Biological Journal of the*  
456 *Linnean Society*, **62**, 239–253.

457 Gaston, K.J. & Fuller, R.A. (2009) The sizes of species' geographic ranges. *Journal of Applied Ecology*,  
458 **46**, 1–9.

459 Gaston, K.J., Chown, S.L., Calosi, P., Bernardo, J., Bilton, D.T., Clarke, A., Clusella-Trullas, S.,  
460 Ghalambor, C.K., Konarzewski, M., Peck, L.S., Porter, W.P., Pörtner, H.O., Rezende, E.L., Schulte,  
461 P.M., Spicer, J.I., Stillman, J.H., Terblanche, J.S. & van Kleunen, M. (2009) Macrophysiology: a  
462 conceptual reunification. *The American Naturalist*, **174**, 595–612. Geczy, B. (1984) Jurassic ammonite  
463 provinces of Europe. *Acta Geologica Hungarica*, **27**, 67–71.

464 Gittleman, J.L. & Kot, M. (1990) Adaptation: statistics and a null model for estimating phylogenetic  
465 effects. *Systematic Zoology*, **39**, 227.

466 Gittleman, J.L., Anderson, C.G., Gates, S.E., Luh, H.K., Smith, J.D., McKinney, M.L. & Drake, J.A.  
467 (1998) Detecting Ecological Pattern in Phylogenies. *Biodiversity dynamics: turnover of populations,*  
468 *taxa, and communities* (ed. by M.L. McKinney and J.A. Drake), pp. 51–69. Columbia University  
469 Press, New York.

470 Gradstein, F.M., Schmitz, M.D., Ogg, G.M. & Ogg, J.G. (2012) *The Geologic Time Scale*, Elsevier,  
471 Boston.

472 Hallam, A. (1969) Faunal realms and facies in the Jurassic. *Palaeontology*, **12**, 1–18.

473 Hallam, A. (1972) Diversity and density characteristics of Pliensbachian-Toarcian molluscan and  
474 brachiopod faunas of the North Atlantic margins. *Lethaia*, **5**, 389–412.

475 Hallam, A. (1977) Jurassic bivalve biogeography. *Paleobiology*, **3**, 58–73.

476 Hallam, A. (2001) A review of the broad pattern of Jurassic sea-level changes and their possible causes in  
477 the light of current knowledge. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **167**, 23–37.

478 Hardy, C., Fara, E., Laffont, R., Dommergues, J.-L., Meister, C. & Neige, P. (2012) Deep-time  
479 phylogenetic clustering of extinctions in an evolutionarily dynamic clade (Early Jurassic ammonites).  
480 *PLoS ONE*, **7**, e37977.

481 Harmon, L.J. & Glor, R.E. (2010) Poor statistical performance of the Mantel test in phylogenetic  
482 comparative analyses. *Evolution*, **64**, 2173–2178.

483 Harvey, P. H. & Pagel, M. D. (1991) *The comparative method in evolutionary biology*, Oxford University  
484 Press, Oxford.

485 Hunt, G., Roy, K. & Jablonski, D. (2005) Species-level heritability reaffirmed: a comment on “On the  
486 heritability of geographic range sizes.”. *The American Naturalist*, **166**, 129–135.

487 IUCN, S.S.C. (2001) IUCN red list categories and criteria: version 3.1. *Prepared by the IUCN Species*  
488 *Survival Commission*. Jablonski, D. (1987) Heritability at the species level: analysis of geographic  
489 ranges of Cretaceous mollusks. *Science*, **238**, 360–363.

490 Jablonski, D. & Valentine, J.W. (1990) From regional to total geographic ranges: testing the relationship  
491 in Recent bivalves. *Paleobiology*, **16**, 126–142.

492 Jones, K.E., Sechrest, W. & Gittleman, J.L. (2005) Age and area revisited: identifying global patterns and  
493 implications for conservation. *Phylogeny and Conservation* (ed. by A. Purvis, J.L. Gittleman and T.  
494 Brooks), pp. 141–165. Cambridge University Press, Cambridge.

495 Joppa, L.N., Butchart, S.H.M., Hoffmann, M., Bachman, S.P., Akçakaya, H.R., Moat, J.F., Böhm, M.,  
496 Holland, R.A., Newton, A., Polidoro, B. & Hughes, A. (2016) Impact of alternative metrics on  
497 estimates of extent of occurrence for extinction risk assessment. *Conservation Biology*, **30**, 362–370.

