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Par
Coraline MONTARIOL

Effet du réchauffement climatique sur la taille et la biogéographie des bivalves à une échelle macroécologique : une approche paléontologique

Thèse présentée et soutenue à Lille, le 25-02-2025
Unité de recherche : E.E.P (Ecologie, Evolution, Paléontologie)

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Written by
Coraline MONTARIOL

Effect of global warming on body size and biogeography of bivalves at macroecological scale: a palaeontological approach

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Résumé

Le réchauffement climatique actuel et ses conséquences sur les espèces terrestres comme marines sont une question écologique clef. Les observations des dernières décennies ont permis de mettre en lumières plusieurs modifications chez certains organismes, comme la tendance à devenir plus petit et plus isolés géographiquement lorsque les températures augmentent. Ces deux paramètres sont capitaux, puisqu'ils influent directement sur le statut de conservation des dites-espèces : en diminuant leur taille ainsi que leur répartition géographique, elles auront plus de mal à se maintenir dans leur milieu, et donc sont plus propices à la disparition. L'objet de ce travail est de déterminer si les observations faites à échelle humaine sont également visibles sur l'ensemble du Phanérozoïque, dans le temps profond. Le principal objectif est d'explorer l'impact et la relation possible entre la température, la taille et la répartition biogéographique des espèces, au travers de l'étude empirique issue du registre fossile d'animaux marins ectothermes - les bivalves. La première étude évalue l'hypothèse que la dynamique de biodiversité des bivalves a été marquée par les changements biotiques et abiotiques du milieu sur l'ensemble du Phanérozoïque. Contrairement à ce qui était attendu, la diversité globale des bivalves ne semblent pas avoir été perturbée, et augmente quasi continuellement jusqu'à aujourd'hui. Cette résilience – notamment face aux cinq crises biotiques majeures – peut être expliquée par la successions de quatre faunes évolutives dans le temps, qui elles, répondent aux changements écologiques globaux. La deuxième étude estime l'influence de la température sur la taille et la répartition biogéographique des bivalves à grande échelle. Similairement à la diversité, les bivalves ne montrent pas de variation de taille ou de répartition géographique lorsqu'on considère l'ensemble des étages du Phanérozoïque ; par contre, les espèces présentent une certaine sensibilité lors des périodes de réchauffement et de refroidissement. La réponse macroécologique est donc complexe, mais tend à suivre ce qui est observé de nos jours. L'étude finale explore donc ce lien entre température, taille et répartition biogéographique au regard de deux règles macroécologiques fondamentales liées à la répartition latitudinale des espèces : les lois de Bergmann et de Rapoport. Contrairement à ce qui serait attendu, les bivalves montrent une diminution de l'aire de répartition géographique aux pôles, mais une augmentation générale de leur taille, et ce, identiquement lors des périodes de réchauffement que des périodes de refroidissement. Ensemble, ces résultats mettent en perspectives les effets du réchauffement climatique observés aujourd'hui, soulignant la complexité des réponses sur de grandes échelles de temps et d'espace.

Keywords : réchauffement climatique, taille, paléobiogéographie, macroécologie, macroévolution, bivalves

Abstract

Global warming and its consequences for both terrestrial and marine species is a key ecological issue. Observations over the last few decades reveal a variety of changes affecting certain organisms, notably the tendency for them to become smaller and more geographically isolated as temperatures increase. These two parameters are crucial, because they directly influence the conservation status of these species: by reducing their body-size and their geographical distribution, it will be more difficult for them to maintain their position in the environment, and therefore they are more likely to become extinct. The aim of this work is to determine whether the observations made on a human scale are also visible throughout the Phanerozoic, in deep time. The main objective is to explore the impact and possible relationship between temperature, body-size and the biogeographical distribution of species, based on an empirical study of the fossil record of marine ectotherms - bivalves. The first study evaluates the hypothesis that the biodiversity dynamics of bivalves were affected by biotic and abiotic changes in the environment throughout the Phanerozoic. Contrary to initial expectations, the overall diversity of bivalves does not appear to have been disrupted, and has increased almost continuously to the present day. This resilience - particularly in the face of five major biotic crises - can be explained by the succession of four evolutionary faunas over time, all responding to global ecological changes. The second study estimates the influence of temperature on the body-size and biogeographical distribution of bivalves on a large scale. Similar to diversity, bivalves do not show variation in body-size or geographical distribution across all stages of the Phanerozoic; however, species show a certain sensitivity to periods of warming and cooling. The macroecological pattern is thus complex, but tends to reflect what is observed today. The final study explores the link between temperature, body-size and biogeographical distribution in the light of two fundamental macroecological rules associated with the latitudinal distribution of species: Bergmann's and Rapoport's rules. In contrast with the expected trend, bivalves show a decrease in their geographical distribution at the poles, but a general increase in their body-size, equally during periods of warming and cooling. Together, these results provide a perspective on the effects of current climate warming, emphasising the complexity of responses over large scales of time and space.

Keywords : warming, body size, paleobiogeography, macroecology, macroevolution, bivalves

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I dedicate this thesis to all the little girls who have heard that their dreams are too big.

Je dédie cette thèse à toutes les petites filles à qui on a dit qu'elles avaient des rêves un peu trop grands.

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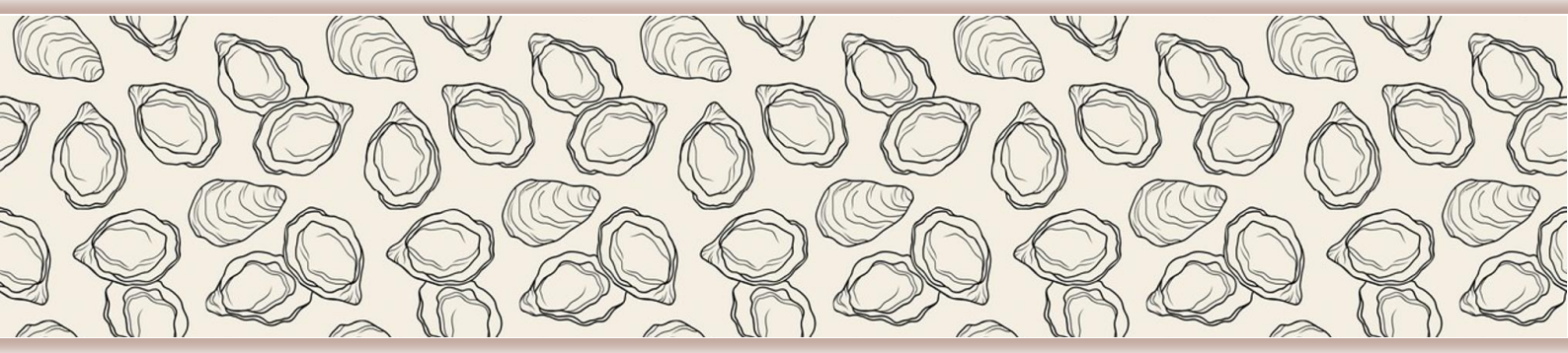


"To anticipate the future, we need to know the past, because the events of this world are always linked to the times that preceded them."

— Nicolas Machiavel

1

General introduction

Preface

The majority of animals are invertebrates (Wilson 1987), and they present a wide diversity of forms and habitats. Due to climate change and anthropogenic modifications, many species are in decline (Dirzo et al. 2014; Eisenhauer et al. 2019). Marine bivalves can clearly highlight the problems associated with the acceleration of extinction phenomena and, more broadly, the profound modification of ecosystems that this entails. Their wide range of traits and ecological adaptations allowed them to be largely distributed worldwide. Because bivalves are suspension-feeding animals, they are commonly used as biomarkers to investigate the presence of heavy metals and dissolved pollutants (Klumpp & Burdon-Jones 1982; Burns & Smith 1981; Rainbow 2018; Cartry et al. 2017). They are also key control of the chemical factor balance of their habitat by participating of the recycling of organic matter (Smyth et al. 2018; Ray & Fulweiler 2020),. In addition, bivalves have been involved in human nutrition since prehistoric times (Bignon et al. 2008; Amesbury 2007). They are known to be the third main part of the current production of fish and seafood (FAO 2015).

Understanding the evolution of this group and the control of its ecological changes over time are crucial issues today, considering the significance of bivalves for humans and their environment. Such questions are largely addressed by paleobiodiversity, where the relative abundance and preservation of these mollusks greatly facilitate the study of their evolution during the Phanerozoic. Consequently, since the early 1970s, a large number of macroecological analyses have been carried out on body-size change, paleogeography and group distribution (Flessa & Jablonski 1985; Crame 2000; Jablonski et al. 2000; Roy et al. 2000; Cope 2002; Jablonski et al. 2006; Damborenea & Echevarria 2015; Tomašových et al. 2016). Bivalves are also used in macroevolutionary models for testing hypotheses such as Cope's rule (Hallam 1975; Jablonski 1997) or extinction risks and survivorship over time (Aberhan & Baumiller 2003; Harnik 2011; Ros & Echevarria 2011; Huang et al. 2015).

As a result, the class of Bivalvia is well documented, although it remains significant spatial and temporal heterogeneity between the various studies, making it difficult to establish a clear overall picture of its evolutionary history. In this PhD project, we aim to fill the aforementioned knowledge gaps by performing macroevolutionary and macroecological studies for the whole Phanerozoic. We want to understand the biodiversity patterns of marine bivalves and their relationship to past climate change, by **(1) documenting the influence of global ecological change on their palaeobiodiversity**; **(2) examining the relationship between size, biogeographic range and temperature**, and **(3) observing latitudinal patterns of size and biogeographic distribution as a function of temperature**.

General introduction

1.1. Biodiversity, ecology, and evolution: historical perspectives

1.1.1. From biodiversity to evolution

Today, simply looking out of your window reveals the vast diversity of life: from plants to animals, from the smallest unicellular organisms to the largest mammals. There are over 8.75 million species on Earth (IUCN 2016; Mora et al. 2011; number revised upwards by Wiens 2023). This diversity in form and size also implies a wide range of habitats and biological processes essential for the survival of each species. Reproduction can be sexual, as in humans, or asexual, as in Holoturians (Dolmatov 2014). Different species have varied feeding habits and unique survival strategies. Despite the immense complexity of life, scientists have recognized a fundamental unity since the 16th century (Belon 1555). This unity was first observed through comparative anatomy (Cuvier et al. 1835) and ontogenetic stages (Haeckel 1866; Gould 1977). In the 20th century, these observations was further supported by molecular composition and successive discoveries about RNA and DNA (Watson & Crick 1953, and Rosalind Franklin's pioneering work the same year; Holley 1965). The unity of all living beings forms the foundational basis of biological classification (Linnaeus 1735; Field et al. 1988).

It is therefore essential to consider life in terms of both its diversity and its unity: this is the principle of evolution. Without the formalization of the theory of evolution in the 19th century (Wallace 1871; Darwin 1859), the accumulation of naturalist observations would have been just a vast record with no connections. By understanding the crucial role of the environment and its changes over time in the diversification of life, a continuous chain can be established between what exists now and what existed in the past. The transmission of traits, as discussed by Charles Darwin and Alfred Wallace, was later incorporated into the modern

synthesis of evolutionary theory. Integrating Mendelian genetics, natural selection, and modern systematics, this synthesis developed between the 1930s and 1950s. It was formalized through the work of scientists such as Theodosius Dobzhansky, Ernst Mayr, Julian Huxley, and George Gaylord Simpson (Huxley 1942 ; Mayr 1942, 1996 ; Simpson 1944, 1953 ; Dobzhansky 1937,1949). This theory unifies the principles of genetics and evolution, explaining how genetic variations within populations can lead to the evolution of species through natural selection and other evolutionary mechanisms.

Nowadays, there are two parameters for investigating the evolution of species: microevolution and macroevolution. Microevolution, as its name suggests, is concerned with the observation of intraspecific variations, and more specifically allelic frequencies within populations. Models are generally living beings with short life cycles (bacteria, insects, plants) that can be grown and maintained in the laboratory (Dobzhansky 1937; Brock 1970; Hendry & Kinnison 2001; Plutynski 2007). Microevolution can be used to examine the influence of different selection pressures or evolutionary mechanisms, for example by modifying access to resources. The choice of living models with short generations is particularly useful for highlighting genetic drift (Kimura 1983; Hallatschek et al. 2007). In addition, across all the experiments conducted, it is also possible to examine the speciation process when mutations have accumulated sufficiently within the populations observed (Irwin et al. 2001).

In contrast, macroevolution is concerned with evolutionary patterns and processes on a larger scale. It focuses on the study of species as a whole, or taxonomic groups of higher rank (Simpson 1944; Gould 1982; Stanley 1979; Mayr 1982). The aim of macroevolution is to answer questions related to the dynamics of a species over large scales of time and/or space, such as the role of extinctions and originations in observable diversity. In short, macroevolution is concerned with the tempo and mode of evolution. Tempo refers to the speed of evolutionary change, whether rapid or slow, while mode describes the manner in

which evolutionary change occurs and accumulates (or does not) over time. This concept considers the relationship between evolutionary change and ecological as well as geological factors (Plutynski 2007 ; Saupe and Myers 2021).

1.1.2. From biodiversity to biogeography

Understanding the distribution of species in space and time is one of the most fundamental questions in ecology and evolution. Theophrastus and even Pliny the Elder formulated the first hypotheses in Antiquity. However, it was not until the 18th and 19th centuries that the first naturalists - driven by the great biological explorations - really began to document variations in the geographical distribution of species. Thanks to these observations, the first known mechanisms were highlighted, such as the latitudinal gradient of biodiversity or provincialism (Wallace 1876; Brown et al. 1996; Gaston 2003). Despite this long history of successive discoveries, the understanding of the main drivers of the distribution of life remains incomplete. The necessity of addressing these issues becomes more urgent in recent decades when it is essential to predict changes in biodiversity patterns in response to global change, from climate change to habitat loss or fragmentation (Brown et al. 1996; Jetz & Rahbek 2002; Whittaker et al. 2005; Gaston 2009; Grill et al. 2019).

Biodiversity, or the image we paint of it, is closely linked with the regions it occupies. The appearance of the term "hotspot" of diversity is a clue to the public understands of a well-known process: life is not uniformly distributed across the Earth. When looking at different regions of the globe, we can expect to find different species but also different degrees of taxonomic richness. This disparity can be fully understood only by taking into account the evolutionary history of species and of the Earth. During the Phanerozoic, the continents constantly joined together and became more or less isolated from each other (Valentine & Moore, 1970 ; Smith & Hallam, 1970). This succession of isolation and convergence has contributed to the various colonisations and diversifications, which form

today's biodiversity (Simpson 1980, Mayr 1982). As a result, these natural cycles have shaped the biodiversity.

