THE RAPOPORT EFFECT AND THE CLIMATIC VARIABILITY HYPOTHESIS IN EARLY JURASSIC AMMONITES

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Abstract: The increase in species range size towards high latitudes, known as Rapoport’s rule, remains one of the most debated and poorly understood macroecological patterns. Numerous studies have challenged both its universality and the main mechanism originally proposed to explain it: the climatic variability hypothesis. Here, we study this pattern using a group of fossil marine organisms: the early Triassic ammonites of the western Tethys. We further take into account the influence of the marked provincialism prevailing at that time, with a Mediterranean province (MED) and a north-west European province (NWE) located on each side of a latitudinally oriented palaeobiogeographical barrier. We find that only species from the NWE province display a Rapoport effect, whereas species from the more tropical MED province show a boundary effect and have larger range sizes on average. This dual pattern can be explained by an alternative climatic variability hypothesis that better captures latitudinal seasonal variations and outlines the influence of the intertropical zone, characterized by stable and homogeneous climate that allows species to disperse over very large areas, regardless of their thermal tolerance. Accordingly, the NWE province probably displayed a gradient of seasonal climatic variations which caused the emergence of a Rapoport effect, whereas the MED province was probably located in the intertropical zone where no gradient in species range size is expected. Our multiscale approach further shows that the Rapoport effect is scale-dependent and may be labile through time. This probably explains the conflicting results of previous studies carried out at various spatiotemporal scales.

Key words: Rapoport effect, range size, latitude, ammonites, Jurassic, climatic variability hypothesis.
equivocal in the southern hemisphere (Rohde 1996; Gaston et al. 1998; Gaston & Chown 1999; Cardillo 2002; Chown et al. 2004; Hernández Fernández & Vrba 2005). Some authors have thus suggested that it could be a ‘local’ phenomenon that essentially applies to the northern hemisphere, out of the tropics (Rohde et al. 1993; Rohde 1996; Blackburn & Gaston 1996; Gaston et al. 1998; Gaston & Chown 1999). For this reason, Blackburn & Gaston (1996) advocated replacing the term ‘Rapport’s rule’ with ‘Rapoport effect’; a terminology that we follow in this work. The debate is still open, but as noted by Gaston & Chown (1999), it is hindered by the non-randomness of the published case studies, which have mainly focused on extant terrestrial vertebrates from the Nearctic, Palaearctic and Australasian biogeographical realms, and have barely investigated low-latitude and deep-time patterns (Table 1). In addition, some confusion has arisen from the diversity of approaches used to investigate the Rapoport effect: (1) empirical tests of the climatic variability hypothesis with known thermal latitudinal gradients (e.g. Morin & Lechowicz 2011; Pintor et al. 2015; Tomašových et al. 2015; Stuart-Smith et al. 2017); (2) empirical tests with both thermal gradient and species thermal tolerances known (e.g. Khalilq et al. 2017; Grünig et al. 2017); and (3) predictions of a Rapoport effect tacitly assuming (or not) the presence of a thermal latitudinal gradient (e.g. Stevens 1989; Rohde 1996; Fortes & Absalão 2004; Weiser et al. 2007; Veter et al. 2013).

Here, we test for the existence of a Rapoport effect among fossil representatives of a marine group of invertebrates: the ammonites (Cephalopoda). Our study focuses on a c. three million-year-long interval in the Early Jurassic (the early Pliensbachian), and covers what was a vast tropical epicontinental sea at that time (present-day Europe, the Middle East and North Africa; Fig. 1). Such a case study presents several advantages. First, it uses one of the most highly resolved fossil datasets available, because the taxonomy of early Pliensbachian ammonites has been thoroughly revised up to the species level by Dommergues et al. (2009) and species occurrences are documented at the scale of the chronozone (i.e. c. 1 million-year-long intervals). As such, it provides a high-resolution palaeontological framework in which to investigate the Rapoport effect through time, hence offering more possibilities than the binary response that can be obtained when studying extant organisms (i.e. existence/absence of a Rapoport effect). This is especially interesting because the end of the early Pliensbachian records climatic changes that affected the phylogenetic conservatism of ammonite range sizes (Zacaï et al. 2017) and could also have modified their latitudinal distribution. Second, the singular configuration of the area under study, divided into two contiguous marine biogeographical provinces (Dommergues 1982; Dommergues & Meister 1991; Meister & Stampfli 2000; Dommergues et al. 2009), allows us to test for the influence of a latitudinally oriented biogeographical barrier on the geographical distribution of species range sizes and on the existence of a Rapoport effect. Third, assuming the validity of the climatic variability hypothesis for extant organisms, the dataset seems appropriate to test for the applicability of this hypothesis and the existence of a Rapoport effect in deep time, because the environmental and supposedly climatic contrast that characterized the two provinces is known to have influenced both ammonite dispersal (Zacaï et al. 2016) and phylogenetic conservatism of species range size (Zacaï et al. 2017). Fourth, it extends the study of the Rapoport effect to the marine realm and to the fossil record, both of which have been largely neglected in previous studies (Table 1). Our goal is thus to test for the existence of a Rapoport effect in ammonites and for the applicability of the climatic variability hypothesis in a fossil marine environment, and to estimate the influence of the singular geographical and environmental configuration of the early Pliensbachian western Tethys on the latitudinal distribution of species range size.

**MATERIAL AND METHOD**

**Dataset**

We used Dommergues et al.’s (2009) dataset of early Pliensbachian ammonites (Early Jurassic, c. 191.36 ± 1 Ma to 187.6 ± 1 Ma; Gradstein et al. 2012; Ogg et al. 2016; Fig. 1A). It consists of 214 revised species distributed among 104 fossil localities of the western Tethys and adjacent areas (present-day Europe, the Middle East and North Africa; Fig. 1B). Palaeocoordinates for each fossil locality were calculated following the procedure thoroughly described by Zacaï et al. (2017). The three successive chronozones of the early Pliensbachian, that is Jamesonian, Ibex and Davoei (Page 2003; Fig. 1A), are represented, respectively, by 88, 94 and 80 localities, at a total of 104 localities. Species occurrences are documented at the scale of the chronozone.