498 Kiessling, W. & Aberhan, M. (2007) Geographical distribution and extinction risk: lessons from Triassic-  
499 Jurassic marine benthic organisms. *Journal of Biogeography*, **34**, 1473–1489.

500 Lawton, J.H. & May, R.M. (1995) *Extinction rates*, Oxford University Press, Oxford.

501 Legendre, P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology*, **74**, 1659–1673.

502 Liu, C., Heinze, M. & Fürsich, F.T. (1998) Bivalve provinces in the proto-Atlantic and along the southern  
503 margin of the Tethys in the Jurassic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **137**, 127–  
504 151.

505 Lockwood, J.L., Russell, G.J., Gittleman, J.L., Daehler, C.C., McKinney, M.L. & Purvis, A. (2002) A  
506 metric for analyzing taxonomic patterns of extinction risk. *Conservation Biology*, **16**, 1137–1142.

507 Longrich, N.R., Scriberas, J. & Wills, M.A. (2016) Severe extinction and rapid recovery of mammals  
508 across the Cretaceous-Paleogene boundary, and the effects of rarity on patterns of extinction and  
509 recovery. *Journal of Evolutionary Biology*, **29**, 1495–1512.

510 Lord, A.R. (1988) Ostracoda of the Early Jurassic Tethyan Ocean. *Evolutionary biology of ostracoda: its  
511 fundamentals and applications. Proceedings of the 9th International Symposium on Ostracoda* (ed. by  
512 T. Hanai, N. Ikeya and K. Ishizaki). *Developments in Palaeontology and Stratigraphy*, **11**, 855–868,  
513 Elsevier.

514 Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Milner-  
515 Gulland, E.J. & Stuart, S.N. (2008) Quantification of extinction risk: IUCN’s system for classifying  
516 threatened species. *Conservation Biology*, **22**, 1424–1442.

517 McAllister, D.E., Schueler, F.W., Roberts, C.M. & Hawkins, J.P. (1994) Mapping and GIS analysis of the  
518 global distribution of coral reef fishes on an equal-area grid. *Mapping the Diversity of Nature* (ed. by  
519 R.I. Miller), pp. 155–175. Springer Netherlands.

520 McArthur, J.M., Algeo, T.J., van de Schootbrugge, B., Li, Q. & Howarth, R.J. (2008) Basinal restriction,  
521 black shales, Re-Os dating, and the Early Toarcian (Jurassic) oceanic anoxic event.  
522 *Paleoceanography*, **23**, PA4217.

523 Meister, C. & Stampfli, G. (2000) Les ammonites du Lias moyen (Pliensbachien) de la Néotéthys et de  
524 ses confins; compositions fauniques, affinités paléogéographiques et biodiversité. *Revue de  
525 Paléobiologie*, **19**, 227–292.

526 Moran, P.A.P. (1950) Notes on continuous stochastic phenomena. *Biometrika*, **37**, 17–23.

527 Morin, X. & Lechowicz, M.J. (2013) Niche breadth and range area in North American trees. *Ecography*,  
528 **36**, 300–312.

529 Mouillot, D. & Gaston, K. (2009) Spatial overlap enhances geographic range size conservatism.  
530 *Ecography*, **32**, 671–675.

531 Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K. & Thuiller, W. (2012)  
532 How to measure and test phylogenetic signal. *Methods in Ecology and Evolution*, **3**, 743–756.

533 Myers, C.E., MacKenzie, R.A. & Lieberman, B.S. (2013) Greenhouse biogeography: the relationship of  
534 geographic range to invasion and extinction in the Cretaceous Western Interior Seaway. *Paleobiology*,  
535 **39**, 135–148.

536 Naglik, C., Tajika, A., Chamberlain, J. & Klug, C. (2015) *Ammonoid Locomotion. Ammonoid*  
537 *Paleobiology: from anatomy to ecology* (ed. by C. Klug, D. Korn, K. De Baets, I. Kruta, and R.H.  
538 Mapes), pp. 649–688. Springer Netherlands, Dordrecht.