The word biogeography, which refers to the "geography of nature" (Lomolino et al. 2010), is in fact a recent legacy. It only began to make sense in the 18th century, when Carl Linnaeus, the father of systematics, began to think about the geography of species distribution. His first demonstrations were still in the embryonic stages, and generally focused on a regionalisation highly permeable to biblical beliefs related to Noah's Ark (Candolle 1820; Nelson 1978). He defined each species as capable, when the waters subsided, of migrating to a preferred environment (Browne 1983). Buffon was quick to oppose him, underlining that species are not perfectly adapted to their environment, but instead their distribution is the result of observed climatic changes (Buffon 1770). This is the "law of distribution of forms", defining that similar environments in two distinct regions can have different species with similar attributes (Browne 1983). Thanks to these two pioneering works, notably Alexander Von Humboldt (Humboldt & Bonpland 1805) produced the first maps of living organisms. This fertile breeding ground of ideas led to the identification of biotic zones and the environmental factors that determine them (Candolle 1820; Lieberman 2012).

This regionalisation of life is quickly followed by concerns about the significance of the historical heritage of species in these regions. Therefore, palaeontology enables scientists to establish the link between the current distribution of a species and its distribution in the fossil record (Sepkoski 1997). This crucial component largely inspired Darwin to explain why species sharing the same area are often more closely related than those found in a distant region (Darwin 1959). Wallace, who proposed a global pattern of species distribution in which the higher taxonomic levels are spread over the globe, while the lower levels are confined to more precise localities (Wallace 1876), later extended this vision. Since then, our understanding of the distribution of species has grown steadily and is now one of the main tools for understanding biodiversity.

1.1.3. Body-size : key parameter to ecology

Body size is one of the most studied life-history traits in ecology. Its investigation goes back even before the creation of the discipline, formalised by Ernst Haeckel in 1866, due to its plastic and genetic characteristics (Wolpert et al. 2000; Crozier & Hutchings 2014). Bergmann (1847), for example, formulated the link between body size and the geographical location of a species for the first time. One of the reasons for this attractiveness is the ease of quantifying the parameter; notably, it allows a large amount of biological information to be obtained. Body size is linked to many fundamental biological properties such as fecundity, locomotion, metabolism and ingestion (Peters 1993; Calder 1996). In addition to individual properties, body size is also involved in population ecology (Kingslover & Huey 2008; Savage et al. 2004). Size can affect the fitness of individuals within a population, making it an essential marker in intraspecific interactions. Nevertheless, it also plays a role in interspecific interactions, directly influencing the dynamics of communities and food webs (Woodward et al. 2005). As a result, body size is not a trivial parameter. It is at the heart of a veritable web of influence that has a more or less direct impact on ecosystems (Brown et al. 2007).

Although body size is an important parameter for organisms, it is subject to directional selection. Responding to environmental factors such as temperature or resource availability, body size can vary in time and space in parallel with these ecological forcings. On the human observation scale, the removal of the largest specimens - particularly through fishing - leads to a significant reduction in size among predators (Shackell et al. 2010). In response, the entire trophic chain is disrupted, leading in the extreme cases to changes in behaviour or in mortality linked to predation (Audzijonyte et al. 2013). The factors controlling body size are numerous and potentially interactive, complicating the prediction of size variations within an ecosystem. Nevertheless, it now seems essential to predict and understand these changes, as body size occupies the epicentre of many biological and ecological properties. In the

context of global warming, it remains important to consider the ecological consequences of possible changes in body size.

1.1.4. Range – body-size relationship and its implications

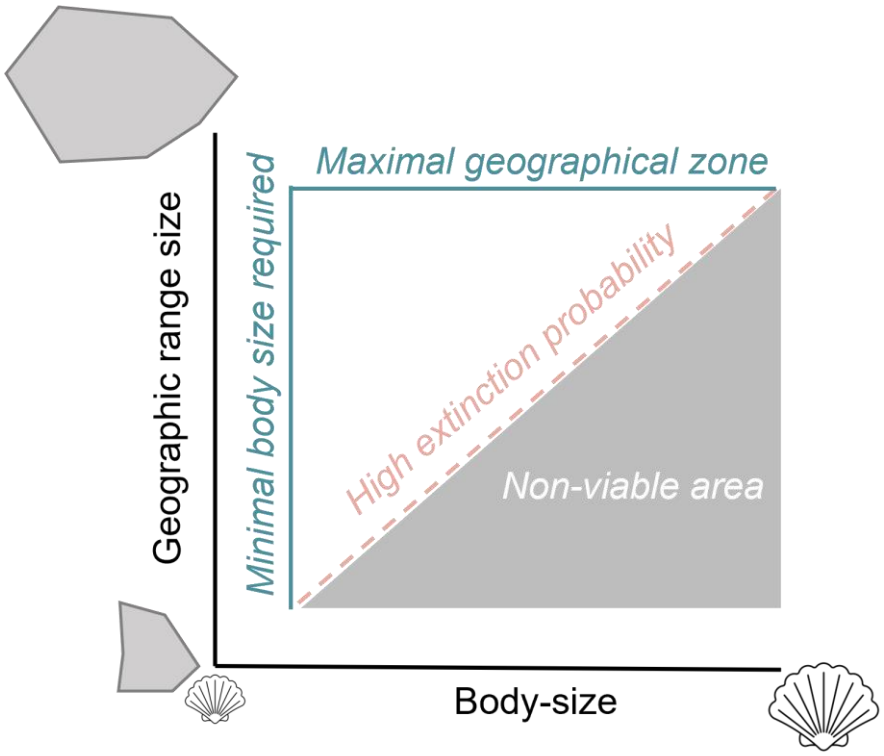


Figure 1 : Empirical model describing the geographic range size–body relationship (modified from Diniz-Filho 2023)

One of the most important parameters explaining the variation in species distribution is body size (Brown 1995; Gaston & Blackburn 2000). Body size is directly dependent on the physical space and resources allocated between species (Brown & Maurer 1987, 1989). This is the cornerstone of fundamental macroecology (Brown 2019). Each species is subject to a certain number of ecological and/or evolutionary constraints, restricting the relationship between range and body size through various processes of colonisation, speciation or extinction (Brown & Maurer 1987, 1989). It is a triangular relationship where the upper horizontal limit corresponds to the maximum geographical area that species can potentially occupy (geographical constraint) and the vertical limit corresponds to the minimum body size that a species can reach (physiological constraint) (Fig 1). The diagonal junction between

both is the minimum viable geographic range for species to persist in the long term (Gaston & Blackburn 1996).

In general, larger organisms are considered to have more extensive ranges, as they disperse faster and more efficiently. Therefore, species with a large body size are better able to fulfil their distribution potential (Gaston 1994; Gaston & Backburn 1996). In addition, larger species have greater energetic demands, and occupying a larger space enables them to acquire sufficient resources to support a viable population size sufficient to maintain itself (Swihart et al, 1988). Smaller species, on the other hand, may have more varied geographical ranges (Gaston & Blackburn, 1996).

Consequently, all species have a zone of non-viability, which is directly linked to their body size and geographical distribution. Beyond the minimum viable geographic range, organisms are liable to extinction or, at least, have a low probability of surviving over time (Gaston & Blackburn, 1996). The more distant a species is from this minimum viable geographic range, the more likely extinction is. It is a relatively reliable and widely used predictor (Rosenfield, 2002; Diniz-Filho et al, 2005; Newsome et al. 2020; Diniz-Filho, 2023).

Moreover, this relationship has significant ecological implications. When the body size decreases in a species, usually in response to environmental pressures such as global warming, the geographical range size may be restricted (Gardner et al. 2011a; Sheridan & Bickford 2011). This reduction can in some cases lead to a decline in genetic diversity and enhanced vulnerability to local perturbations (Jenkins et al. 2013; Purvis et al. 2000). A reduced geographical range can also limit essential ecological interactions, such as pollination and seed dispersal, thereby affecting the structure and deep functioning of ecosystems (Klein et al. 2007; Memmott et al. 2004). Understanding these interdependent mechanisms is still incomplete, but it is essential for studying past and future ecosystems.

1.2. Linking ecology and evolution at large scales

1.2.1. Macroevolution : Phanerozoic, radiation events and biological crises

While current ecologists are interested in the evolutionary dynamics of populations, this is also one of the major issues in palaeontology: what was the diversity of the different groups currently known? What mechanisms influence their dynamics? What role does the fossil record occupy in the history of life? These issues, highlighted by the first theories of evolution (Darwin 1859), underline the importance of considering the fossil record in order to understand the entire evolutionary history of a species. The objective is to document evolutionary trends over long-term, geological timescales, going well beyond the simple observation on a human scale (Foote et al. 2007a).

The first diversity curves covering the entire Phanerozoic were established towards the end of the 19th century (Raup & Sepkoski 1982; Sepkoski 1981). These studies revealed various major events affecting the biodiversity and species. Major periods of radiation or crisis have profoundly influenced the biosphere, redistributing the cards and changing both the composition and interactions of communities (Hallam & Wignall 1997; Jablonski 1986, 2001). Although there is an evolutionary continuum within each species, biological crises lead to major extinctions and radiation events, often associated with faunal renewal (Bambach 2006; Bambach et al. 2004; Sepkoski 1986).

Most biotic crises are the consequence of large-scale environmental disturbances of varying magnitude and severity (Hallam 1998; Bond & Grasby 2017). As today, past biodiversity is primarily driven by major environmental changes (Roberts & Mannion 2019). The fossil record contains a large number of variations in richness over time, but five crises are widely recognised as outweighing all others: the so-called 'Big Five' (Raup & Sepkoski 1982; Erwin 2006; Fig 2).... Today, it is recognised that the largest of these events occurred at the end of the Permian (Baresel et al. 2017; Benton 2015a; Erwin 2006), with a generic

extinction rate over 50%, equivalent to three quarters of all species (Bambach 2006; Stanley 2016). Nevertheless, the others, respectively at the end of the Ordovician, Devonian, Triassic and Cretaceous periods, had also a major impact on biodiversity. Although the statistics vary depending on the authors and the period (Raup & Sepkoski 1982; Barnosky et al. 2011; Escarguel et al. 2011), there is a consensus about the fact that during these periods the greatest number of extinctions occurred (Benton 2003; Erwin 2006; Stanley 2016).

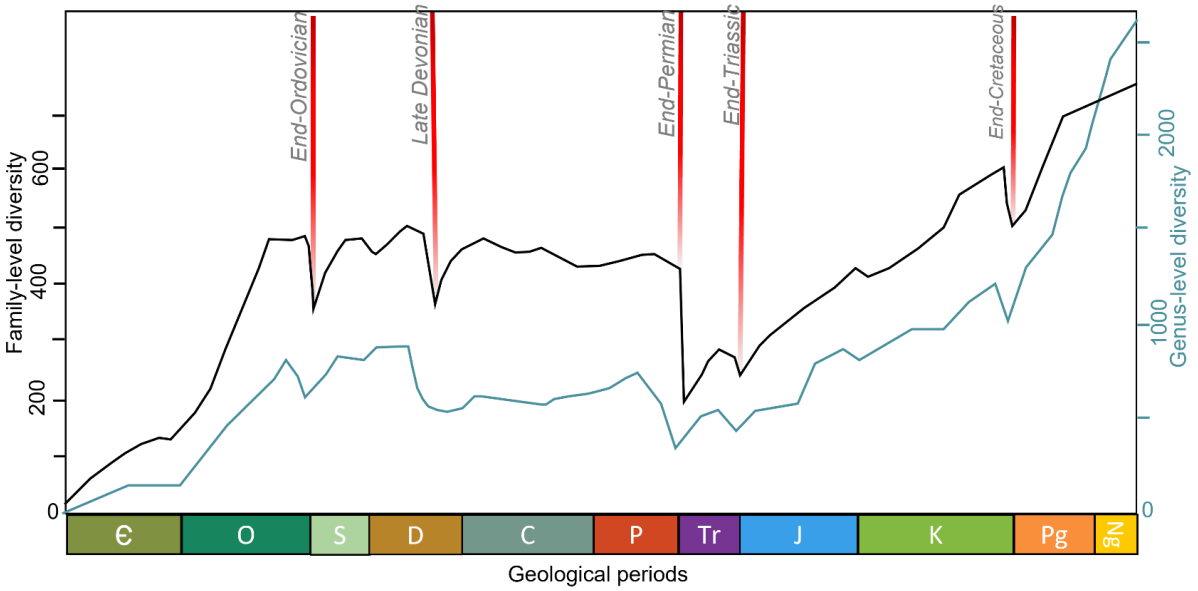


Figure 2 *: Evolution of the taxonomic diversity through the Phanerozoic. Vertical red lines indicate the 'Big Five'* marine mass extinctions, in black the family and in blue the genus diversity (modified from Raup & Sepkoski 1982 and Alroy et al. 2008)

This overview, allowed by macroevolution, is the subject of numerous debates in the scientific community. The intensity of extinctions, as well as their rate or the possibility of a cycle specific to each species, is still the focus of lively discussion among specialists (Barnosky et al 2011; Eldredge 1976). This is also the case for the processes leading to the extinction of a species, whether in the context of a major biotic crisis or 'naturally' (Alvarez et al. 1979; Flessa & Jablonski, 1985; Barnosky 2001; Alroy 2008; Bond & Wignall 2014).

However, in addition to the major biotic crises, biodiversity has never been as important as it is today (Fig 2). This is due to the frequent emergence of new species, particularly during periods of low diversity (Alroy 2008). This paradox is closely linked to the

ability of 'survivors' to colonise new ecological niches vacated by the disappearance of other species, and then to diversify. This theory, formulated by Erwin (1993; 2001), is one of the preferred hypotheses for explaining the dynamics of radiation following mass extinctions. Thus, when a species colonises a new area, it will be prone to either ecological diversification or morphological diversification. This is known as adaptive radiation (Erwin 2015; Jablonski 2017). But not all taxa are equal and do not tend to have the same dynamics. Some will enjoy extensive radiation, while others will never recover; they remain depleted and tend to disappear gradually (Jablonski 2002; Barnes et al. 2021).

The research work that constitutes the current corpus of knowledge is becoming increasingly necessary as global change in the 21st century precipitates the decline of many species and their habitats (Barnosky et al. 2011; Bellard et al. 2012; Briggs 2017; Worm & Lotze 2021): a real challenge, already described as the 6th mass extinction. Understanding the mechanisms intrinsic to past extinctions and origination/radiation phenomena is a major issue in predicting future trends.