The early Pliensbachian is a time of marked faunal provincialism between two marine areas: the Mediterranean Tethys (MED) in the south, located approximately between 25°N and 45°N, and north-west Europe (NWE) in the north, located approximately between 40°N and 65°N (Fig. 1B). These two provinces have been identified for ammonites (Donovan 1967; Hallam 1969; Dommergues 1982; Geczy 1984; Dommergues & Meister 1991; Meister & Stampfli 2000; Dommergues et al. 2009), bivalves (Hallam 1977; Liu et al. 1998), brachiopods (Ager 1973; Vörös...
**Table 1.** Synthesis of a survey of published studies treating the relationship between range size and latitude.

| Taxon                  | Region                | R     | M   | P | Lat. range | Support  | References                          |
|------------------------|-----------------------|-------|-----|---|------------|----------|-------------------------------------|
| Birds                  | North America         | a     | m   | x | 25–60°N   | 25–40°N  | Brown (1995, p. 113)                |
| Birds                  | Global                | l     | m   | x | ?          |          | Cardillo (2002)                     |
| Birds                  | Global                | l_a   | s,m |   | c. 90°S–90°N | 0–90°N  | Orme *et al.* (2006)                |
| Birds                  | New World             | l     | s   |   | c. 60°S–80°N | 0–60°S  | Tomasových *et al.* (2016)         |
|                        |                       |       |     |   |            |          | (genus level)                       |
| Birds                  | Soviet Union          | l     | s   |   | 40–80°N   |          | Stevens (1989)                      |
| Non-migratory birds    | Soviet Union          | l     | s   |   | 40–80°N   | 40–80°N  |                                    |
| Birds                  | New World             | a     | s   |   | 55°S–70°N | 17–70°N  | Blackburn & Gaston (1996)          |
|                        |                       |       |     |   |            |          |                                    |
| Wildfowl               | Global                | a     | m   |   | 55°S–70°N |          |                                    |
| *Phylloscopus*         | Old World             | l     | m   |   | 15–65°N   | 15–65°N  | Price *et al.* (1997)              |
| Mammals and birds      | North America         | l     | s   |   | c. 10–70°N | c. 30–65°N | Sax (2001)                         |
| Mammals                | North America         | l     | s   |   | 35–80°N   | 35–80°N  | Stevens (1989, 1992)              |
| Mammals                | North America         | a     | m   |   | 5–80°N    | 5–80°N  | Pagel *et al.* (1991)             |
| Mammals                | Palaeartic            | l_a   | s   |   | 20–80°N   | 30–80°N  | Lether & Harvey (1994)            |
| Mammals                | Australia             | l     | s   |   | 10–40°S   |          | Smith *et al.* (1994)             |
| Mammals                | South America         | l     | s   |   | c. 0–60°S | 40–50°S  | Sax (2001)                         |
| Mammals                | North America         | l     | s   |   | ?          |          | Arita *et al.* (2005)             |
| Mammals                | Africa                | l_a   | m   |   | 40°S–40°N | 0–40°N  | Hernández Fernández & Vrba (2005) |
| Mammals                | North America         | l     | s,m |   | c. 0°–70°N |          | Lyons & Smith (2010)              |
| Mammals (weak support) | Australia             | l     | m   | x | 11–39°N   | 11–39°N  | Johnson (1998)                     |
| Primates               | Africa                | l     | m   | x | c. 37°S–37°N | c. 0–37°N | Cowlishaw & Hacker (1997)         |
| Bats                   | New World             | l     | s   |   | 60°S–65°N | 60°S–65°N | Lyons & Willig (1997)             |
| Forest mammals         | Australia             | l     | m   | x | 45°S–45°N | 15°N–45°N | Johnson (1998)                     |
| Fossil mammals (Cenozoic) | North America       | l     | m   |   | c. 25°–60°N |          | Vetter *et al.* (2013)            |
| Carnivora, primates    | South America         | l     | s   |   | 55°S–10°N | 55°S–10°N | Ruggiero (1994)                    |
| Artiodactyla, Hystriognathini, marsupials | South America | l     | s   |   | 55°S–10°N | 55°S–10°N** |                                    |
| Marsupials             | New World             | l     | s   |   | 60°S–45°N | 0°–45°N  | Lyons & Willig (1997)             |
| Mammals and vascular plants | Europe               | l     | s   |   | 55°S–25°N |          | Sax (2001)                         |
| Reptiles and amphibians | North America        | l     | s   |   | 30–65°N   | 30–60°N  | Stevens (1989, 1992)             |
| Lizards                | Australia             | l     | s,m |   | 40°S–10°S | 2 out of 3 clades | Pintor *et al.* (2015)      |
| Snakes                 | Global                | a     | s/m |   | c. 90°S–90°N | c. 90°S–90°N | Böhm *et al.* (2017)               |
| *Brachinus* beetles    | North America         | l_a   | m   | x | ?          |          | Juliano (1983)                     |
| Moths                  | Switzerland           | l     | m   | x | 600–2400 m |          | Beck *et al.* (2016)              |
| Human pathogens        | Global                | l     | m   |   | c. 35°S–60°N | c. 20°S–30°N | Guernier & Guégan (2009)            |