539 Neumayr, M. (1872) Ueber Jura-Provinzen. *Verhandlungen der Kaiserlich-Königlichen Geologischen*  
540 *Reichsanstalt*, **3**, 54–57.

541 Ogg, J.G., Ogg, G.M. & Gradstein, F.M. (2016) *A Concise Geologic Time Scale: 2016*, Elsevier.

542 Page, K.N. (2003) The Lower Jurassic of Europe: its subdivision and correlation. *Geological Survey of*  
543 *Denmark and Greenland Bulletin*, **1**, 23–59.

544 Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.

545 Paradis, E. (2012) *Analysis of phylogenetics and evolution with R*, Springer New York, New York.

546 Pateiro-López, B., & Rodríguez-Casal, A. (2010) Generalizing the convex hull of a sample: the R  
547 package alphahull. *Journal of Statistical Software*, **34**, 1–28.

548 Powell, M.G. (2007) Latitudinal diversity gradients for brachiopod genera during late Palaeozoic time:  
549 links between climate, biogeography and evolutionary rates. *Global Ecology and Biogeography*, **16**,  
550 519–528.

551 Purvis, A. (2008) Phylogenetic approaches to the study of extinction. *Annual Review of Ecology*,  
552 *Evolution, and Systematics*, **39**, 301–319.

553 Qian, H. & Ricklefs, R.E. (2004) Geographical distribution and ecological conservatism of disjunct  
554 genera of vascular plants in eastern Asia and eastern North America. *Journal of Ecology*, **92**, 253–265.

555 R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R  
556 Foundation for Statistical Computing, Vienna, Austria.

557 Rapoport, E.H. (1982) *Areography: geographical strategies of species*, Pergamon Press, Oxford.

558 L. J. (2012) Phytools: an R package for phylogenetic comparative biology (and other things). *Methods*  
559 *in Ecology and Evolution*, **3**, 217–223.

560 Ritterbush, K.A., Hoffmann, R., Lukeneder, A. & De Baets, K. (2014) Pelagic palaeoecology: the  
561 importance of recent constraints on ammonoid palaeobiology and life history: pelagic palaeoecology  
562 of ammonoids. *Journal of Zoology*, **292**, 229–241.

563 Rosales, I., Quesada, S. & Robles, S. (2004) Paleotemperature variations of Early Jurassic seawater  
564 recorded in geochemical trends of belemnites from the Basque–Cantabrian basin, northern Spain.  
565 *Palaeogeography, Palaeoclimatology, Palaeoecology*, **203**, 253–275.

566 Rosenzweig, M.L. (1995) *Species diversity in space and time*, Cambridge University Press, Cambridge.

567 Smith, P.L. & Tipper, H.W. (1986) Plate tectonics and paleobiogeography; Early Jurassic (Pliensbachian)  
568 endemism and diversity. *PALAIOS*, **1**, 399–412.

569 Tomašových, A., Jablonski, D., Berke, S. K., Krug, A. Z. & Valentine, J. W. (2015) Nonlinear thermal  
570 gradients shape broad-scale patterns in geographic range size and can reverse Rapoport's rule. *Global*  
571 *Ecology and Biogeography*, **24**, 157–167.

572 Udvardy, M.D.F. & Papp, C.S. (1969) *Dynamic zoogeography, with special reference to land animals*,  
573 Van Nostrand Reinhold, New York.

574 Valentine, J. W., Jablonski, D., Kidwell, S. & Roy, K. (2006) Assessing the fidelity of the fossil record by  
575 using marine bivalves. *Proceedings of the National Academy of Sciences*, **103**, 6599–6604.

576 Vörös, A. (1977) Provinciality of the Mediterranean Lower Jurassic brachiopod fauna: causes and plate-  
577 tectonic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **21**, 1–16.

578 Waldron, A. (2007) Null models of geographic range size evolution reaffirm its heritability. *The American*  
579 *Naturalist*, **170**, 221–231.