1.2.2. Macroecology : spatial component of large-scale evolution

Since Linnaeus, many intrinsic and extrinsic factors have been identified as possible explanations for variations in the geographical range size of species. Two scales can be distinguished: the ecological scale, which is based on human observation time, and the historical scale (Brown & Lomolino 1998; Sheth et al. 2020). While ecological observation has highlighted current pressures on flora and fauna, many questions require a more global approach. How did a species reach its current geographical distribution? Is there a link between the geographical distribution of an ancestral species and its descendants? What are the biogeographical responses of taxa to environmental disturbances? Is there evidence of similar behaviour to what we find in today's biodiversity?

De facto, to answer these questions we cannot extract the observations from a temporal dimension (Vogler et al. 2003, Escarguel et al. 2011). The evolution of a species' range sizev is closely linked to its evolutionary history, as well as to large-scale variations. The removal or creation of physical barriers can lead to profound changes in the geographical range of a species. Areas that were previously isolated can be connected to new regions, while those that were connected could gradually become isolated. This encourages exchanges between communities or, conversely, leads to endemism or even speciation (Vermeij 1991; Hoorn et al. 2010).

Initially, it was considered that a species saw its geographical range expand throughout its existence, creating a relationship between the age of a taxon and its biogeography (Willis 1922). Thanks to the fossil record and its study, today it is possible to understand that the relationship is not as linear as imagined at the beginning of the 20th century. In fact, when a species is considered, it first tends to extend its geographical range and then, over time, decline until it becomes endemic and disappears (Foote et al. 2007a; Liow et al. 2010). Range size is also known to be sensitive to speciation events (Jablonski & Roy 2003; Pigot et al. 2010). The greater the number of species living in the same ecology in a given area, the less space is available. The relationship between the geographical range size and the rate of diversification of the same species is negative.

The study of geographical ranges is neither as simple nor as clear-cut as one might think. A multitude of factors need to be taken into account, depending on both the species itself and its surroundings, as well as the global environment. A deep understanding of biodiversity patterns cannot be achieved without this holistic approach (Morueta-Holme & Svenning, 2018; Sheth et al. 2020). This is the foundation of macroecology as defined by MacArthur (1984). To understand the entire ecological distribution of a taxon, it is necessary to study it as a whole (Brown, 1995). Macroecology is primarily a research method based on

observation or statistical modelling between organisms and their environment (Brown, 1995; Gaston & Blackburn, 2000).

The challenge is even greater when we look at deep time. The existence of palaeogeographic and palaeoenvironmental changes constitutes a crucial parameter in the influence of past climates on the geographical range of species (Janis 1993; Alroy et al. 2000; Erwin, 2015). Just as the dynamics of a species cannot be considered without taking into account a large temporal scale, macroecology is entirely dependent on time and space (Rosenzweig 1995; Escarguel et al. 2011). Conserving almost 500 million years of ecosystem history enables us to follow the temporal distributions of a taxon from almost the origin of all the clades present in today's biodiversity. The palaeobiogeography of a taxon can be compared not only with its evolutionary dynamics, but also with all the major events to which it is related (Hannisdal & Peters, 2011 ; Benson et al. 2015) Thus the palaeontological studies carried out are an essential key to the comprehension of the phenomena observed by ecologists (e.g. Kiessling & Aberhan 2007; Fritz et al. 2013).

1.2.3. Connecting macroecology and macroevolution: environmental changes

Two key dimensions connecting macroevolution and macroecology influence environmental variations: space and time. Initially, ecological research focused on how spatial differences in environments affected species distribution. In contrast, temporal variation impacts both the ecology and evolution of organisms. While spatial influences are relatively straightforward to observe within a human scale, temporal influences are more elusive and are thus more effectively studied through palaeoecology, which offers a long-term perspective on populations and their environmental contexts.

A multitude of environmental parameters can affect biodiversity. Observing them and defining the time scale is therefore essential to understanding the trends and patterns of living organisms. Species can respond to these environmental variations in different ways,

adapting their strategies or life habits accordingly, as well as the intensity of this response. A drastic change will generally generate a response of the same magnitude in the organism in question, or its decline if it is unable to cope with the changes.

Over the past few decades, there has been increasing interest in studying life-history traits in response to environmental variations (Angilletta et al. 2004). Examining biological patterns on a large geographical scale enables researchers to engage with both ecological theories and evolutionary concepts. The hypotheses explaining the interaction between life traits and environmental parameters are linked to speciation and adaptation for example. Despite the extensive research conducted on both past and recent biodiversity, understanding how environmental factors influence species remains a complex and broadly challenging question.

1.3. Environmental variations and constraints on biodiversity

1.3.1. Climate change

Extensive research over recent decades has examined climate change and weather variations (Intergovernmental Panel on Climate Change 2019; Urban et al. 2016; Foden et al. 2018). It is well-established that global temperatures are rising, and since the mid-19th century, both the polar ice caps and spring snow cover in the Northern Hemisphere have been decreasing. Global mean temperatures are now approaching the upper bound of what has been observed over the past 2 million years (Callendar 1938 ; Steffen et al 2018).

However, what is climate change? Firstly, it refers to a worldwide change in climate over time. Climatic changes at all scales are fundamental to the Earth's evolution. There are a multitude of factors explaining these changes, which can be both extrinsic and intrinsic to the Earth system. These include solar radiation, volcanism and even the position of the continents. Over the past four billion years, the Earth has experienced greater climate

variability than that suggested by the last few hundred thousand years of observation (Scotese et al. 2021; Song et al. 2019 ; Fig 3).

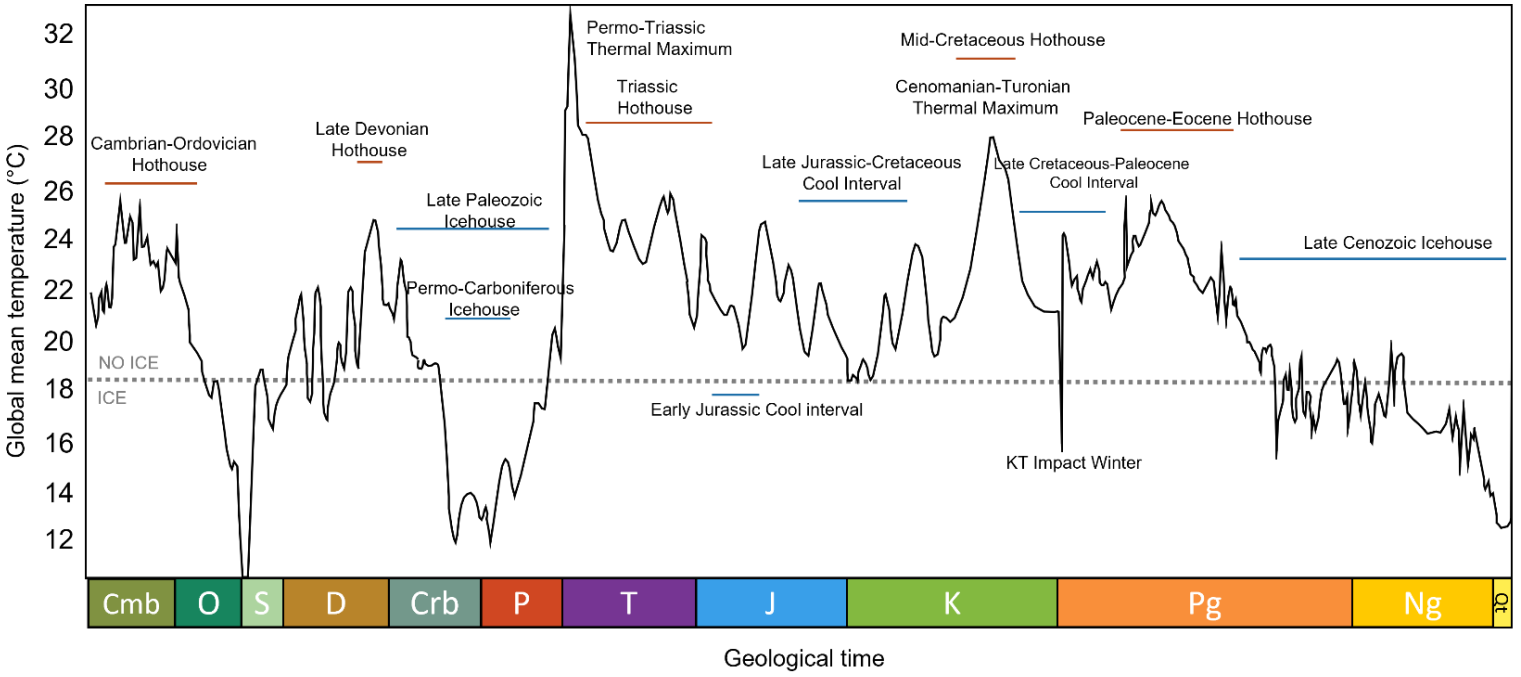


Figure 3 : Global atmospheric temperature through the Phanerozoic (from Scotese et al. 2021). The doted line represent the shift between periods with no permanent icecap (<18°) and those with permanent icecap (>18°).

Climate is rightly related to atmospheric CO_2 levels. Since the industrial revolution, human activities have played a large part in the increase in CO_2, and by extension in the greenhouse effect and the alarming global warming of recent years. However, given past variations, it is vital to understand the mechanisms of climate change over the long term, using geochemical tracers from sedimentary records. The palaeoclimatology and geology communities have long studied these geochemical tracers. The nature and form of these markers vary widely. They can range from the density of stomata (Konrad et al. 2020) to the indirect measurement of an isotope. Nevertheless, the most successful studies do not hesitate to consider a series of geochemical tracers to trace the carbon cycle in relation to tectonic constraints, including $\delta^{18}O$,$\delta^{13}C$,$\delta^{34}S$, the $^{87}Sr/^{86}Sr$ ratio and Mg/Ca (Van der Meer et al. 2022; Mills et al. 2019).

Nowadays, it is undeniable that the climate changes highlighted above are linked to evolution on a broader scale. The relationship is further complicated by the often positive or negative feedback from one side to the other (Erwin 2009). Profound biological changes often have climatic repercussions, and conversely, changes in the environment can disrupt ecosystems and biodiversity (e.g; Parmesan 2006 ; McGaughran et al. 2021).

1.3.2. Effect of the climate on biodiversity

1.3.2.1. Abiotic factors: climate change impacts marine ecology

The distribution of the continents is the first-order control on climate change. The arrangement of the continents is directly linked to the circulation of the air-ocean system (Rohmstorf, 2002). Consequently, the fragmentation or assembly of supercontinents throughout the Phanerozoic may have led to glaciation events or warm periods (e.g. Crowell 1978; Ramstein et al. 1997; Donnadieu et al. 2014; Brune et al. 2017). Plate tectonics also modifies the topography and interrelationship of the continents, resulting in a change in the surface area of the latter in the tropics and in the height of the mountain ranges. Acting like a cycle, these parameters together allow for the establishment of ocean floors, with less dense crust, but also shallower basins with large epicontinental seas (Thiede, 1982; Kauffman, 1984; Shaw, 2016.).

In addition, the existence of ice at the poles is crucial in maintaining the global heat balance. The albedo phenomenon effectively reflects insolation (Stephens et al. 2015). Therefore, the loss of ice and the cryosphere reduces this albedo effect. Solar radiation is less refracted, leading to a gradual increase in global temperatures from the poles to the equator. Seawater ice is also important in the ocean's freshwater and salt balances (Polyakov et al. 2020). Salt concentration is increased by the formation of these ice caps. The formation of icebergs drifted by currents and winds transports large quantities of freshwater to more temperate zone where it can melt.

The melting of glaciers and icecaps and the release of stored land water into the sea cause a global rise in sea level (Miller et al. 2005). This variation in global mean sea level is a direct result of climatic variations. During periods of warming, the sea level will rise, while during periods of cooling, the formation of ice reduces the volume available. By creating these marine transgression and regression events, the length of available coastline and the presence of islands can be affected. The alteration of these habitats has a direct impact on the organisms relying on them, particularly island endemic fauna and flora or coastal communities (Hughes & Connell, 1999; Zong & Tooley, 2003; Fitzerald et al. 2008).

Global warming has a directly linked incidence on carbon dioxide (CO2) concentrations. This is mainly due to the greenhouse effect, which causes not only an increase in atmospheric temperatures but also oceanic temperatures through absorption by surface waters, creating significant changes in the marine system across the globe. The oceans are considered to be 'carbon pumps', absorbing up to 25% of CO2 emissions since pre-industrial times (Gruber et al. 2019; Garcia-Soto et al. 2021). Atmospheric CO2 will tend to increase the formation of carbonic acid, lowering the pH that causes ocean acidification (Caldeira & Wickett 2003). And because this acidification exists, numerous studies carried out over the last few decades have shown a negative (albeit variable) effect on calcifying organisms such as bivalves (Kroeker et al. 2010; Hoegh-Guldberg et al. 2017; Lemasson et al. 2017).

And in parallel with carbon dioxide levels, oxygen concentration also plays a key role in the oceans. As the basis of life for the majority of living organisms, oxygen is essential for defining the environmental and ecological limits of these organisms: there is a critical threshold for each species, below which it cannot live and develop properly (Childress & Seibel, 1998 ; Pörtner, 2001 ; Seibel & Deirssen, 2009 ; Pörtner & Lanning, 2009). In the marine system, oxygen is acquired in the most superficial layers of the water column, mainly through photosynthesis or gas exchange with the atmosphere, and its concentration

decreases as we consider deeper layers of water. The increase in temperature reduces the solubility of oxygen, and therefore its availability in surface waters. Photosynthesis and, more generally, biological activity are reduced, upsetting oceanic stratification and other parameters which, in the end, put in place a negative feedback on dissolved oxygen levels (Schmidtko et al. 2017; Stramma & Schmidtko 2021).