(continued)
TABLE 1. (Continued)

| Taxon                      | Region                      | R     | M  | P  | Lat. range | Support | References                                      |
|----------------------------|-----------------------------|-------|----|----|------------|---------|------------------------------------------------|
| Plants                     | New World                  | a     | –  | –  | ?          | North   | Morueta-Holme et al. (2013)                     |
| Trees                      | North America              | l     | s  | –  | 25–70°N   | 25–70°N | Stevens (1989, 1992)                           |
| Trees                      | North America and Europe   | l     | m  | –  | 15°–71°N  | 15°–71°N| Morin & Lechowicz (2011)                       |
| Trees                      | North America              | l,a   | m  | x  | 6.4°N–74.3°N|         | Lane (2007)                                    |
| Temperate rainforest trees | South America              | l     | s  | x  | 38–54°S   | 38–54°S | Arroyo et al. (1996)                           |
| Woody plants               | New World                  | l     | s,m| –  | c. 60°S–75°N| c. 40°–60°N| Weiser et al. (2007)                           |
| *Eucalyptus*               | Australia                  | l,a   | m  | ( )| ?          | –       | Edwards & Westoby (1996)                       |
| *Eucalyptus*               | Australia                  | l,a   | m  | x  | 10–45°S   | –       | Hughes et al. (1996)                           |
| *Pinus*                    | North America              | l     | s  | –  | 5–70°N    | 15–70°N | Stevens & Enquist (1998)                       |
| Columnar cacti             | Argentina                  | l,a   | m  | x  | 23–33°S   | –       | Moulere & Ezcurra (1997)                       |
| Columnar cacti             | Mexico                     | l     | m  | x  | 15–28°N   | 15–28°N | –                                               |
| Fishes                     | North America              | l     | s  | –  | c. 30–60°N| c. 30–60°N| Sax (2001)                                     |
| Freshwater fishes          | North America              | l     | s  | –  | 0°–85°N   | 35–85°N | Rohde et al. (1993)                            |
| Freshwater fishes          | Northern Europe            | l     | m  | x  | 0°–70°N   | 25–60°N | –                                               |
| Freshwater fishes          | Australia                  | l     | s  | –  | 45–10°S   | –       | –                                               |
| *Cyprinella* minnows       | North America              | a     | m  | ( )| ?          | ✓       | Taylor & Gotelli (1994)                        |
| Freshwater amphipods       | North America              | l     | s  | –  | 30–70°N   | 30–70°N | France (1992)                                 |
| Freshwater crayfish        | North America              | l     | s  | –  | 25–65°N   | 25–65°N | –                                               |
| Freshwater and coastal fishes | North America          | l     | s  | –  | 25–80°N   | 35–80°N | Stevens (1989, 1992)                           |
| Marine fishes              | Pacific Ocean             | l     | s  | –  | 30–65°N   | –       | Stevens (1996)                                 |
| Marine teleost fishes      | Atlantic                   | l     | s  | –  | 55°S–90°N | –       | Rohde & Heap (1996)                            |
| Marine teleost fishes      | Indo-Pacific               | l     | m  | x  | 45°S–75°N | –       | –                                               |
| Marine teleost fishes      | Various                    | l     | s  | –  | 55°S–75°N | –       | Rohde et al. (1993)                            |
| Teleosts                   | East Atlantic              | l     | s  | –  | 35°S–70°N | 35°S–70°N| Macpherson & Duarte (1994)                      |
| Corals and fishes          | Indo-Pacific               | l     | m  | –  | c. 35°S–35°N| –       | Connolly et al. (2003)                         |
| Fishes and invertebrates   | Atlantic                   | l     | s  | –  | 70°S–80°N | –       | MacPherson (2003)                              |
| Elasmobranchs              | East Atlantic              | l     | s  | –  | 35°S–70°N | –       | MacPherson & Duarte (1994)                      |
| Marine molluscs            | North America              | l     | s  | –  | 25–70°N   | 25–70°N | Stevens (1989, 1992)                           |
| Marine molluscs            | Western Atlantic and eastern Pacific | l   | s,m| –  | 90°S–90°N | –       | Fortes & Abalsan (2004)                        |
| Marines bivalves            | Western & eastern Pacific and western Atlantic | l   | s  | –  | 77°S–83°N | –       | Tomasovych et al. (2015)                       |

(continued)
also supports the hypothesis of a physical boundary between the two provinces. The NWE province corresponds to an epicontinental sea not exceeding 200 m in depth, surrounded by continents and punctuated by numerous archipelagos (Fig. 1B). This singular configuration led to a strong influence of numerous perturbations, such as freshwater influxes, nutrient inputs, anoxia, incursions of cold and warm waters and changes in water currents (Rosales et al. 2004a; Wignall et al. 2005; Arias 2007; McArthur et al. 2008; Dera et al. 2009a, b, 2011a; Dommergues et al. 2009). Conversely, the MED province corresponds to a series of deep interconnected basins influenced by warm and nutrient-rich surface waters from the Tethys Ocean and therefore represents a physically more stable open-marine palaeoenvironment (Hallam 1972; Smith & Tipper 1986; Dommergues et al. 2009; Dera et al. 2011a). For all these reasons, the most largely accepted hypothesis regarding the nature of the biogeographical barrier separating the NWE and MED province is that it comprised a narrow chain of emerged or shallow areas, acting as a full physical barrier or a faunal filter, depending on sea-level fluctuations (Dommergues 1982; Dercourt et al. 1985; Dommergues & Meister 1991; Meister & Stampfli 2000; Dommergues et al. 2009; Dera et al. 2011b).