- 580 Webb, T.J. & Gaston, K.J. (2003) On the heritability of geographic range sizes. *The American Naturalist*,  
581 **161**, 553–566.
- 582 Webb, T.J., Kershaw, M. & Gaston, K.J. (2001) Rarity and Phylogeny in Birds. *Biotic Homogenization*  
583 (ed. by J.L. Lockwood and M.L. McKinney), pp. 57–80. Springer US, Boston.
- 584 Westermann, G.E.G. (1996) Ammonoid Life and Habitat. *Ammonoid Paleobiology* (ed. by N.H.  
585 Landman, K. Tanabe and R.A. Davis), pp. 607–707. *Topics in Geobiology*, **13**, Springer US.
- 586 Wignall, P.B., Newton, R.J. & Little, C.T. (2005) The timing of paleoenvironmental change and cause-  
587 and-effect relationships during the Early Jurassic mass extinction in Europe. *American Journal of*  
588 *Science*, **305**, 1014–1032.
- 589 Yang, W., Ma, K. & Kreft, H. (2013). Geographical sampling bias in a large distributional database and  
590 its effects on species richness–environment models. *Journal of Biogeography*, **40**, 1415–1426.
- 591 Zacaï, A., Brayard, A., Dommergues, J.-L., Meister, C., Escarguel, G., Laffont, R., Vrielynck, B. & Fara,  
592 E. (2016) Gauging scale effects and biogeographical signals in similarity distance decay analyses: an  
593 Early Jurassic ammonite case study. *Palaeontology*, **59**, 671–687.

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## 597 **SUPPORTING INFORMATION**

598 Additional Supporting Information may be found in the online version of this article:

599 **Appendix S1** References for Table 1, palaeocoordinates of the 104 studied fossil localities and species-  
600 level phylogenetic trees for each chronozone of the early Pliensbachian with and without branch length  
601 recalculation

602 **Appendix S2** Species latitudinal range size and extent of occurrence for each subdataset and evaluation  
603 of the robustness of species range size conservatism according to the potential uncertainty in range size  
604 estimates

605 **Appendix S3** Spatial autocorrelation of species range sizes estimated using Moran's *I*, and phylogenetic  
606 conservatism of species range size measured by Moran's *I* on subtrees without branch length  
607 recalculation

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**BIOSKETCH**

Axelle Zacaï is a palaeontologist with broad interests in macroecology. Her PhD thesis focused on the biogeographical patterns of Early Jurassic ammonites, on their evolution through time and on the influence of intrinsic (e.g. morphology, phylogenetic relatedness) and extrinsic (e.g. environment, climate, palaeogeography) factors on these patterns.

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**Table 1** Studies of range size phylogenetic conservatism for various clades and time intervals.

Clade	<i>n</i>	Analytical method	Use of a phylogeny	Phylogenetic signal	Range variable	Source
Molluscs (fossil)	172	Spearman's rank correlation of sister species pairs	Yes	Yes	Geographic range in km	Jablonski, 1987
Birds: Australian	559	Nested ANOVA (orders)	Yes	Yes	Grid cells	Cotgreave & Pagel, 1997
Birds: New World	3901	Nested ANOVA	Yes	No	Grid cells	Gaston & Blackburn, 1997
Birds: Anseriformes	46	Spearman's rank correlation of sister taxon pairs	No (pairs of sister taxa only)	No	Grid cells	Webb <i>et al.</i> , 2001
Sunfish	21	Pagel's $\lambda$	Yes	No	Area	Freckleton <i>et al.</i> , 2002, reanalysing Pyron, 1999
Suckers	47	Pagel's $\lambda$	Yes	Yes	Area	Freckleton <i>et al.</i> , 2002, reanalysing Pyron, 1999
Australian marsupials	165	Pagel's $\lambda$	Yes	Yes	Grid cells	Freckleton <i>et al.</i> , 2002, reanalysing Johnson, 1998
Lepidoptera (UK)	38	Pagel's $\lambda$	Yes	No	Latitudinal range (based on grid cells)	Freckleton <i>et al.</i> , 2002, reanalysing Dennis <i>et al.</i> , 2000
Birds	103	Range size asymmetry of sister taxon pairs	No (pairs of sister species only)	No	Grid cells	Webb & Gaston, 2003