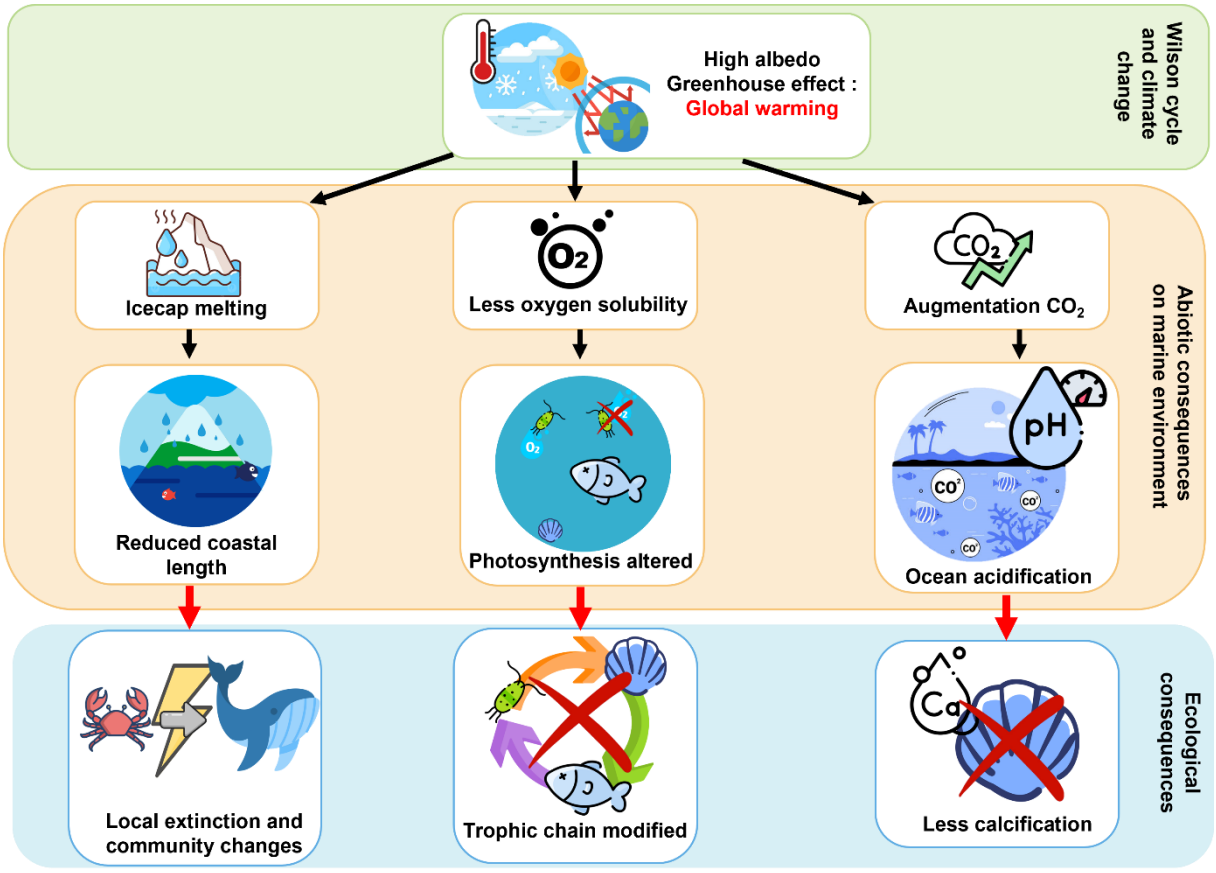


Figure 4 : Abiotic factors that affect the marine ecology. Initial triggers are placed on the top, cascading in a large variety of consequences along the marine environment.

Changes in physico-chemical parameters linked to climate change in marine ecosystems trigger biological responses that can differ according to the spatiotemporal scale considered (Lett et al. 2010; Lefort et al. 2014; Woodin et al. 2013 ; Fig 4). Temperature, as well as pH, carbon dioxyde concentration and even shelf area, fundamentally impacts all physiological processes and influences essential metabolic activities, enzymatic reactions and even cell membrane permeability (Hochachka & Somero 2002).

1.3.2.2. Modification of biotic traits of life

To address climate change, a species might exhibit adaptive behaviors. When confronted with environmental fluctuations and their challenges, individuals may either (i) tolerate or adjust to these changes and adapt accordingly, or (ii) fail to adapt, experiencing direct or indirect impacts on their life history traits and population dynamics.

Long-term trends in environmental conditions can, after a certain threshold, create local mismatches between the biology, needs and tolerance of individuals and their direct living environment. The first universal response to these changes is the ability of individuals to move and track more favourable environmental conditions. However, this response is not without consequences for population dynamics, as it can lead to new dynamics in both the extinction process and the population colonisation process (Chen et al. 2011; Lenoir & Svenning 2015), modifying communities and ecosystems entirely. There are several examples in today's species that have shifted their biogeographic range in response to climate change trends, corroborating the impact that such variations can have on populations (e.g. Hitch & Leberg 2006; Berteaux, 2004; Poloczanka et al. 2016; Blowes et al. 2019). However, this response is limited by the species' ability to move or even the availability of resources in refuge habitats. In addition, the specialisation of certain taxa to their habitat (such as polar organisms) places them at the extreme limit of their distribution. This endemism leads to an increasingly significant reduction in their range, and by extension, local population extinction (Parmesan & Yohe 2003; Parmesan 2006). Species then have only one other option for coping with these trends: to adapt.

Changes in environmental conditions can directly affect the selection pressures exerted on populations, and consequently induce alterations in life-history traits. Phenotypical changes can be expected in particular as a direct response to climate variations. Recent work has highlighted the large decline in body size observed in many organisms, which has been linked to the global increase in temperature over recent decades

(Gardner et al. 2011a; Gardner et al. 2011b ; Sheridan & Bickford 2011). This change in body size is one of the three universal responses to global warming (Daufresne et al. 2009; Gardner et al. 2011a; Sheridan & Bickford 2011), and called the Temperature-Size Rule (TSR; Atkinson 1994).

This general rule for ectothermic organisms suggests that a taxon living in a warm environment will have a higher initial growth rate and, consequently, a smaller size compared to a taxon in a colder environment. Numerous studies have investigated how environmental factors influence the biological processes that modify body size in response to temperature changes. Two main causes have been identified. The first hypothesis suggests a limiting metabolic relationship between size and oxygen during climatic warming. For ectothermic organisms, oxygen limitation acts as a selective pressure to reduce body size (Atkinson et al. 2006; Frazier et al. 2001; Hoefnager & Verberk 2015). The second hypothesis relates to resource availability (Gardner et al. 2011a). Organisms in warmer conditions face constraints in the abundance, diversity, or quality of available resources. Nutrient intake, crucial for growth, determines the body size of individuals (Elser, 2003). Thus, changes in the quality or quantity of resources could lead to changes in body size.

For endothermic species, such as birds and mammals, the reduction in body size observed is interpreted in accordance with Bergmann's rule (Bergmann 1847), which predicts a negative relationship between temperature and body size. A larger body size is preferred in colder environments because it increases heat retention (Lindstedt & Boyce 1985; Millar & Hickling 1990). In contrast, a smaller body size facilitates heat dissipation (Blackburn et al. 1999). The same ecological rule has since been tested on ectothermic organisms (Partridge & French, 2010). As the majority of biological processes are linked to body size, its decreases observed during climate warming inevitably have ecological consequences for individuals, populations, communities and, more broadly, for ecosystems.

However, these adaptive changes can be constrained. Each species has its own adaptive potential, leading to disparities in the ability of individuals to cope with climate change (Hoffmann & Sgro 2011). At the same time, species with low population turnover are expected to be less resilient to continuous or rapid changes in their environment (Gamelon et al. 2014). In addition, taxa with a low growth rate tend to recover more slowly from external disturbance, and to be more sensitive to global change (Lebreton 2011). They will therefore have a greater risk of extinction, compared with smaller organisms with a shorter overall lifespan (Cardillo 2003 , 2005).

However, some studies suggest that these phenotypic changes are not necessarily the result of phenotypic plasticity but instead of a non-adaptive response to changes in several environmental factors such as temperature or resource availability or even quality (Teplisky & Millien 2014). For example, the decline in body size may be linked to the increased survival of smaller individuals after a harsh season or to the overconsumption of larger individuals (Ozgul et al. 2009). The profound change in biotic traits is the result of a combination of mechanisms (Daufresne et al. 2009). In addition, the age structure of a population can be modified, in particular by increasing the presence of juveniles relative to adults (Daufresne et al. 2009).

1.3.3. Environmental conditions, modified larval characteristics leading to biogeographic changes in modern Bivalves

In this context, coastal environments generally exhibit wide spatio-temporal variations in physico-chemical conditions (Hoffmann et al. 2011). As a result, these particular environments are subject to significant environmental change, while their social and economic importance increases. Almost 40% of the world's population has settled on the coasts (Neumann et al. 2015), and 775 million people are strongly dependent on these systems and their services (Selig et al. 2019). Therefore, current climate change implies

drastic alterations to organisms belonging to these systems, which contribute more than 60% of the total economic value of the biosphere (Martinez et al. 2007; Kroeker et al. 2013).

Recent recognition of these issues has led the scientific community to take an increasing interest in the main ecological players of these environments. Bivalves (class: Bivalvia) represent one of the most diverse groups and are recognised for their reef bioconstruction, which is beneficial to global biodiversity (Fariñas-Franco and Roberts 2014; McAfee et al. 2017). In addition to their ability to create new substrates, bivalves are also filter feeders capable of reducing pollution in the water column (Smyth et al. 2018). By their presence, they improve or modify local productivity (Donnarumma et al. 2018; Strain et al. 2021), in particular through the selective elimination of phytoplankton species (Ward & Shumway 2004), but they also play a key role in the marine carbon cycle (Smyth et al. 2013; Smyth et al. 2018; Ray & Fulweiler 2020). In addition, bivalves now occupy most of the world's seas and oceans. They are able to thrive in extreme environments, with cold waters (Petersen et al. 2003; Ambrose et al. 2012; Ballestra-Artero et al. 2017), as well as in warmer waters at lower latitudes (e.g. Roy & Martien 2001; Campos 2016). The cosmopolitan nature of bivalves is particularly important as they represent the second most important seafood in human consumption (Smaal et al. 2019). Consequently, bivalves are excellent models for studying the influence of climate change.

Numerous works have already highlighted the importance of understanding climate variations in their larval phase, making it possible to predict more accurately changes in population size, organism body size, and dispersal, as well as distribution patterns. Current knowledge about how bivalves respond to different climatic stressors is based on both field studies and laboratory experiments. The majority of these studies are based on responses to the two environmental challenges we are currently facing: acidification and ocean warming. Moreover, both climate variations have a synergistic effect, inducing a reduction in growth rates in calcifying marine organisms (Kroeker et al. 2010; Knights et al. 2020; Sampaio et al.

2021). In general, bivalves show a negative relationship with these parameters (Kroeker et al. 2013; Harvey et al. 2013; Sampaio et al. 2021; Leung et al. 2022): the growth of organisms is reduced with climate change.

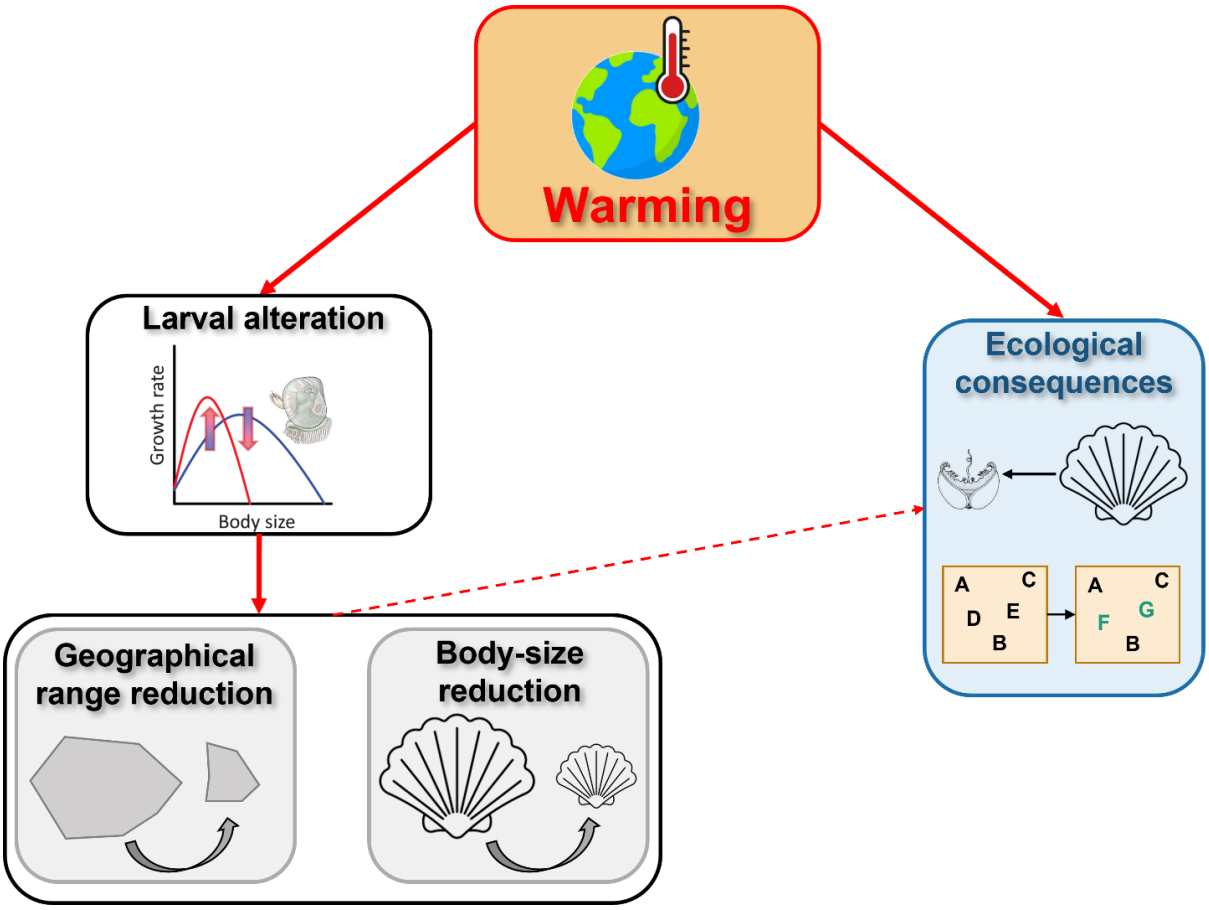


Figure 5 : Thermal effects, both direct and indirect, are influenced by reductions in body size and geographical range. Direct temperature impacts on bivalves' physiology and ecology are indicated by bold red arrows, while indirect ecological effects are shown.