**Relationship between range size and latitude**

Stevens (1989) initially documented the positive relationship between species latitudinal range size and latitude by

| Taxon                      | Region                   | R* | M† | P‡ | Lat. range§ | Support¶ | References                                      |
|----------------------------|--------------------------|----|----|----|-------------|----------|------------------------------------------------|
| Marine bivalves            | Western & eastern        | 1  | s  | –  | c. 80°S–80°N | species-rich genera | Tomašových et al. (2016) and Tomašových & Jablonski (2017) |
| Pacific and western       | Atlantic                 |    |    |    |             |          |                                                |
| Marine prosobranch gastropods | Western Atlantic        | 1  | m  | –  | 5°S–65°N    | –        | Roy et al. (1998)                               |
| Prosobranchs              | and eastern Pacific      |    |    |    |             |          |                                                |
| Coastal cephalopods        | Atlantic                 | 1  | s  | –  | 0–70°N      | –        | Roy et al. (1994)                               |
|                           | & depth                  |    |    |    |             |          |                                                |
|                           | Western & eastern        | 1  | s  | –  | c. 60°S–70°N | Western Atlantic | Rosa et al. (2008)                               |
|                           | Atlantic                 |    |    |    |             |          |                                                |

*Range size measure: l, latitudinal extent; a, range area.
†Method used to test for Rapoport effect: s, Stevens method; m, midpoint method.
‡If the midpoint method was used, whether or not the phylogenetic non-independence of species was accounted for; ‡ indicates that a phylogenetic effect was considered but not explicitly controlled for.
§The approximate latitudinal range over which Rapoport effect was tested.
¶The approximate latitudinal range over which there was evidence for a Rapoport effect (there is an element of subjectivity in these judgments in several cases); ‡‡, there was evidence for the pattern but it is not clear over what latitudes; –, there was no evidence for the pattern. Where this range embraces the equator, there was evidence for a Rapoport effect in both hemispheres.
**The pattern is found across all species, but across species in only three of seven orders when analysed separately.
††Separate analyses for families and genera did not find evidence for a Rapoport effect.
‡‡‡Of separate analyses for elasmobranchs, and for deep-living, littoral and pelagic teleosts, only the last found evidence for a Rapoport effect.

(Continued)
comparing the average range size of species occurring in 5° latitudinal bands. This approach has been criticized because it suffers from several statistical problems (Rohde et al. 1993; Colwell & Hurtt 1994; Letcher & Harvey 1994; Gaston et al. 1998), the most salient being the non-independence of mean range sizes since large-range species contribute to mean range size at multiple latitudes (Rohde et al. 1993; Letcher & Harvey 1994; Connolly 2009). To circumvent this problem, Rohde et al. (1993) proposed a different approach called the ‘midpoint method’, which associates species latitudinal range sizes with their latitudinal midpoints and treats them as independent data. However, this method is affected by triangular geometric constraints, which implies that: (1) small variations in range size of species at the boundaries of the area under study will have higher weight in the analyses than substantial variations in range size of species distributed more centrally within the study area; and (2) large-range sizes are more susceptible to being located at the centre of the study area (Blackburn & Gaston 1996; Lyons & Willig 1997; Lyons & Smith 2010; Pintor et al. 2015). As noted by Rohde et al. (1993), Fortes & Absalão (2004) and Connolly (2009), the midpoint approach can be misleading in some particular cases, especially when there are many species with very large ranges. A survey of the literature reveals that the Stevens and midpoint methods have had the same appeal to researchers despite their respective advantages and drawbacks (Table 1). About half of the published studies failed to consider the issue of the non-independence of statistical observations. When taken into account, this dependence can be treated either spatially (e.g. Tomásovych et al. 2015, 2016), or phylogenetically (e.g. Morin & Lechowicz 2011, Beck et al. 2016, Böhmer et al. 2017), or by the mean of null model simulations through bootstrapping approaches (e.g. Arita et al. 2005, Pintor et al. 2015). Overall, at least 17 different statistical approaches have been used to investigate the relationship between range size and latitude, making the published studies hardly comparable (Table 1). Here, we adopt the midpoint method and we control for the phylogenetic dependence of statistical observations. To allow for future investigations, we also provide data matrices corresponding to the Stevens method and to the study of the subsequent spatial non-independence of observations (Zacai et al. 2018, table S1).

We analysed the relationship between species range size and latitude using generalized estimating equations (GEE; see Morin & Chuine 2006 and Morin & Lechowicz 2011). GEE fit regression models by taking into account the
relatedness among observations (Liang & Zeger 1986). Paradis & Claude (2002) proposed using GEE in the context of comparative analyses, the relatedness among observations (i.e. species) being computed from the phylogeny. These authors also underlined the ability of GEE to deal with phylogenies containing polytomies, which is the case in our dataset (see Zacaï et al. 2018, fig. S1, and Hardy et al. 2012). Here, we fit a GEE model to explain variation in species latitudinal range size (response variable) depending on variation of species latitudinal midpoints (explanatory variable), while removing phylogenetic autocorrelation. Considering the continuous nature of the response variable, we used a Gaussian error distribution for this variable, with an identity link function in the GEE model. This model has the following form (Paradis & Claude 2002):

$$E[y_i] = \beta_0 + \beta_1 x_{it},$$

where $E[y_i]$ is the expectation of the response variable (latitudinal range) for the $i$th species; $\beta_0$ and $\beta_1$ are the coefficients of the model (i.e. intercept and slope, respectively); and $x_{it}$ is the explanatory variable (species latitudinal midpoint). We computed this model using the compar.gee function (Paradis & Claude 2002) as implemented in the R package ape (Paradis et al. 2004; R Core Team 2016), with a significance level set at $a = 0.05$.

We determined palaeolatitudinal range size (i.e. the difference, in degrees of latitude, between the northernmost and southernmost points of a geographical range) and midpoint (i.e. mean of these two extremes) of each species for the early Pliensbachian and for the three chronozones of this substage. These range sizes correspond to ‘maximal’ species range sizes as they are calculated based on the sum of species occurrences for the early Pliensbachian and for each chronozone. Thus, they do not represent instantaneous ranges but rather the whole range explored by a species during its lifetime or during a specific time interval (Zacaï et al. 2017).