<b>Molluscs (fossil)</b>	56	Range asymmetry of ancestor-descendant pairs	No (pairs of ancestor-descendant only)	No	Geographic range in km (no further details)	Webb & Gaston, 2003, reanalysing Jablonski, 1987
Birds: Psittaciformes	349	Moran's <i>I</i> at various taxonomic ranks	No (taxonomy)	Yes (species and genera)	Area, grid cells and latitudinal range	Blackburn <i>et al.</i> , 2004
Herbaceous and woody plants	57	Nested ANOVA at various taxonomic ranks	No	No	Latitudinal range and area (based on grid cells)	Qian & Ricklefs, 2004
<b>Molluscs (fossil)</b>	172	Spearman's rank correlation of ancestor-descendant pairs	Yes	Yes	Geographic range in km	Hunt <i>et al.</i> , 2005, reanalysing Jablonski, 1987
Birds	103	Spearman's rank correlation of ancestor-descendant pairs	No (pairs of sister species only)	Yes	Grid cells	Hunt <i>et al.</i> , 2005, reanalysing Webb & Gaston, 2003
Terrestrial mammals	4745	Moran's <i>I</i> and Pagel's $\lambda$	Yes	Yes	Area	Jones <i>et al.</i> , 2005
Birds: Sylviidae	26	Regression associated to Mantel tests	Yes	No	Area	Böhning-Gaese <i>et al.</i> , 2006
Birds: North American	65 pairs of sister species	Randomization test on range size symmetry	Yes	Yes	Latitudinal range	Waldron, 2007
Carnivores, Artiodactyla and Primates	891	GLS model incorporating spatial and phylogenetic components and Pagel's $\lambda$	Yes	Yes (but weak)	Area	Freckleton & Jetz, 2009
Birds	1136	Spearman's rank correlation of sister species pairs	No	Yes	Area	Mouillot & Gaston, 2009
<b>Mammals (fossil)</b>	220	Blomberg's <i>K</i> statistic and Pagel's $\lambda$	Yes	Yes (genera) No (species)	Proportion of localities of occurrence area	Carotenuto <i>et al.</i> , 2010
Water beetles (10 lineages)	174	Blomberg's <i>K</i> and phylogenetic eigenvector regression	Yes	Yes but weak and not for all lineages	Area	Abellan & Ribera, 2011
South American avifauna	2869	Comparison of species-range size distribution of simulated and empirical data (Kolmogorov-Smirnov two-sample $D^*$ statistic) and Pagel's $\lambda$	No	Yes but not directly	Grid cells	Borregaard <i>et al.</i> , 2011
<b>Trilobites</b>	38	Pagel's $\lambda$ and Blomberg's <i>K</i>	Yes	Yes	Coastal distance (km) and latitudinal extent	Hopkins, 2011

Terrestrial carnivorans	231	Blomberg's <i>K</i> , Pagel's $\lambda$ and Moran's <i>I</i>	Yes	Yes but driven by the size of geographic domain	Area	Machac <i>et al.</i> , 2011
North American trees	598	Blomberg's <i>K</i> and Moran's <i>I</i>	Yes	Yes (but weak)	Area + latitudinal range	Morin & Lechowicz, 2013

Detailed references are given in Appendix S1 in the Supporting Information. Abbreviations: *n*, number of taxa; PS, phylogenetic signal indicating whether a significant positive phylogenetic correlation has been reported for the range size data of each clade.

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**Table 2** Phylogenetic conservatism of species range size as measured by the Moran's *I* and Pagel's  $\lambda$ .

Temporal interval	Range variable	Spatial scale					
		MED		NWE		Western Tethys	
		Moran's <i>I</i>	Pagel's $\lambda$	Moran's <i>I</i>	Pagel's $\lambda$	Moran's <i>I</i>	Pagel's $\lambda$
Early Pliensbachian	<i>n</i>	43 sp		22 sp		117 sp	
	Extent of occurrence	<b>0.113**</b>	<b>0.395**</b>	-0.040	7.933e-05	<b>0.021**</b>	0.180
	<i>n</i>	66 sp		29 sp		147 sp	
	Latitudinal range	<b>0.085***</b>	<b>0.393***</b>	<b>0.024*</b>	5.074e-05	<b>0.034**</b>	<b>0.346**</b>
DAVOEI	<i>n</i>	14 sp		5 sp		33 sp	
	Extent of occurrence	-0.081	7.933e-05	-0.228	0.925	-0.052	7.437e-05
	<i>n</i>	17 sp		7 sp		38 sp	
	Latitudinal range	0.015	0.062	-0.184	4.745e-05	0.016	5.706e-05
IBEX	<i>n</i>	22 sp		11 sp		57 sp	
	Extent of occurrence	<b>0.145**</b>	0.390	-0.154	4.745e-05	<b>0.022*</b>	0.197
	<i>n</i>	29 sp		13 sp		66 sp	
	Latitudinal range	<b>0.191**</b>	<b>0.656**</b>	-0.003	0.597	0.004	0.036
JAMESONI	<i>n</i>	33 sp		12 sp		67 sp	
	Extent of occurrence	<b>0.143**</b>	<b>0.487**</b>	-0.155	4.745e-05	<b>0.042*</b>	<b>0.261*</b>
	<i>n</i>	49 sp		16 sp		87 sp	
	Latitudinal range	<b>0.024*</b>	<b>0.439**</b>	-0.063	6.919e-05	<b>0.058***</b>	<b>0.455***</b>