Climate change affects all development stages, but larval stages seem to be the most affected compared with adults, for which the impact is more moderate (Kruft-Welton et al. 2023). So the most primordial stages are the most vulnerable to changes in their environment. The larval phase of bivalves is unique because of the pelagic performances of this developmental stage. Thanks to this key period, bivalves can reach new ecosystems and are able to relocate to fulfill their environmental needs (CITATIONS). However, elevated

temperatures and marine heatwaves have been shown to compromise the development, behavior, and survival of larvae (Olabarria et al 2016). Exposure to extreme heat events alters physiological and behavioral traits in mytilid mussels, particularly in early life stages, impacting both viability and recruitment potential. Gleason et al. (2018) demonstrated that thermal tolerance in juvenile Mytilus californianus exhibits significant plasticity, but that this plasticity is tightly linked to growth rate—suggesting a trade-off between thermal adaptation and growth performance.

Through various metabolic processes, environmental change leads to a reduction in movement speed (Czaja et al. 2023), and these alterations can also trigger changes in the overall dispersal of organisms (North et al. 2008; Burgess et al. 2021). This is particularly concerning as dispersal during the larval stage governs the geographic range of many bivalve species. Reduced dispersal limits gene flow and population connectivity, increasing the risk of local extirpations and reducing species' adaptive potential to future conditions (Jablonski & Lutz 1983; Jablonski 1986). Bivalves from different thermal environments exhibit distinct thermal tolerance ranges, pointing to the possibility that populations from less variable climates may be more vulnerable to rapid warming (Campton et al 2007). Sorte et al. (2011) further support this by demonstrating significant intraspecific variation in temperature tolerance across geographic ranges, suggesting some populations may serve as potential refugia or sources of adaptive traits. By reducing dispersal capacity, the entire biogeography is affected. Species become less cosmopolitan, communities more isolated as the geographical range size of species is reduced (Jablonski 1986; Lester et al. 2007). Furthermore, as growth is altered by temperature, we can expect a reduction in the average body size of adults, as in most ectotherms, in line with the temperature-size rule (Atkinson et al. 2006; Frazier et al. 2001; Hoefnager & Verberk 2015). The smallest organisms have reduced dispersal, thereby reducing their potential to colonise environments (Roy et al. 2001a).

These changes may be further compounded by genetic and ontogenetic differences in thermal resilience. Both developmental stage and genetic background are key to understanding inter-population variability in thermal sensitivity, offering insights into which populations might be more adaptable in the face of escalating climate pressures (Delorme et al.2024). Masanja et al. (2023) and Steves et al. (2018) illustrate how repeated or prolonged marine heatwaves can cause cumulative physiological stress, leading to reduced reproductive success and delayed population recovery. The long-term performance of bivalve species under future climatic regimes will likely depend on this complex interplay between plasticity, genetic adaptation, and environmental variability. All of these causal factors suggest that they must be taken into account to understand the ecological consequences of global climate change (Fig. 5). This is especially true for species of economic and ecological importance, such as bivalves, whose vulnerability at early life stages may act as a bottleneck for future population viability and ecosystem resilience.

1.4. Aims of the thesis

In addition to the relative knowledge of the current climatic impact on bivalves, there are still some grey areas, particularly concerning the link between temperature and body size and body size and geographical distribution. This is why palaeontology plays a key role; by looking at similar environmental variations, it is possible to get a clearer idea of the patterns governing current biodiversity. The interest of bivalves, in addition to the points made above, is that they are abundant in the fossil record, and appear since the Cambrian. Their high conservation levels make them an excellent candidate for answering the question of the influence of climate change, especially temperature, on biogeographical and body size responses throughout the Phanerozoic.

Therefore, the aim of this thesis is to characterise not only the temporal dynamics of bivalves but also their spatial and body size dynamics from the Ordovician (485.4 Ma) to near-present-day ecosystems (Neogene; 2.58 Ma), to substantially improve our

understanding of the macroecological patterns of these mollusks and identify their main drivers (Fig. 6). Most of the studies carried out to date do not concern bivalves, or focus solely on shorter periods of time, corresponding to major biological events (e.g. Jablonski & Raup 1995 ; Tu et al. 2016 ; Schaal et al. 2016 ; Foster et al. 2020 ; Huang et al. 2023). There are, however, a few preambular studies that draw parallels between the relatively recent fossil record (Pleistocene 2.58 Ma - 0.0117 Ma) and present-day faunas (e.g. Jablonski & Valentine 1990 ; Kaustuv et al. 2001). So nowadays it is essential to obtain a broader view of the evolutionary and ecological consequences of environmental change. Consequently, this thesis is dedicated to the study of large datasets of spatiotemporal occurrences of bivalve fossils, using methods derived from macroecology. Each chapter explores one aspect of the influence of climate change on an evolutionary, physiological or biogeographical response, and measures its effects on fossil populations.

1.4.1. Database presentation

1.4.1.2. Database presentation : biases and limitations

This thesis conducted macroecological and macroevolutionary analyses of body size and biogeographic range in fossil bivalves using a comprehensive dataset compiled by Payne and Heim (2021), originally derived from the Paleobiology Database (PBDB). The database aggregates a large number of genus-level occurrences from the Phanerozoic fossil record, incorporating associated information such as estimated body size, stratigraphic age, and paleoenvironmental context. By synthesizing data drawn from published literature, museum collections, and previous compilations, this dataset provides a valuable framework for examining long-term evolutionary patterns and ecological responses of bivalves to global environmental changes. In particular, it enables quantitative assessment of trends in body size evolution, extinction selectivity, biogeographic shifts, and trait-environment relationships across hundreds of millions of years.

Despite its breadth and utility, the database, like all large-scale fossil compilations, is shaped by several inherent limitations and potential biases that warrant careful consideration in any analytical interpretation (e.g., Lloyd et al. 2011; Butler et al. 2011; Valentine et al. 2006). One significant constraint lies in the unevenness of the fossil record itself. Temporal and geographic sampling intensity varies considerably due to rock availability, research history, and collector effort. Some stratigraphic intervals and regions, particularly those with well-exposed marine sediments in Europe and North America, are disproportionately represented, whereas others, such as tropical regions or poorly studied basins, remain undersampled. This spatial and temporal heterogeneity can skew diversity and trait-based analyses, favoring taxa that were more likely to be preserved or more extensively studied. Preservation biases further complicate the interpretation of ecological and morphological patterns. The fossilization process favors taxa with robust, heavily calcified shells, which are more likely to survive the taphonomic filter.

Furthermore, differential preservation linked to shell mineralogy (e.g., aragonite dissolution), depositional environment, and ecological strategy disproportionately affects specific taxa. As a result, the fossil record systematically underrepresents bivalves with delicate or lightly calcified morphologies, such as small-bodied infaunal species, which may have played significant roles in past ecosystems (Ros & Renzi 2004; Foote et al. 2015). Consequently, while apparent trends in body size or taxonomic richness may, in general, be influenced by differential preservation, multiple empirical studies demonstrate that such biases have limited influence on macroecological analyses of bivalves. Preservation biases complicate the interpretation of fossil assemblages in many invertebrate groups. The taphonomic selectivity exerts only a modest impact on bivalves, mainly due to their wide range of shell types and the extensive fossil record spanning nearly all marine environments. Several lines of evidence support the high fidelity of the bivalve fossil record in reflecting actual patterns of ecological and morphological diversity. Bivalves exhibit a strong

correspondence between fossil and living assemblages in terms of both taxonomic richness and ecological composition (Valentine et al. 2006). The relative proportions of life modes (e.g., infaunal vs. epifaunal) and taxonomic representation were remarkably consistent between modern death assemblages and their corresponding fossilized counterparts, even after taphonomic filtering. Similarly, Ros & Renzi (2004), focusing specifically on preservation biases in Bivalvia, concluded that although some preferential loss of aragonitic and thin-shelled forms does occur, this effect is generally coherent across depositional settings and stratigraphic intervals, and therefore does not significantly distort long-term evolutionary or ecological trends. Their results indicate that shell mineralogy exerts only a secondary influence compared to other factors such as sampling intensity and taxonomic assignment. Moreover, studies of modern death assemblages reinforce the conclusion that post-mortem biases introduce limited distortion into bivalve communities' size structure and taxonomic composition (Kidwell & Rothfus 2016). Proportional abundance and trait distributions are maintained across death and fossil assemblages, even in dynamic shallow-marine settings. These findings suggest that the ecological and morphological signals retained in the fossil record broadly represent original living communities, particularly for bivalves, which are more consistently preserved than many other marine invertebrates due to their relatively high mineral content and sedimentary ubiquity.

A further source of uncertainty stems from how body size is recorded within the dataset. In the foundational work by Heim et al. (2015), which serves as the empirical basis for the dataset used in this thesis, body size estimates were systematically compiled for fossil marine bivalves based on maximum linear shell dimensions, principally shell length, but also height or width when length was unavailable. These measurements were derived from original data (i.e., specimen measurements from museum collections) and published sources (monographs, taxonomic descriptions), with values typically representing the maximum observed size for each genus. The rationale behind this approach was to ensure

comparability across a broad taxonomic and temporal scope, as maximum linear dimensions are generally the most consistently reported and accessible metric across paleontological literature (Jablonski 1996; Finnegan et al. 2012). However, while practical and reproducible, such linear metrics offer only partially approximation of body size, particularly when considering physiological or ecological proxies such as biomass, metabolic rate, or surface-area-to-volume ratio (Peters 2005; Payne et al. 2009). Linear size does not scale isometrically with volume or mass, especially in bivalves, where shell morphology is highly variable among taxa. A genus with a long, thin shell (e.g., Solen) may have the same length as one with a compact, thick shell (e.g., Cardium), yet exhibit vastly different volumes and ecological functions (Brown et al. 2004). Consequently, reliance on maximum linear dimensions likely underrepresents three-dimensional morphological variation and may obscure trait-environment relationships that depend on more functionally relevant measures (e.g., volume, mass, or area). Moreover, Heim's dataset focuses on adult shell size, based on the largest available specimens per genus. This focus is an ordinary and necessary compromise in macroevolutionary and macroecological studies, which require standardization and comparability across clades and time intervals. However, it introduces biases related to ontogenetic stage, intraspecific variability, and sexual dimorphism. For example, genera exhibiting marked size polymorphism or sexual dimorphism may be misrepresented by a single maximum value, especially when the fossil record preferentially preserves only one morphotype. Similarly, species with complex growth trajectories or prolonged juvenile phases may appear disproportionately small or large relative to their ecological role. Nonetheless, such simplifications are defensible within the context of deep-time comparative studies. The large-scale patterns revealed by genus-level averages tend to be robust to variation in measurement source or orientation, particularly when statistical analyses incorporate broad temporal bins and large sample sizes (Heim & Peters 2011; Finnegan et al. 2012). Furthermore, the consistency of the measurement protocol across

taxa ensures that any residual error is non-directional, thus making it unlikely to systematically bias trends over macroevolutionary timescales.

Temporal resolution represents another important constraint in large-scale analyses based on fossil occurrence data. In the present study, stratigraphic information is primarily resolved to the geological stage level, corresponding to intervals that typically span 2 to 10 million years. While this resolution is among the finest consistently available across the Phanerozoic, it nonetheless imposes a coarse temporal framework that limits our capacity to detect short-lived ecological or evolutionary events. Particularly in the context of climatic and environmental perturbation, such as marine heatwaves, rapid carbon injection events, or transient episodes of ocean anoxia or acidification, the coarse binning of occurrence data may obscure biologically significant but temporally narrow responses. This issue is well documented in the paleobiological literature. Stratigraphic binning across multi-million-year intervals leads to temporal averaging, which can mask elevated extinction episodes or origination over much shorter timescales (Foote 1994 ; Bambach et al. 2004). Binning also reduces the ability to detect punctuated evolutionary changes, often smoothing abrupt morphological shifts into gradual trends (Hunt 2006). In the context of bivalves, whose ecological and physiological traits are known to respond rapidly to environmental change (e.g. Pörtner 2006b; Pinsky et al 2020), the inability to resolve responses at sub-stage scales could lead to an underestimation of trait volatility or the lagged detection of ecological disruption. This is particularly relevant to the goals of the present thesis, which seeks to characterize the relationship between climatic regimes and macroecological traits such as body size and biogeographic range. Abrupt climatic transitions, such as those associated with early Toarcian warming, the Paleocene-Eocene Thermal Maximum (PETM), or end-Permian ocean acidification events, are known to produce rapid, biologically impactful changes in marine ecosystems (e.g., Jenkyns 2010; Clapham & Payne, 2011).

However, when these events are embedded within broader temporal bins, their ecological signature may be diluted by background conditions. For instance, a brief episode of range contraction or dwarfing during a warming pulse may be rendered invisible if followed by a subsequent recovery phase within the same stage. Such temporal smoothing can attenuate or entirely mask rapid biological responses, leading to potential underestimations of the magnitude and speed of ecological perturbations. Nevertheless, it is important to recognize that temporal binning, while coarse, also provides methodological consistency across datasets and regions. Geological stages represent standardized chronostratigraphic units supported by robust biostratigraphic and radiometric frameworks. They offer a practical compromise that balances resolution with data coverage, enabling meaningful comparisons across taxonomic groups and paleogeographic provinces. In the specific context of this thesis, which aims to reconstruct broad-scale evolutionary and ecological trajectories of bivalves about major climatic transitions, the use of stage-level bins serves an essential function. It allows for the detection of general patterns and trends, such as the contrasting trajectories of body size and biogeographic range between hothouse and icehouse intervals, while reducing the influence of noise introduced by localized or short-term fluctuations. Notably, using such a coarser temporal resolution does not preclude the integration of finer-scale analyses in future work. Rather, shorter and longer time bins should be seen as complementary tools, each suited to answering different scales of biological questions. While fine-scale resolution is better suited to capturing ecological responses to transient climatic events, coarser bins are appropriate for tracking the cumulative effects of those events and for identifying persistent evolutionary or ecological responses. The broad patterns identified in this study, emerging across hundreds of genera and multiple climatic regimes, thus represent robust signals of long-term biotic responses, rather than artifacts of single events or sampling irregularities. This integrative approach allows the thesis to contribute

meaningfully to understanding how marine biodiversity has historically responded to sustained environmental change.

1.4.1.2. The robustness of deep-time analyses

A central strength of this thesis lies in using a large, globally distributed dataset, comprising tens of thousands of bivalve occurrences spanning the Phanerozoic. The breadth of the database allows for taxonomically and geographically inclusive large-scale analyses and enables statistically robust assessments of body size and geographic range dynamics under changing climatic regimes. Even after filtering for locality density and taxonomic representation, many occurrences per time bin minimizes stochastic noise, increases the signal-to-noise ratio, and supports applying higher-level comparative models. Abundant and taphonomically resilient bivalves offer some of the most reliable data for long-term ecological inference, especially when occurrence density is sufficient to average out sampling irregularities (Valentine et al. 2006; Kidwell & Rothfus 2016). The high volume of data is particularly critical for addressing macroecological questions that depend on trait variation across time and space, such as those concerning biogeographic range contraction or body size reduction under climatic stress. Some sensitivity analyses are required to ensure trends remain stable when thresholds for the number of occurrences and spatial distance are applied, underlining the statistical robustness of the observed patterns. The stability across filtered subsets of the data should confirm that the results are not merely artefacts of uneven sampling, rare taxa, or spatial autocorrelation, but instead reflect consistent biological responses across a broad taxonomic and environmental spectrum.