We conducted the analyses: (1) at the scale of the western Tethys, with no distinction between species occurring exclusively in one province (hereafter referred as ‘MED species’ and ‘NWE species’) and those occurring in both provinces (transprovince species); and (2) at the province scale, that is, considering either MED or NWE species only. For the temporal scale, we conducted the analyses for the entire early Pliensbachian but also for each of its chronozone in order to track potential changes in Rapoport effect through time. We paid special attention to the Davoei chronozone because it records several climatic and environmental changes, including an increase in sea-surface temperatures (Rosales et al. 2004a; Dera et al. 2009a, b, 2011b; Price et al. 2016), a sea-level rise (Hallam 2001) and more humid climatic conditions (Dera et al. 2009b). For analyses on chronozone/province subdatasets, interspecies phylogenetic distances were calculated on subtrees containing only species occurring in the chronozone/area of interest (see Zacaï et al. 2018). Analyses were conducted on ‘complete’ dataset and subdatasets, meaning that all species were conserved, even those showing only one occurrence and thus null latitudinal range sizes. We also conducted analyses on datasets containing only species showing more than one occurrence in order to evaluate the influence of null range sizes on the relationship between species range size and latitude.

RESULTS

At the scale of the early Pliensbachian, latitudinal range sizes of western Tethys species increase significantly with latitude (Fig. 2A; Table 2) and thus show a Rapoport effect. However, when species are separated according to their province of occurrence (i.e. MED, NWE and transprovince species), only NWE species exhibit such a pattern (see Fig. 2C, Table 1 and Zacaï et al. 2018, table S2) for analyses of transprovince species). This positive relationship between NWE species range size and latitude could be driven by an outlier, that is, the species showing the largest range at the highest latitude (Boweniceras luridum Simpson, 1855). However, it remains significant even when this species is removed from the dataset analysed (Zacaï et al. 2018, table S2). The relationship observed at the scale of the western Tethys is therefore probably driven by NWE species. MED species have their largest latitudinal range sizes near the centre of the province, and those ranges decrease towards the northern and southern province boundaries (Fig. 2B). This distribution pattern certainly results from a triangular geometric constraint (see Material and Method).

For the Jamesoni chronozone, only the analysis at the spatial scale of the western Tethys shows a significant Rapoport effect (Fig. 2I; Table 2). When considered separately, neither the NWE and MED species nor the transprovince species display an increase in range size with latitude (Fig. 2K–L; Zacaï et al. 2018, table S2). For the Ibex chronozone, only NWE species show a significant Rapoport effect (Fig. 2I; Table 2). However, this relationship is no more significant when the outlier represented by Boweniceras luridum is removed from the analysis (see Zacaï et al. 2018, table S2). For the Davoei chronozone, NWE species show a clear increase in their range sizes with latitude but this relationship is only almost significant ($p = 0.059$; Fig. 2F), probably because of the small sample size (8 species). Conversely, analyses at the scale of the western Tethys and MED province exhibit a significant decrease in species range size with latitude (Fig. 2D–E and Table 2). Results of analyses conducted on datasets
containing only species with more than one occurrence are consistent with those conducted on complete datasets (Zacaï et al. 2018, table S3), indicating that endemic species do not have a noticeable influence on the overall latitudinal distribution of species range sizes and on the emergence of a Rapoport effect.

**DISCUSSION**

**Rapoport effect during the early Pliensbachian and the modified climatic variability hypothesis**

In the climatic variability hypothesis, Stevens (1989) regarded seasonal climatic variations as the main factor generating a Rapoport effect: lower seasonal climatic variability observed between the tropics is favourable to stenotopic species, while greater seasonal climatic variability at high latitudes favours eurytopic species, thereby resulting in an increase of species range size with latitude. Gaston & Chown (1999) later added the mean annual temperature as an explicative agent of this pattern and also revised its form. Today, mean annual temperatures increase from the poles to a latitude of about 20–25° north and south, after which they level off (Terborgh 1973; Gaston & Chown 1999; Colwell et al. 2008). Thus, environmental/climatic conditions are more homogeneous across the tropics (i.e., over a very large latitudinal extent). For this reason, the difference of thermal tolerances between tropical and temperate species anticipated under Janzen’s (1967) hypothesis should not produce a Rapoport pattern within the tropics. Indeed, a tropical species with a narrow temperature tolerance may theoretically have a broader latitudinal range than a temperate species with a greater temperature tolerance, given the thermal plateau observed between 20–25°S and 20–25°N (Terborgh 1973; Gaston & Chown 1999; Colwell 2011; Jablonski et al. 2013). This modified climatic variability hypothesis implies that large latitudinal ranges are also expected at low latitudes and that the decreasing trend of species range size from high to low latitudes should vanish in the intertropical zone. A broad dispersal has been observed in many extant groups of tropical species such as neotropical birds, mammals and reptiles (Terborgh 1973), American wasps (Richards 1978), insects (Gaston 1991), Costa Rican hymenoptera (Gaston & Gauld 1993; Gaston 1996) and marine bivalves (Jablonski et al. 2013; Tomasových et al. 2015, 2016; Tomasových & Jablonski 2017). Some groups even show the pattern expected under Gaston & Chown (1999) hypothesis, that is broader latitudinal extents towards lower latitudes, or at least a breakdown of the Rapoport effect towards lower latitudes (e.g., teleost fishes, Rohde et al. 1993; molluscs from the eastern Pacific, Roy et al. 1994; North American birds and mammals, Sax 2001).

**FIG. 2.** Relationship between species latitudinal midpoint and latitudinal range size for early Pliensbachian ammonites of the western Tethys and adjacent areas, estimated with GEE. A–C, analyses at the scale of the substage (early Pliensbachian). D–L, analyses at the scale of the chronozone (Jamesoni, Ibex and Davoei). Trend lines show significant relationships (see Table 2 for details). Colour online.