Abbreviations: *n*, number of species considered in the analyses; sp, species; MED, Mediterranean province; NWE, North-West European province. Note: \*\*\**p* < 0.001, \*\**p* < 0.01, \**p* < 0.05, no symbol = not significant.

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625 **FIGURES**

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627 **Figure 1** Biostratigraphical and palaeogeographical context of the early Pliensbachian. (A) Ammonite  
 628 chronozones (Page, 2003; Gradstein *et al.*, 2012) and their approximate absolute ages (Gradstein *et al.*,  
 629 2012 ; Ogg *et al.*, 2016). (B) Palaeogeographical reconstruction of the western Tethys and adjacent areas  
 630 with the palaeolocation of the 104 fossil localities used here. NW European localities are represented by  
 631 circles and Mediterranean localities are represented by squares. Abbreviations: Ad, Adria bloc; Africa,  
 632 African bloc; Anatolia, Anatolian bloc; Eurasia, Eurasian bloc; Ib, Iberian bloc.

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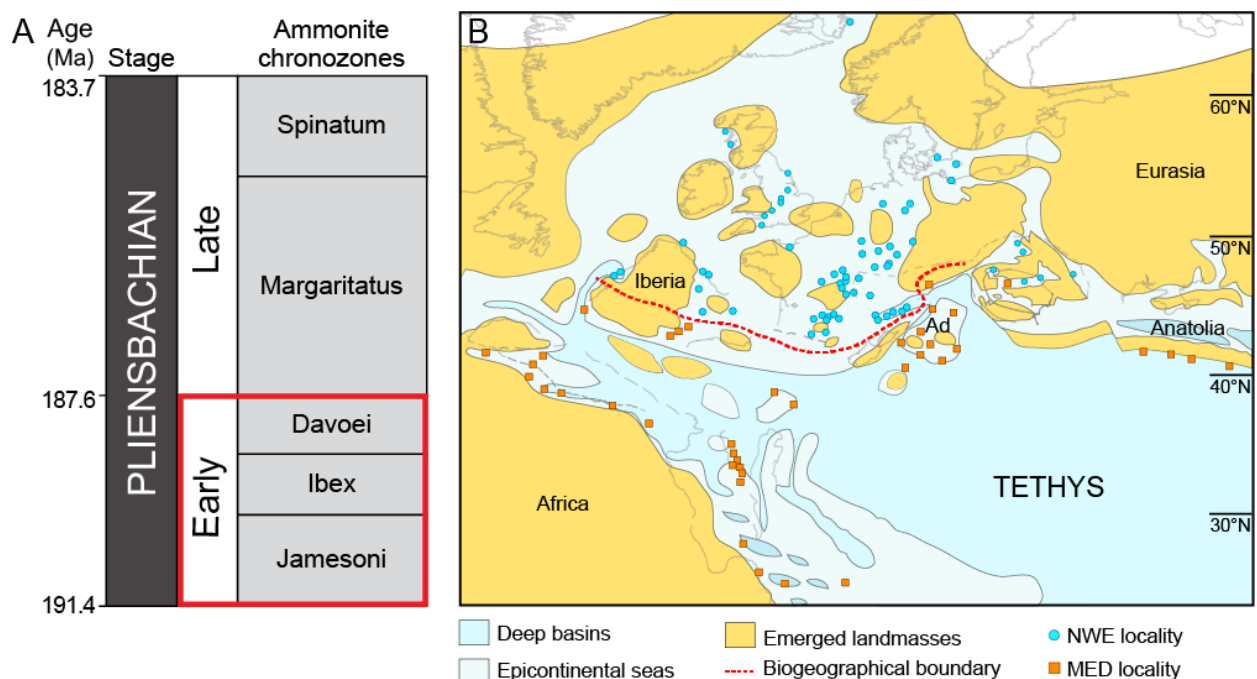
634 **Figure 2** Species-level phylogenetic hypothesis for early Pliensbachian ammonites (after Hardy *et al.*,  
 635 2012) together with their province(s) of occurrence. Inter-species phylogenetic distances correspond to  
 636 branch lengths between each species pair in the phylogeny. Abbreviations: MED, Mediterranean; NWE,  
 637 North-West European.