A second pillar of the analytical framework concerns the climate classification scheme used to interpret biotic patterns. In this thesis, climate regime partitioning is based on the absolute and relative temperature reconstructions (Scotese 2016 ; Scotese et al. 2021). By integrating multiple proxies, these reconstructions estimate global mean annual surface temperatures at million-year intervals across the Phanerozoic. These include $\delta^{18}O$ data from

marine carbonates, clumped isotopes, and sedimentological indicators with paleogeographic modeling. Their approach combines empirical geochemical data with climate simulation outputs from general circulation models (GCMs), yielding smooth, temporally continuous temperature variation curves. While this model provides one of the most comprehensive and widely adopted global paleotemperature reconstructions, it is important to recognize its inherent limitations. Absolute temperature estimates derived from isotopic proxies are subject to uncertainties associated with diagenetic alteration, secular trends in seawater composition, and assumptions regarding the isotopic baseline (Veizer et al. 2000; Grossman & Joachimski 2022). Moreover, the global averages proposed by Scotese et al. represent smoothed macroclimatic conditions. They may obscure significant regional and seasonal variability, which could have influenced biotic responses at more localized scales. As such, the classification of hothouse, greenhouse, transitional, and icehouse intervals—while valuable for identifying global trends—should be interpreted as general climatic envelopes rather than precise thermal thresholds. Despite these caveats, integrating temperature partitionings with the bivalve dataset remains a methodologically sound and conceptually appropriate approach for investigating long-term evolutionary and ecological responses to climate. Coarse resolution of palaeotemperature data and fossil occurrences is in line with epistemology: both operate on the scale of intervals of several million years, allowing consistent comparisons across deep time.

In order to examine the evolutionary and ecological responses of bivalves to climatic variability, this thesis employed a climatically explicit partitioning of the fossil dataset, following the absolute paleotemperature reconstructions provided by Scotese et al. (2016, 2021). This approach enabled the extraction of targeted subsets of occurrence data corresponding to specific climate phases, including intervals of global warming, global cooling, and sustained hothouse and icehouse conditions. These categories were not merely temporal bins, but thermally informed frameworks, allowing for hypothesis testing about how

biodiversity patterns varied under different global climatic regimes. Warming and cooling intervals were identified based on the direction of temperature change in consecutive time slices to isolate biologically meaningful trends. In contrast, hothouse and icehouse intervals were distinguished by their absolute mean annual surface temperatures. The thresholds applied for hothouse and icehouse intervals are grounded in the paleotemperature reconstructions. These specific cutoffs correspond to major climatic modes in Earth's history. Hothouse intervals, exceeding 24°C in global mean temperature, are associated with low equator-to-pole temperature gradients, ice-free poles, high eustatic sea levels, and extensive shallow marine habitats (e.g., the Cambrian–Ordovician and mid-Cretaceous). In contrast, icehouse intervals, falling below 17°C, reflect periods of global glaciation, steeper latitudinal gradients, and greater climatic seasonality (e.g., the Late Paleozoic Ice Age and the Neogene). These thresholds are ecologically significant because they correspond to qualitatively different Earth system states with consequences for ocean circulation, nutrient cycling, and biotic stress regimes (e.g., Pörtner, 2006b; McClain et al., 2018).

By structuring the analyses around these climate partitions, this thesis could test for non-random body size and range size patterns that correlate with large-scale environmental modes, rather than simply tracking secular trends over time. This climate-based binning scheme provides a biologically relevant framework for interpreting large-scale change. It supports the hypothesis that bivalve responses, like dwarfing and range shifts, are strongly modulated by the thermal context in which they occur. In addition, the approach enabled comparison of evolutionary dynamics between absolute climatic states and during transitional phases, thereby capturing both background trends and responses to directional environmental forcing.

1.4.2. General summary of the thesis

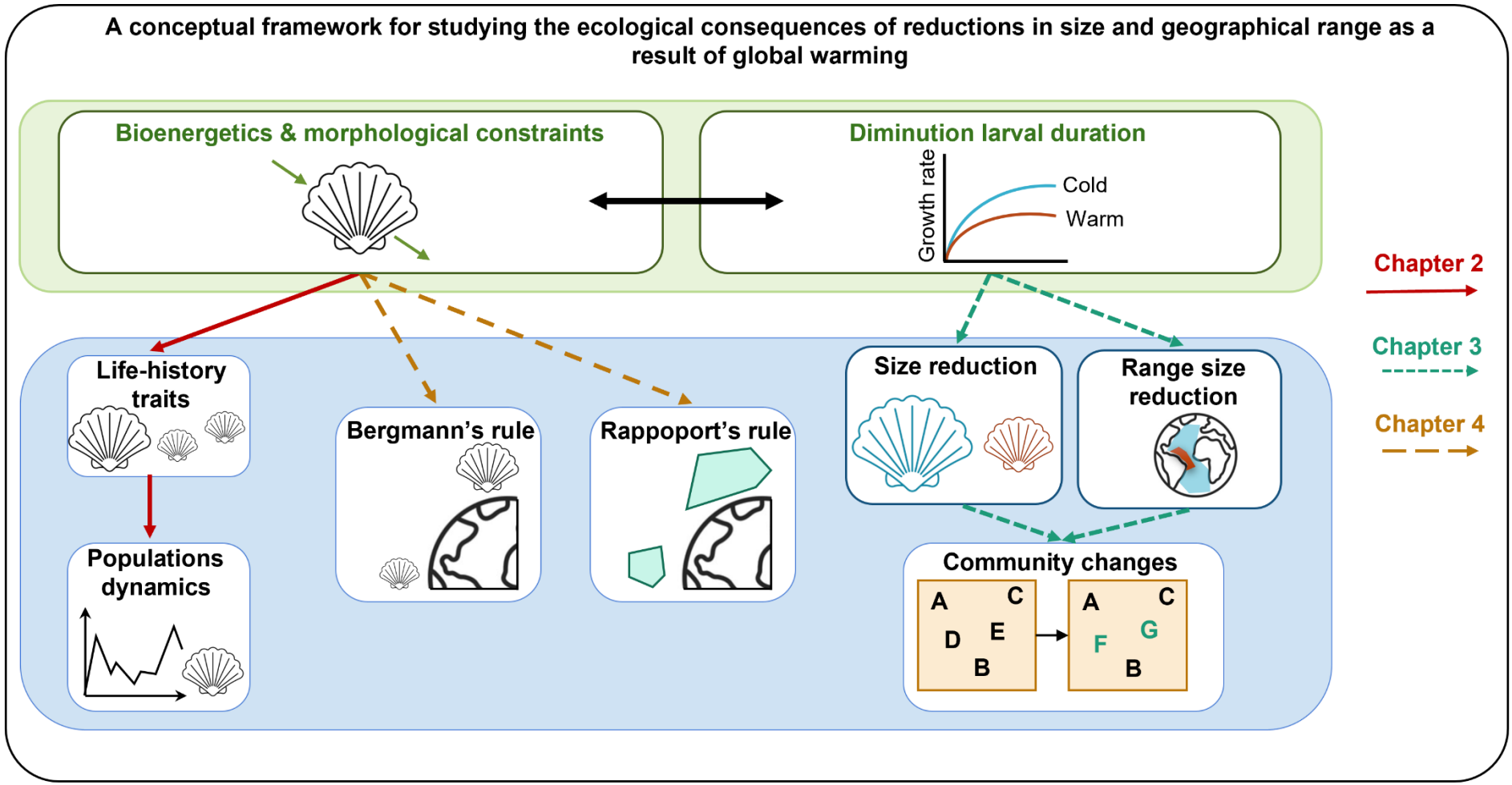
Chapter II (Montariol et al. submitted) focuses on the evolutionary dynamics of bivalves on a global scale. The 'evolutionary fauna' model has been revisited using data

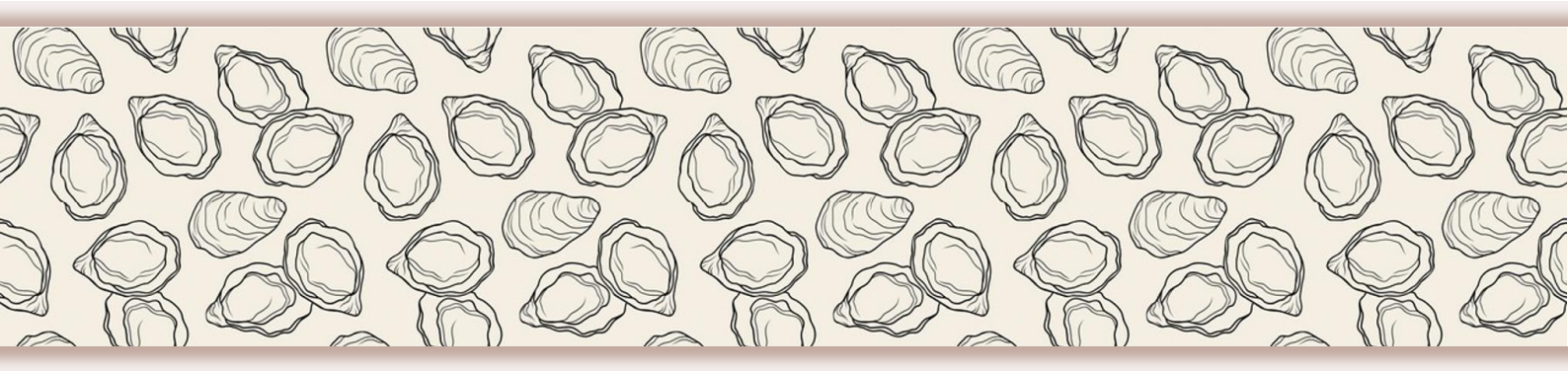
extracted from Payne & Heim (2020), focusing on the entire Phanerozoic to give a more detailed picture of the turnovers affecting bivalves. This analysis was supplemented by an observation of the ecospace of each family involved, to describe the ecological changes that occurred over time. The results were then compared with global climatic and ecological variations, including abiotic factors (temperature, sea level, etc.) and biotic factors (plankton diversity, evolutionary flora, etc.).

Chapter III focuses on the response to variations in body size and range size of bivalves during the Phanerozoic. Correlations were established between these intrinsic parameters of fossil organisms and global temperature. This study is based on different climate partitionings, observing patterns both globally and during 'hothouse' or 'icehouse' episodes, in order to consider the full complexity of the influence of the temperature parameter on biological responses. This chapter is completed by an exploration of the biogeographical connectivity of bivalves over time, and thus of the influence of climate change on communities, after highlighting the importance of body size and geographic range size.

Finally, the last chapter is devoted to the study of two known biogeographical phenomena observed in current biodiversity: Rappoport's rule and Bergmann's rule. The aim here is to determine the existence of both of these effects on the body sizes and range sizes of fossils species. The large-scale demonstration of such distribution patterns in the fossil record plays a major role in macroecology; these two proposed rules help to put forward palaeoecological hypotheses, such as the temperature-dependence of species, but also palaeoenvironmental hypotheses (e.g. latitudinal gradient of diversity) explaining the spatial and temporal distribution patterns of species, in accordance with the thermal variations observed between high and low latitudes.

Figure 6 : Conceptual framework of the thesis, exploring the relation between body size, geographical range size and climate change during the Phanerozoic. The chapter II analyses diversity trends and intrinsic ecological changes of bivalves and their drivers. The chapter III focuses on the impact of temperature change on body size and geographical range size of bivalves, and the consequences on communities through time. The last chapter of this thesis test two major biogeographical rules : *Rappoport's rule and Bergmann's rule during different climatic periods, to better understand distributional patterns linked with temperature*.





2

Clams over time : imprint of global climate changes on the Phanerozoic paleobiodiversity of bivalves

Abstract

Marine bivalves are a key component of marine benthic ecosystems since the Cambrian Explosion (ca. 520 Ma) and are an amazing model organism to study macroevolution and macroecology such as the relationships among global climate change, species geographic range, body size, and/or latitudinal gradients of biodiversity. However, the paleobiodiversity of bivalves remains poorly evaluated, except a well-known pattern of quiet and ever-increasing global richness. To evaluate diversity dynamics of marine bivalves at a geological timescale, this chapter quantifies the genus richness among their families throughout the Phanerozoic stages by establishing/deciphering their so-called evolutionary faunas. A factor analysis identifies, for the first time, four consecutive temporally correlated assemblages of taxa: an Ordovician–Devonian fauna, a Carboniferous–Permian fauna, a Triassic–early Cretaceous fauna, and a late Cretaceous–Cenozoic fauna. Comparison of this four-phased diversity pattern with the bivalve ecospace (mobility, feeding and tiering) shows a striking decoupling. In addition, these evolutionary faunas are compared to major biotic events and time series of abiotic factors to evaluate their potential drivers. Only one transition among these evolutionary faunas is abrupt and coincides with the Permian/Triassic boundary, which records the main mass extinction of the Phanerozoic. Otherwise, the transitions are gradual and protracted during several millions years and coincide with major gradual turnover in phytoplankton stoichiometry. Thus, this study strongly suggests these ships (bivalve evolutionary faunas) that pass in deep time over a macroevolutionary timescale are primarily fueled by plankton evolution, which is in turn mainly driven by continental fragmentation and its environmental consequences.

Keywords: Bivalvia, Biodiversity, Evolutionary faunas, Ecospace, Macroevolution, Phanerozoic

2.1. Phanerozoic paleobiodiversity of bivalves

2.1.1. Paleobiodiversity curves

Data informations

The database used was created and published by Payne and Heim (2020), and consists of an extract from the Paleobiological Database (PBDB, www.paleobiodb.org) of several marine metazoans from the Tremadocian to the present day. The original data contained a set of classes that were filtered to create a dataset that only contained bivalve occurrences. Then data was cleaned to remove any non-marine orders, families or genera. Although the 'pull of the recent' effect has been shown to have a little impact on the diversity observed in the fossil record for our group of interest (Jablonski et al. 2013), all post-Piazencian occurrences were discarded and will not be considered in our analysis.