**TABLE 2.** Results of GEE models testing the relationship between species latitudinal midpoint and range size.

| Temporal interval | Spatial scale | Western Tethys | MED | NWE |
|-------------------|---------------|----------------|-----|-----|
| Early Pliensbachian | n = 214 | 214 | 110 | 52 |
| Estimate | $b_1 = 1.29 \times 10^{-1}$*** | $b_1 = -9.42 \times 10^{-2}$ | $b_1 = 7.64 \times 10^{-1}$*** |
| SE | 3.86e $\times 10^{-2}$ | 6.33 $\times 10^{-2}$ | 1.39 $\times 10^{-1}$ |
| Davoei | n = 45 | 45 | 23 | 8 |
| Estimate | $b_1 = -9.89 \times 10^{-1}$*** | $b_1 = -2.13$*** | $b_1 = 1.15$ |
| SE | 1.92 $\times 10^{-1}$ | 2.63 $\times 10^{-1}$ | 3.36 $\times 10^{-1}$ |
| Ibex | n = 103 | 103 | 56 | 23 |
| Estimate | $b_1 = 7.56 \times 10^{-2}$ | $b_1 = 1.75 \times 10^{-2}$ | $b_1 = 1.06$** |
| SE | 7.78 $\times 10^{-2}$ | 1.07 $\times 10^{-1}$ | 2.16 $\times 10^{-1}$ |
| Jamesoni | n = 132 | 132 | 81 | 29 |
| Estimate | $b_1 = 2.53 \times 10^{-1}$*** | $b_1 = 9.34 \times 10^{-2}$ | $b_1 = -3.39 \times 10^{-1}$*** |
| SE | 4.33 $\times 10^{-2}$ | 8.08 $\times 10^{-2}$ | 3.99 $\times 10^{-1}$ |

Phylogenetic linear regression of species latitudinal range size against latitudinal midpoint for early Pliensbachian ammonites of the western Tethys calculated with GEE.

n, number of species considered in the analysis; SE, standard error; $b_1$, slope of the regression; MED, Mediterranean province; NWE, north-west European province.

***p < 0.001; **p < 0.01; *p < 0.05; no symbol = not significant.
However, it is important to note that the majority of these groups are terrestrial, and more generally, that the climatic variability hypothesis has been established for the terrestrial realm (Stevens 1989).

The latitudinal distribution of species range sizes for early Pliensbachian ammonites of the western Tethys and adjacent areas is consistent with the pattern corresponding to the modified climatic variability hypothesis of Gaston & Chown (1999). At the scale of the early Pliensbachian, a Rapoport effect is observed for NWE species, that is for species with range midpoints located at mid- to high latitudes (between c. 43°N and 55°N), whereas MED species, that is species with midpoints located at lower latitudes (between c. 25°N and 45°N), do not show any increase in their range size with latitude (Fig. 2; Table 2), but they disperse over larger distances than the northern ones on average (Fig. 3). In the marine realm, the influence of climatic variability is: (1) essentially limited to the epipelagic zone (i.e. between 0 and about −200 m); (2) of lower amplitude than in terrestrial environments; and (3) stronger at mid-latitudes corresponding to temperate zones (c. 35–60°N and S) than in polar regions (Helmuth et al. 2002; Parmesan et al. 2005; Clarke 2009). The influence of seasonal climatic variations on water temperature during the early Pliensbachian was thus probably very different between the NWE and MED provinces, because of their latitudinal position but also of their palaeogeographical configuration. The shallowness of the epicontinental sea and the proximity of emerged lands (Fig. 1B) probably made the NWE province much more sensitive to seasonal climate changes (Arias 2007) than the MED province. The latter was probably much less subject to seasonal variations in temperature and much more stable and homogeneous in terms of climate and environments, due to its more tropical position (Stevens 1989).

Regarding the studied area, the loss of a Rapoport effect in the intertropical zone expected under Gaston & Chown (1999) hypothesis should thus have been shifted to the north during this interval. Additionally, in our case, the presence of a latitudinally oriented biogeographical barrier largely limiting faunal exchanges in the western Tethys (Fig. 1B) may blur the existence of such a break in the graph resulting from the analysis at the scale of the early Pliensbachian (Fig. 2A). However, considering the distinct patterns of species range size distribution observed between the two provinces (Fig. 2B, C), we assume that the limit of the intertropical zone where the Rapoport effect should have vanished was located approximately at the same latitude as the biogeographical barrier (i.e. between 40°N and 45°N; Fig. 1B). Accordingly, the NWE province would have been characterized by a latitudinal gradient of temperatures and marked seasonal variations, and the MED province would have corresponded to a much more stable and homogeneous environment in terms of temperature fluctuations.

Differences in environmental stability during the Pliensbachian have been documented for these two provinces based on sedimentary, geochemical and palaeontological data (Hallam 1972; Smith & Tipper 1986; Dommergues & El Hariri 2002; Wignall et al. 2005; Arias 2007; Dera et al. 2009a, b; Dommergues et al. 2009; Dera et al. 2011a). Although several studies have estimated seawater palaeotemperatures for the NWE province (Saelen et al. 1996; Rosales et al. 2004a, b; van de Schootbrugge et al. 2005; Arias 2007; Dera et al. 2009a, 2011a), they did not formally establish the existence of a temperature gradient in this province during the early Pliensbachian. As for the MED province, samples (oyster shells and belemnite rostra) are apparently not well enough preserved to conduct geochemical analyses to estimate palaeotemperatures (Dera 2009). However, data based on palaeobotany, sedimentary indices, clay mineralogy, modelling experiments, and oxygen isotope analyses reveal a marked division of climatic zones for the longer interval of the Early Jurassic (Chandler et al. 1992; McArthur et al. 2000; Rees et al. 2000; Bailey et al. 2003; Wignall et al. 2005; Dera et al. 2009a, b, 2011a). The NWE province was characterized by a subtropical humid climate affected by seasonal mega monsoons leading to frequent northerly freshwater influxes, whereas warm and semiarid conditions prevailed in the MED province. Furthermore, the northern latitudinal position of the NWE province and the presence of connections with cold waters via the Viking Corridor to the north (e.g. Westermann 1993; Arias 2006; Dera et al. 2009a, 2015) and with warm waters of the Tethys Ocean via the Austro-Alpine and
Pontic provinces to the south (Dommergues & Meister 1991; Dera et al. 2009a; Dommergues et al. 2009) strongly suggest the presence of a latitudinal gradient of temperatures in the NWE province. As for the MED province, palaeoclimatic simulations have shown that: (1) the warmer sea-surface temperatures prevailing during the Jurassic implied larger heat transfers to the poles (Chandler et al. 1992); and (2) the peculiar geomorphology of the western Tethys margin (i.e. a north-westward bottleneck) was prone to tropical cyclone development (Marsaglia & Klein 1983; Krencker et al. 2015), which also favoured north-western heat transport and thus a homogenization of seawater temperature in this area. This supports the hypothesis of a Rapoport effect driven by climatic variability in the NWE province; the MED province belonging to the climatically more stable and homogeneous intertropical zone during the early Pliensbachian.