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639 **Figure 3** Distribution of latitudinal ranges and extent of occurrences for early Pliensbachian ammonites  
 640 of the western Tethys and adjacent areas. Note the typical strongly right-skewed distribution.

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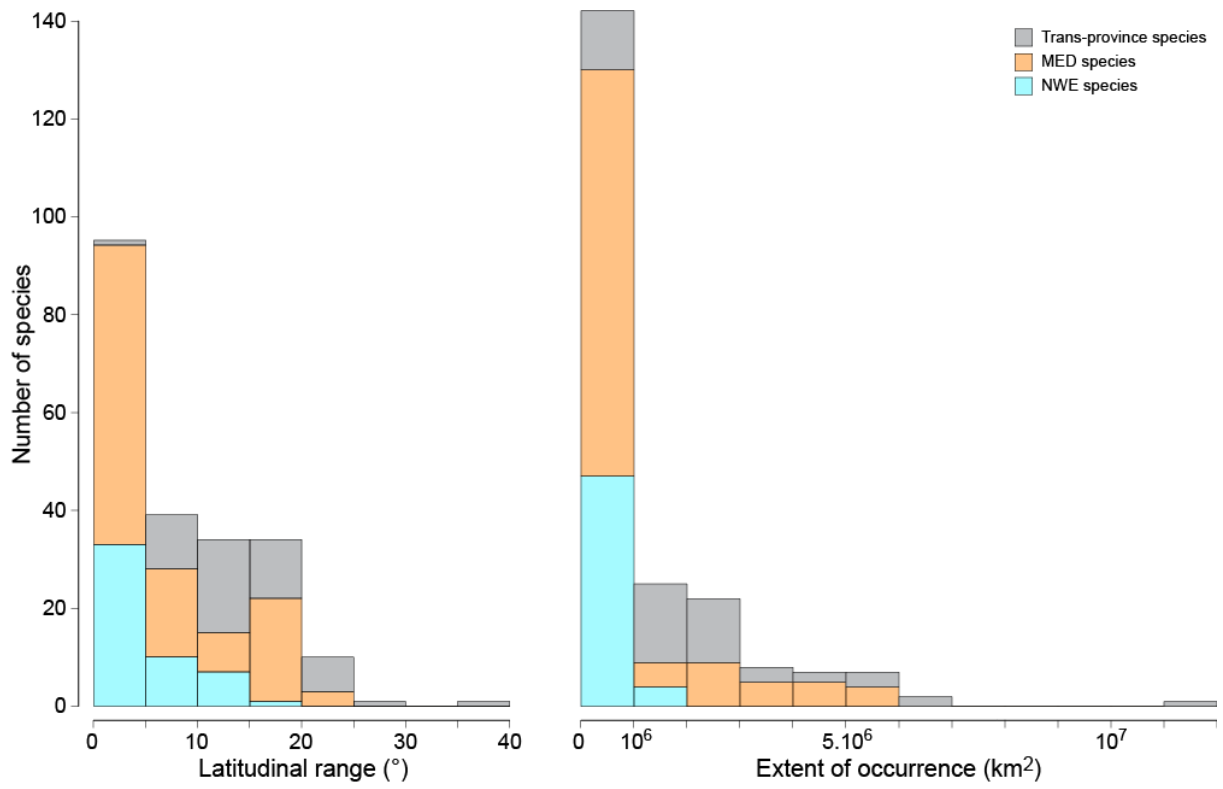


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