The construction of diversity curves is influenced by the quality of the taxonomic data (Sepkoski 1997). Therefore, it is necessary to deal with the biases correlated to the sampling effort, the quality of preservation of the fossil record (Cherns et al. 2009) or the number of studies conducted on the subject (Alroy, 2010a; 2010b). These long-established and highlighted issues have led to a real consideration of how to correct these problems through different analytical methods (Close et al. 2018). However, none of them will be applicable without a taxonomic standardisation of sources, as pointed out by Mondal and Harries (2016). The present study will focus on the genus level, due to the often disparate quality of data at lower taxonomic levels (Valentine 1974 ; Prothero 2015; Reddin et al. 2020). Some occurrences are given as suborder rank in our database, so they have been modified to match the required taxonomic level. In addition, as the taxonomic assignments in the PBDB are not always up-to-date, a revision of the taxonomy was made. Although bivalve systematics is widely studied especially in molecular phylogeny (Campbell 2000; Steiner & Hammer 2000; Giribet & Wheeler 2002), it remains highly debated and most of the works are focused on the order or family level (Hautmann 2001; Wood et al. 2007; Borges et al. 2012;

Combosch & Giribet 2016 ; Liu et al 2018). We opted to base our taxonomic framework on the publications of the Bivalvia's Compendium (Bouchet et al. 2010; Bieler et al. 2010) with some updates. First of all, the data are compared with those compiled in participative open access databases (Molluscabase, www.https://molluscabase.org ; World Register of Marine Species, www.https://www.marinespecies.org ; Worldwide Mollusc Species Database, www.bagniliggia.it/WMSD/WMSDhome.htm). If the results obtained diverge, then a literature review is carried out to assign the genus to the most recent classification. The same exercise is performed to correct synonyms. Secondly, some genera are not associated with any order or family in the database. Searches are made to find the original publication, and if necessary correct the information.

To generate the curves presented hereafter, we also removed from the analysis occurrences belonging to historical or local chronostratigraphic units to standardise it according to the International Chronostratigraphic Chart 2019 (Cohen et al. 2013, updated). Once this is achieved, stratigraphic distribution of genera are checked. When a taxon has a distribution considered anomalous (e.g. early appearance, or late disappearance, after an absence in the fossil record over several stages), it will only be considered present around its peak abundance. Occurrences present in remnant stages will be removed from the analysis. The final file includes 71,729 occurrences, belonging to 183 families distributed in 1119 genera, spread over the whole Phanerozoic.

Construction of paleobiodiversity curves

Taxonomic richness is intrinsically related to the quality of the fossil record, but also to the analysis method used to reconstruct past diversity. It is therefore essential to adopt methods to correct the known biases highlighted in the literature (Sepkoski 1997 ; Foote 2000 ; Alroy 2010a ; Mondal et al. 2016). In this work, the diversity of bivalves during the Phanerozoic is assessed at the genus level, using two analytical methods. The first is a classical approach: we look at the taxonomic richness within predefined time intervals. This allows the calculation

of range-through diversity (RT), by considering not only the taxa physically present in the time interval but also those whose presence is interpolated from the discontinuous record of a taxon (Foote 2000).

However, while this approach is one of the more intuitive, it does not reflect the quantitative reality of biodiversity. Some periods have been largely prioritised in palaeontological studies (particularly around major biological crises), or because of easy access to the field. Consequently, the number of individuals sampled is directly linked to the effort made by the scientific community. A large number of individuals recorded undoubtedly leads to an increase in the number of taxa registered in the time period considered. This is known as "sampling intensity bias" (Fischer et al. 1943 ; Sepkoski 1993 ; Vilhena & Smith 2013). Therefore, in parallel, we computed a shareholder quorum subsampling (SQS) diversity (Alroy 2010a ; Alroy 2020). By subsampling the data, sampling inequalities within a time interval are smoothed out. This is now considered a robust method of correcting for preservation and sampling heterogeneity in the fossil record (Close et al. 2018 ; Benson et al. 2021).

More broadly, diversity is driven by the balance between extinctions and origination rates of taxa during the Phanerozoic (Sanderson and Donoghue 1996 ; Foote 2001 ; Bambach et al. 2004). When the origination rate is greater than the extinction rate, then global diversity increases. Thus, we estimated standardised extinction and origination rates for bivalves, based on the per-capita rate (Foote 2000). In addition, we performed poly-cohorts analyses on the bivalve families. The purpose of a poly-cohort is to look at either survivorship (i.e. poly-cohort survivorship) or pre-nascence (or 'backward survivorship'). In the first case, it indicates the percentage of a cohort (i.e. an assemblage of taxa in a predefined time interval) in later time intervals (Raup 1978). In our analysis, we look at the percentage of taxa of a family that survive from one stage to the next. On the other hand, prenascence is the proportion of an assemblage in a given time interval that was also

present in previous intervals. In other words, it refers to the taxa that originate throughout the period studied. Poly-cohort analysis documents extinction and origination rates in another way (Raup 1978 ; Foote 2001); linear curves indicate a constant rate (no change in the cohort) while a change from one stage to another can be interpreted as a change in rate within the cohort. In this work, the poly-cohorts cover all Phanerozoic stages and are plotted on a logarithmic scale.

All these analyses were performed with the 'epaleo' package (v. 0.8.41; Monnet, unpub.), using the R statistical environment (v. 3.6.2; R Core Team 2019; https://cran.r-project.org/).

2.1.2. Phanerozoic diversity estimates

During the entire Phanerozoic, the global diversity of bivalves shows particular trends, expressed in the taxonomic richness curves (Fig. 7) as well as in the origination and extinction curves (Fig. 8). The trends observed in both total richness (RT) and sample-standardized (SQS) diversity are very similar. The lowest values recorded are from the Ordovician, reaching maximum values in the Neogene. However, the increase in diversity did not occur in a single step. Some visible fluctuations highlight 7 outstanding temporal patterns over time: (1) from the Tremadocian to the Emsian there is an increase in taxonomic richness, followed by (2) a plateau in the first part of the Carboniferous. Then one finds (3) an increase in overall diversity until the end of the Palaeozoic, (4) marked by an abrupt decrease between the Lopingian and the Induan. This diminution returns the taxonomic richness to values analogous to the ones known for the beginning of the Ordovician. Nevertheless, (5) the Triassic allows a rapid recovery in bivalve diversity. The Late Triassic is characterised by (6) an almost constant rise in overall diversity from one stage to the next until the mid-Cretaceous. Finally, (7) from the mid-Cretaceous onwards, the diversification of genera seems to progress even more quickly, and this continues for the whole of the Cenozoic to its highest value

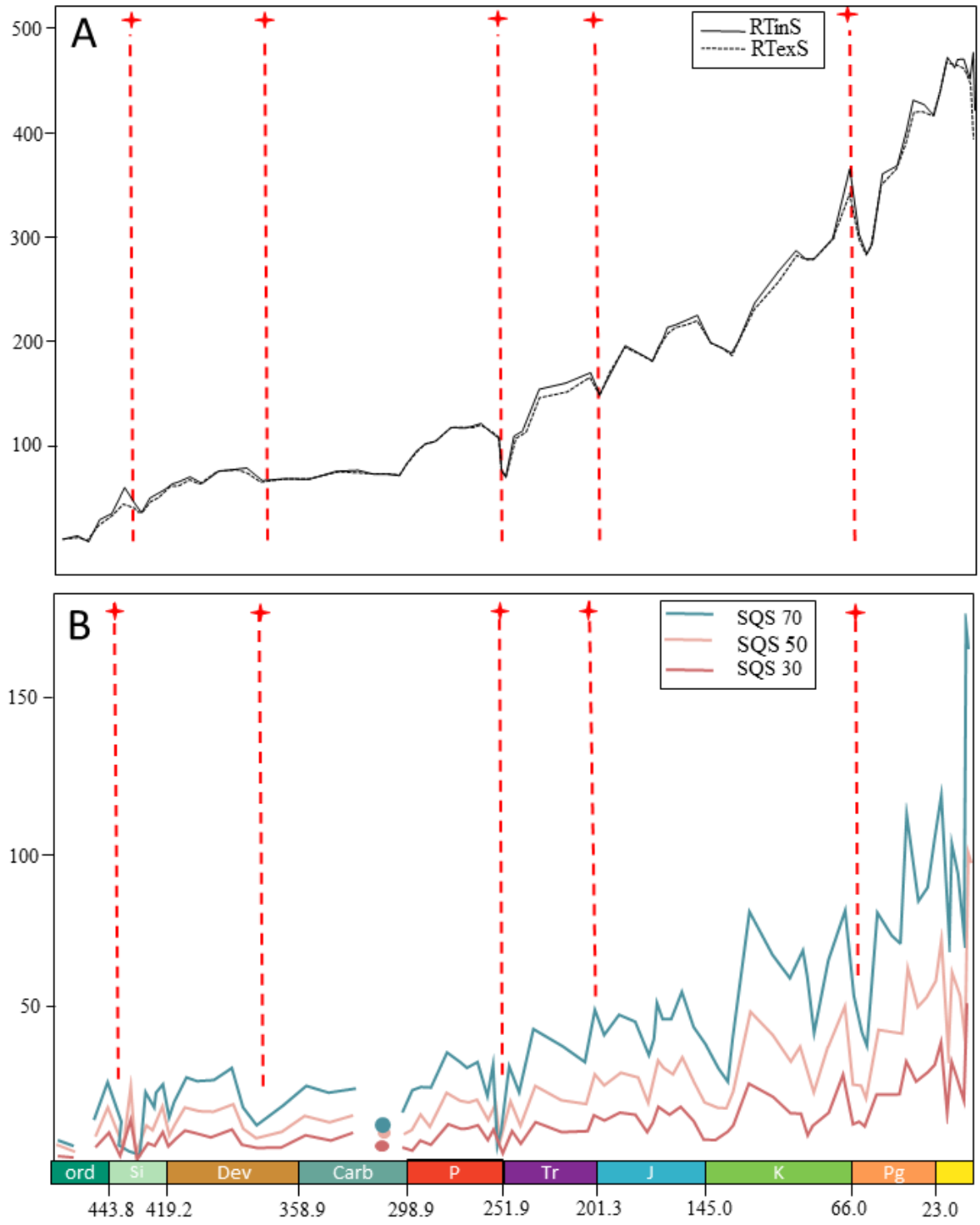


Figure 7: Global diversity of bivalves throughout the Phanerozoic. The curves show a global increase of the taxonomic richness. A) range-through diversity including singletons (RTinS) and excluding singletons (RTexS). B) diversity based on shareholder quorum sub

There are very few genera at the beginning of the Ordovician (about a dozen). From the Dapingian, the taxonomic richness increases until the end of the Pragian, attaining more or less 80 genera per stage. Over the Ordovician, Silurian and Devonian periods, a

progressive rise in diversity can be observed. However, this increase is characterised by significant variations, particularly visible on the SQS, possibly suggesting a lack of data for these periods. There is a succession of peaks in the Darriwilian, then in the Hirnantian/Rhuddanian transition and in the transition between the Silurian and Devonian. Diversity almost drops to zero around the Telychian. From the Pragian to the end of the Pennsylvanian, taxonomic diversity seems to be stable around 80 genera per stage.

However, when looking closely at the SQS curve, this stability can be discussed; a decrease in the number of genera is visible at the Frasnian/Fammenian stages and then at the Serpukhovian/Bashkirian. The curve obtained in the SQS is in contrast to the results of the total diversity curve (RT). It seems probable that the SQS method is more impacted by a too limited data set. The early Carboniferous is perhaps not well documented. Between the Carboniferous and Permian, the global diversity of bivalves increases again, with nearly 120 genera per stage at the end of the Permian. A very sharp decrease in taxonomic diversity occurred at the transition between the Palaeozoic and Mesozoic. This is the greatest extinction peak observed for the entire Phanerozoic in bivalves. This event is clearly shown by both SQS and global diversity, leading to a minimum of genera, with recorded diversity values equal to the early Ordovician. After the extinction event, diversity recovers quickly, with a significant peak at the beginning of the Triassic. The taxonomic richness is about 160 genera per stage. The early Mesozoic, and up to the middle of the Cretaceous, is highlighted by a gradual rise in diversity, doubling the number of bivalve genera recorded in the Aptian. This general increase is periodically interrupted by small decreasing events of taxonomic diversity, well illustrated on the RT curve; in particular, there is a drop in the number of genera per stage at the Triassic/Jurassic boundary, but also in the Toarcian and between the Jurassic and Cretaceous. Although detectable, these changes remain marginal, with a loss of rarely more than twenty genera. Interestingly, the resampling approach (SQS) suggests that these events are somewhat more pronounced, but their trend is identical to the overall

diversity (RT). From the Aptian, there is a more important diversification of bivalves. This acceleration leads to a maximum of diversity in the Neogene, with nearly 500 genera per stage. Once again, this general trend is punctuated by decreasing events of taxonomic diversity. Thus, there is a slight drop at the Cretaceous/Paleogene transition, with a recovery in the Danian. Based on the SQS data, a significant decline was already occurring in the Campanian, and continued during the transition. However, these decreases do not change the general shape of the curve; the recovery of taxonomic richness is almost as sudden as the loss of genera, often limited to a few dozen. Finally, the Cenozoic exhibits a more erratic pattern, with an increase in diversity in consecutive peaks, first in the Selandian, then in the Lutetian and Langhian. Each time, these peaks are interspersed with very minor reductions in taxonomic richness.

2.1.3. Taxonomic change

The rates of origination and extinction highlight the major macroevolutionary trends in bivalves across the Phanerozoic. The highest rates of origination are documented during the Palaeozoic (Fig. 8), and reflect three successive phases: a first during the Ordovician, a second in the Silurian and a third at the Permian/Triassic boundary. Smaller genus appearance events occur during the entire Mesozoic and Cenozoic. At the same time, extinction events are broadly synchronous with origination events. For each time interval corresponding to taxonomic diversification, there is also a relative extinction of genera. Noticeably, there are no significant differences between extinction and origination rates; generally the same order of magnitude is found between them. Furthermore, the per-taxon and per-capita rates follow the same trends.

On closer examination, there are several time intervals where the origination rate is greater than the extinction rate and vice versa. The latter are shown in the rate of net taxon change (Fig 8) ; 0 is no change, while a positive number is a taxon gain from the previous stage and a negative number is a taxonomic loss. During the Palaeozoic, five events of

genus gain are recorded, the most prominent one occurring between the Dapingian and Darriwilian. The four following events, between the Aeronian and the Lochkovian, the Emsian and the Givaetian, the Fammenian and the Tournaisian and finally from the Kasimovian to the Capitanian are half as important, with an increase in taxonomic richness of around ten genera. Concerning the loss of taxa in the Palaeozoic, six events can be identified. The transition between the Permian and the Triassic is the event with the greatest taxonomic decline, with nearly 40 genera disappearing between the Capitanian and the Changhsingian.