Rapoport effect through the early Pliensbachian

The early Pliensbachian corresponds to a climatically stable interval, except for its last chronozone during which several palaeoclimatic and palaeoenvironmental changes are recorded in the NWE province. The Davoei chronozone is indeed characterized by an increase in sea-surface temperatures of about 4°C (Rosales et al. 2004a; Dera et al. 2009a, b, 2011b; Price et al. 2016), a sea-level rise (Hallam 2001), more humid climatic conditions (Dera et al. 2009b) and a potential incursion of warm water masses from the Tethys Ocean (Dera et al. 2009a, 2015). These modifications probably obliterated the phylogenetic conservatism of ammonite range sizes (Zacaï et al. 2017) and could also potentially have modified their latitudinal distribution (this work).

Latitudinal range sizes of NWE species do not increase with latitude during the Jamesoni chronozone but show a significant Rapoport effect during the Ibex chronozone and obviously increase with latitude during the Davoei chronozone, although the relationship is not significant (Fig. 2; Table 2). This lack of significance is probably due to the low species richness characterizing the Davoei chronozone (Dommergues et al. 2009; Hardy et al. 2012; Table 2) and to a slightly less even spatial distribution of fossil localities during this chronozone compared to the two previous ones (Zacaï et al. 2018, fig. S2). This decrease in species richness could be related to the increase in sea-surface temperatures previously mentioned and to a fall in origination rates (Dera et al. 2010). Hence, contrary to what could have been expected based on the analysis at the scale of the early Pliensbachian (Fig. 2C) and on the known palaeoclimatic changes, the only chronozone that does not show a Rapoport effect for the NWE province is not Davoei but Jamesoni. For the MED province, each chronozone shows a different pattern of latitudinal distribution of species range

**FIG. 3.** Distribution of species latitudinal range sizes of ammonites from the western Tethys and adjacent areas for the three chrono-zones of the early Pliensbachian. Colour online.
size: no particular trend during Jamesoni, a boundary effect similar to the one observed at the scale of the early Pliensbachian during Ibex, and a significant decrease in range size with latitude (i.e. inverse of a Rapoport effect) during Davoei (Fig. 2). Latitudinal midpoints of MED species being exclusively located in the northern half of the province during the Davoei chronzone, this decrease in species range size with latitude could simply have resulted from a geographical bias: if no occurrences are recorded in the southernmost localities during this interval, only the northern half of the boundary effect recognized during the Ibex chronzone and at the scale of the early Pliensbachian (Fig. 2H and B, respectively) would be visible (Fig. 2E). However, the southernmost localities of the MED province do record several occurrences, meaning that this pattern does not result from a geographical bias. It is probably related to the absence of endemic species (i.e. species showing only one occurrence and thus null range sizes) in those southernmost localities. Those that occurred during Ibex went extinct, and no other endemic species replaced them. The climatic change is likely to have played a role in these extinctions and in the absence of new endemic species in these southern localities.

At the higher scale of the entire western Tethys, we observe a Rapoport effect during Jamesoni, no noticeable pattern during Ibex and an inverse Rapoport effect during Davoei (Fig. 2). These patterns are hardly interpretable as such because of the existence of the biogeographical barrier, but they can be compared with those found at the smaller scale of the province and are not predictable based on the latter (Fig. 2). For instance, the distribution of species latitudinal range sizes at the scale of the western Tethys shows a Rapoport effect, whereas it does not at the scale of the MED and NWE provinces (Fig. 2J–L). We may have concluded the existence of a genuine Rapoport effect and of a latitudinal gradient of climatic variability at the scale of the western Tethys if the biogeographical structuring had not been documented by previous studies (e.g. Dommergues 1982; Dommergues & Meister 1991; Meister & Stampafl 2000; Dommergues et al. 2009). Similarly, without knowledge of the biogeographical barrier, we could have ignored the existence of a Rapoport effect at the scale of the NWE province. This suggests that the influence of climatic variability on species latitudinal distribution is confined to ‘consistent’ biogeographical areas where species dispersal is not limited by physical barriers, which can explain previous findings stating that the Rapoport effect is a local phenomenon that essentially applies to the northern hemisphere, out of the tropics (Rohde et al. 1993; Blackburn & Gaston 1996; Rohde 1996; Gaston et al. 1998; Gaston & Chown 1999).

Temporal scale effects are also observed; patterns observed at the scale of the early Pliensbachian (Fig. 2A–C) do not result from the addition of patterns observed at the scale of the chronzone, regardless the geographical area under study (Fig. 2D–L). Thus, conclusions drawn at a given temporal scale can be inconsistent at another temporal scale. This calls for a multiscale approach when studying spatial distribution of extant species range size, in order to distinguish scale effects from genuine macroecological signal.

**Climatic variability hypothesis and species thermal tolerance**

Acknowledging the fact that climatic variability influences species range size means recognizing that the size and limits of their geographical ranges relate to their temperature tolerance. In the case of marine invertebrates, this relationship remains poorly known (Witman & Roy 2009). Because ammonites are extinct organisms, one can only rely on: (1) indirect evidence of such a relationship as an empirical tests are impossible; and (2) current knowledge of modern coleoids such as squids and octopods, to which ammonoids are more closely related than to nautiloids (e.g. Ritterbush et al. 2014 and references therein). Zacai et al. (2016) showed that long-distance dispersal of early Pliensbachian ammonites of the western Tethys was not related to morphological features (i.e. shell size and shape) but rather to environmental characteristics of the province to which they belong, and thus indirectly to temperature. In a series of studies on Early Triassic ammonoid biogeography, Brayard et al. (2006, 2007, 2009) argued that temperature directly influences species dispersal and distribution, meaning that these organisms were temperature-dependent. Numerous analyses of ammonoid shell δ18O show variation through ontogenetic stages, which probably means that these were exposed to different temperatures during their life (e.g. Lukeneder 2015 and references therein). Studies on the relationship between ocean temperature and cephalopod species range size are very scarce, although temperature might play an important role in the spatial distribution of these poikilothermic organisms (Lee et al. 1998; Boyle & Rodhouse 2005). In their study of Atlantic cephalopod biogeography, Rosa et al. (2008) have shown that the combined latitudinal and bathymetric range size of western neritic cephalopods increases with latitude and is strongly associated with the sea-surface temperature gradient and the extension of coral reef regions. According to Voss (1983) and Rathjen & Voss (1987), temperature is the prime factor controlling aspects of squid and octopod migration; and studies in the English Channel and the North Sea have shown that temperature and climatic variability play an important role in squid distribution and abundance (Robin & Denis 1999; Challier et al. 2005; van der Kooij et al. 2016).
Expanding this relationship to marine invertebrates shows that a consensus is far from being reached. For Briggs (1995), even if distribution patterns in local situations may be affected by factors such as food, salinity and oxygen, it is temperature that primarily controls species distribution on an oceanic or global scale. Sunday et al. (2012) studied the relationship between species temperature tolerance and range size for more than a hundred marine ectotherms and found that: (1) their observed geographical range boundaries closely match their potential latitudinal ranges (estimated on the basis of their thermal tolerance and extreme temperatures across latitudes); and (2) this relationship may lie as much with temperature as with factors closely correlated to temperature, such as dissolved oxygen availability. The analysis of Belanger et al. (2012) indicated that the large-scale geographical distribution of shallow marine bivalves (i.e. molluscs) can be predicted with 89–100% accuracy by temperature plus salinity and productivity (the last two having lesser but significant effects). Tomašových et al. (2015) showed that bivalve species inhabiting seasonally variable mid-latitude environments have broader thermal ranges than species inhabiting less seasonal tropical environments, supporting Stevens’ (1989) climatic variability hypothesis. By contrast, in a study based on shallow marine invertebrates of the northern hemisphere, Pappalardo et al. (2015) found that range limits predicted from water temperature and species temperature tolerance did not match well with real observations but rather corresponded to patterns of ocean circulation. In addition, using the marine mollusc database of Roy et al. (1998), Parmesan et al. (2005) showed the absence of correlation between seasonal variations in temperature at a given latitude and the median range of species living there, probably because of the broad ranges of tropical species associated with low seasonal variations. These contrasting results show that the relationship among ocean temperature, species temperature tolerance and species range size is not straightforward and may be taxon-specific and scale-dependent. For the early Pliensbachian ammonites of the western Tethys and adjacent areas, temperature seems to be an important controlling factor of their latitudinal distribution.

CONCLUSIONS

Known to biogeographers for more than a century, belatedly popularized by Stevens (1989) and extensively studied since then, Rapoport’s rule remains one of the most controversial patterns in macroecology. Numerous studies, mainly focusing on extant terrestrial vertebrates, have cast doubts on both its ubiquity and on the reliability of Stevens (1989) climatic variability hypothesis as an explanatory mechanism. The study of early Pliensbachian ammonites range sizes reveals patterns that are not as straightforward as those expected according to Stevens’ (1989) hypothesis. Early Pliensbachian ammonites have a dual pattern of distribution of latitudinal range sizes: in the northern biogeographic province (NWE), species range sizes show a Rapoport effect, while in the more tropical province (MED), they show a boundary effect and are in average larger than those of the NWE species. Considering the palaeoclimate, palaeoenvironment and the palaeogeographical configuration of the two provinces, this dual pattern can be explained by the alternative climatic variability hypothesis proposed by Gaston & Chown (1999). The latter better captures latitudinal seasonal variations and outlines the existence of a large intertropical zone with stable and homogeneous climate. Since climate was globally warmer in the Early Jurassic than in the Recent, the northern limit of this intertropical zone was certainly located at a higher latitude than today and probably coincided with the biogeographical barrier separating the NWE and MED provinces. This could explain both the larger dispersal of MED species, essentially limited by the presence of emerged lands in the northern and southern margins of the province, and the increase in species range sizes with latitude in the NWE province. This increase probably corresponds to a gradient of seasonal variations of temperatures from mid to high latitudes within this province. These results support the hypothesis that the Rapoport effect is a phenomenon that occurs mainly out of the tropics (Rohde et al. 1993; Blackburn & Gaston 1996; Rohde 1996; Gaston et al. 1998; Gaston & Chown 1999). Our multiscale approach further shows that this macroecological pattern is scale-dependent and may be labile through time. This probably explains the conflicting results of previous studies carried out at various spatiotemporal scales.

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DATA ARCHIVING STATEMENT

Data for this study (including phylogenetic hypothesis, locality distribution, dataset and GEE model results) are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.dh46139

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