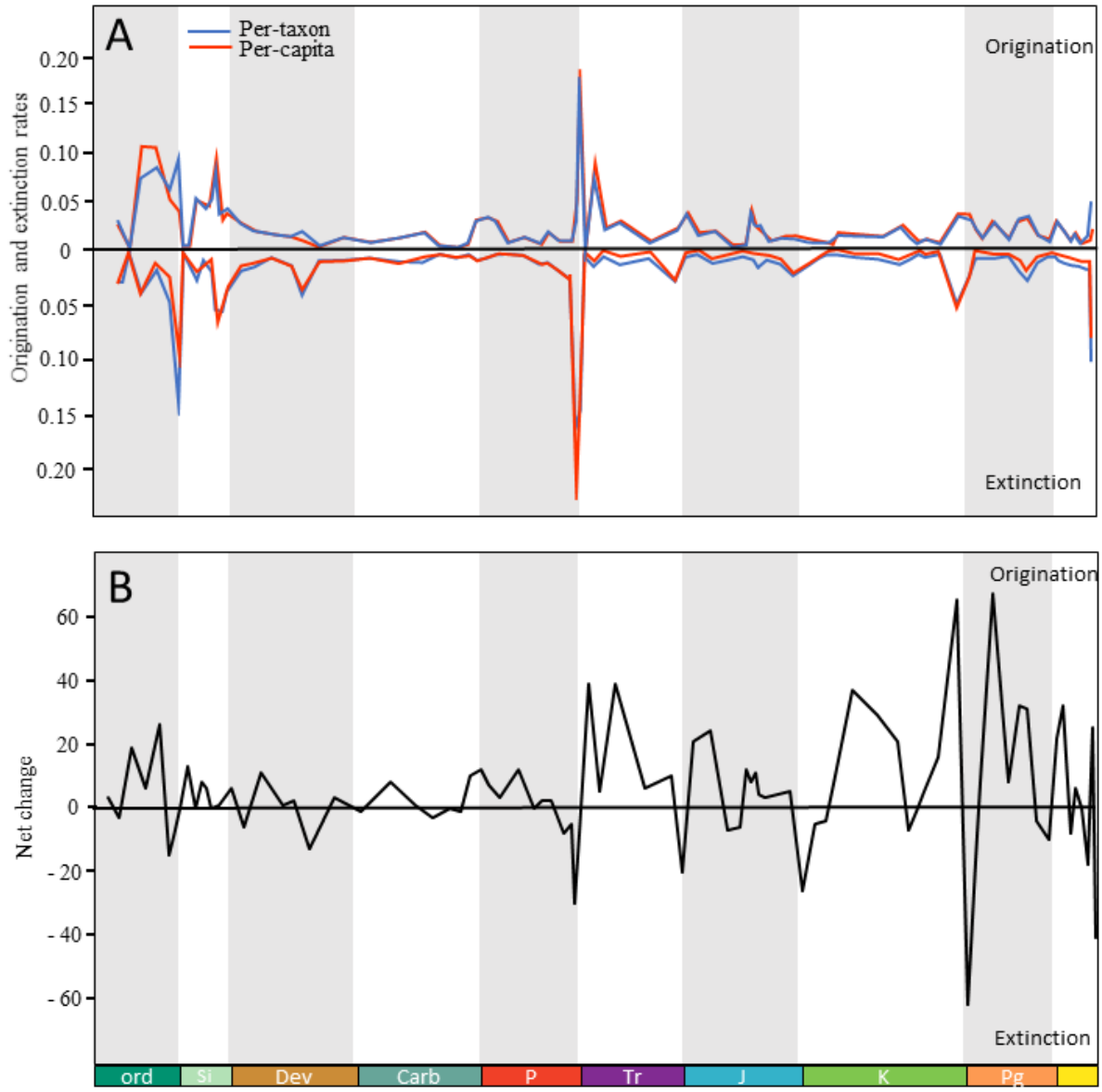


Figure 8 : Taxonomic changes of global Phanerozoic bivalves genus diversity per stage. A) origination and extinction rates. B) net change per stage, corresponding to the number of origination of genus minus the number of extinction genus.

More moderate decreases are noticeable between the Katian and Aeronian as well as between the Givetan and Famenian (about 15 genera lost). Finally, the last three events are marginal, with less than ten lost genera: between the Tremadocian and Dapingian, the Lockhovian and Emsian, and between the Serpukhovian and Gzhelian. During the Mesozoic, after the Permian/Triassic taxonomic drop-off, there are five time intervals with an increase in the number of taxa, separated by genus loss events. In contrast to the Palaeozoic, the events of taxonomic diversity acquisition are more pronounced with three of them presenting a gain of 40 or more genera. This is notably the case for the Triassic (Olenekian - Rhaetian), the Hauterivian - Cenomanian interval and the Coniacian - Maastrichtian interval. The intervals from the Hettangian to the Toarcian and from the Aalenian to the Tithonian are more moderate increases. The events of taxon loss (from the Rhaetian to the Sinemurian, from the Pliensbachian to the Aalenian and from the Tithonian to the Hauterivian, respectively) represent a maximum taxonomic decrease of about twenty genera. Finally, the Cenozoic records the greatest genus diversity, during the Cretaceous-Paleogene boundary, with nearly 60 bivalve genera lost between the last Mesozoic stage and the Danian. Just after this event, the largest taxonomic increase in the Phanerozoic for bivalves is found, from the Selandian to the Rupelian. However, although it remains the largest, the rate of positive change is broadly equivalent during the Late-Cretaceous increase. Increases in the number of taxa are visible until the end of the era, between the Chattian and Burdigalian, then the Langhian and Tortonian and finally from the Messinian to the Zanclean.

Poly-cohort survivorship documents some intervals with major extinctions (Fig. 9). The Ordovician shows a fairly rapid decline in the survival rate of genera until the Hirnantian. A major drop-off is visible in the Hinantian, recording an extinction event at the boundary between the Ordovician and Silurian. Until the middle of the Devonian, survival rates registered are rather stable, with a clear break between the Pragian and Eifelian. From the

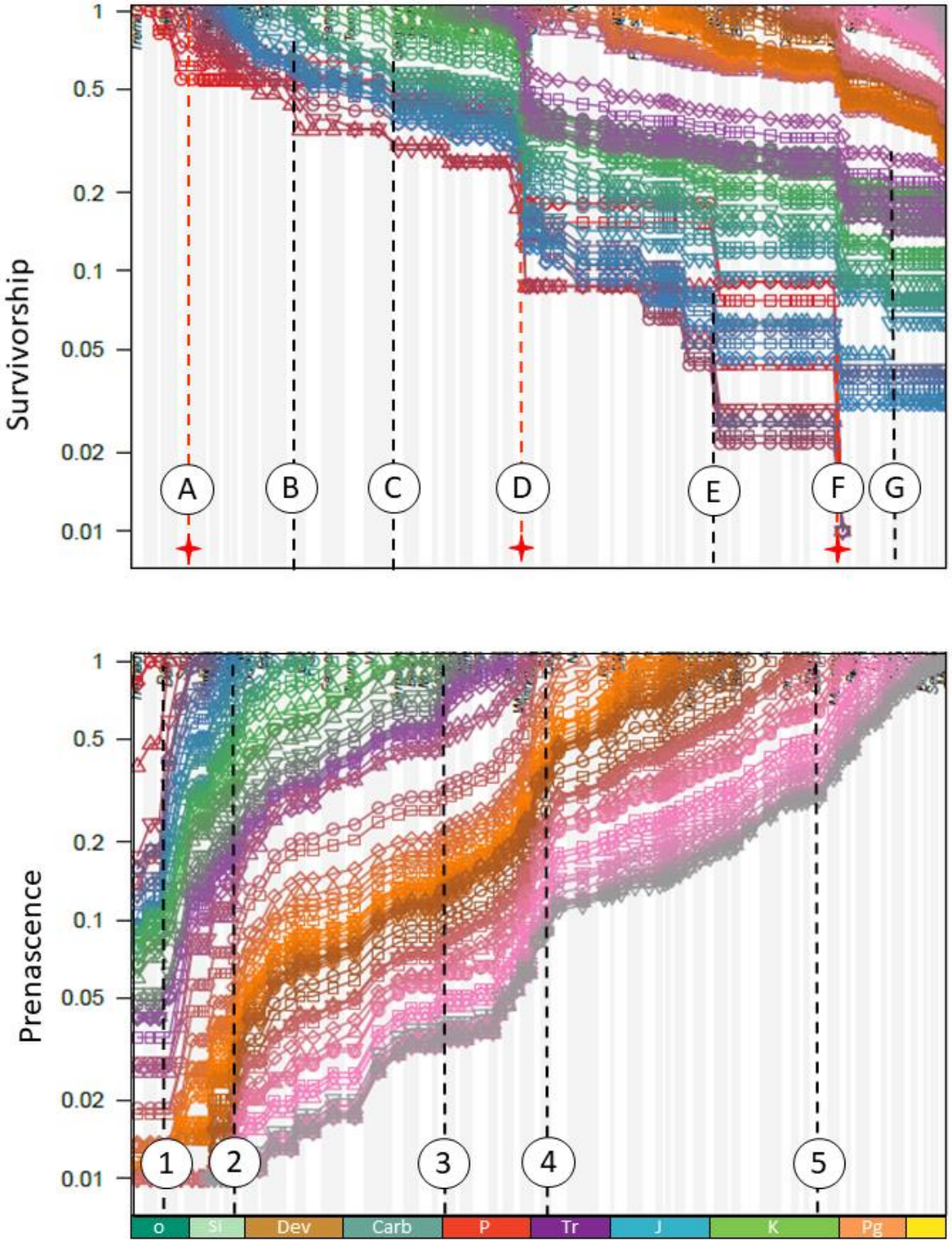


Figure 9 : Poly-cohort analyses reporting the constancy of extinction and origination rates through the time intervals. The cohort survivorship indicates the percentage of a cohort (assemblage of taxa in a given stage) that is still present in the next intervals - the ones which can survive through time. The cohort prenascence highlights the proportion of an assemblage in a given interval present in earlier time bin. It is the proportion of taxa originating through time. Non linear curves would imply changing rates. A to G are several events correlated to a loss of genus richness and 1 to 5 are several events correlated to a gain of genus richness

Eifelian to the Visean the slope is gentle suggesting a reasonably good survival of the genera, punctuated at the end (between the Visean and the Serpukhovian) by a more rapid decline. This event remains minor, since a constant rate is maintained until the end of the Permian. The Permian/Triassic interval is an abrupt change in survival rates, with a significant decrease. The slopes are relatively smooth up to the Tithonian, occasionally showing minor, barely perceptible events, making the decline a little more rapid in the Jurassic. A sharp drop in survival rate is visible between the Jurassic and the Cretaceous (Tithonian/Berriasian) and then between the Cretaceous and the Paleogene. Between these two significant falls, survival rates are mostly unchanged. In the Cenozoic, the decline of certain genera is a bit more pronounced, with a more or less sharp decline between the Lutetian and Bartonian. The prenascence curves point to various significant changes in the composition of the bivalves (Fig. 8). A first change is visible in the middle of the Ordovician. The rate of prenascence increases quite rapidly to the interval between the Pridoli and Lochkovian. This second noteworthy event is followed by a more regular and gentle increase until the transition between the Carboniferous and Permian. Two further events are remarkable after this: the first between the Induan and the Olenekian and the second between the Aptian and the Albian.

2.2. Marine bivalves evolutionary faunas and ecospace

This part of the chapter 2 is a slightly modified version of an article submitted in Earth Science Review called "**Marine bivalves paleobiodiversity : the four big ships that pass in deep time**".

2.2.1. Introduction

Understanding biodiversity dynamics through time and space and their driving processes is a key challenge and central goal of macroevolution (Simpson 1944; Gould 2002; Alroy et al. 2008; Aberhan & Kiessling 2012; Ezard et al. 2016). Because the fossil record provides the only direct window into how Earth's biodiversity has changed over the past 540 million years of the Phanerozoic, estimating paleobiodiversity dynamics has been addressed historically

with datasets of fossil occurrences (Raup & Sepkoski 1982; Benton 1995; Alroy 2008; Alroy et al. 2008; Fan et al. 2020) and now is also complemented with phylogenies (Quental & Marshall 2010; Morlon et al. 2011; Benton 2015b). In addition to such fundamental questions in paleobiology (how diversity changed over geological timescale and what are the rules governing these diversity changes), there are obvious implications for current societal concerns about biodiversity loss and recovery resulting from human impacts and climate changes (Erwin 2009; Barnosky et al. 2011; Bellard et al. 2012; Tekwa et al. 2023; Kiessling et al. 2023). Because the diversity of life on Earth is controlled by hierarchical processes that interact over wide ranges of timescales (Stanley 1979; Jablonski 2008a; Gould 2002), deep time series are needed to answer pressing questions including whether the rate, magnitude and direction of modern changes documented by living experiments or human-scale time series (Wernberg et al. 2024) differ and still hold in the fossil record over million years (Lewandowska et al. 2020; Reddin et al. 2020).

Since several decades marine bivalves have become a key model system for macroevolutionary and macroecological analyses both in the fossil record and living organisms (Stanley 1975; Miller & Sepkoski 1988; Jablonski et al. 2006; Valentine et al. 2006; Krug et al. 2009; Valentine & Jablonski 2010; Tomašových et al. 2016; Payne & Heim 2020; Opazo & Twitchett 2022; Yan et al. 2023; Zhou et al. 2023; Foote et al. 2024). The Class Bivalvia is one of the most successful invertebrate groups, having originated in the mid-Cambrian (Skovsted 2004; Fang & Sanchez 2012; ca. 520 Ma) and having prospered particularly since the Middle Ordovician (ca. 470 Ma), leaving a rich and excellent shell-based fossil record spanning the entire Phanerozoic (Fraiser & Bottjer 2007; Mondal & Harries 2015). These mollusks have a large range of traits and ecological adaptations allowing them to be largely distributed all around the world today in marine aquatic environments, and are generally small, slow-moving or sedentary animals with low-energy requirements when compared with other large and active mollusks (Stanley 1975; Gosling

2015). Interestingly many studies highlighted that bivalves achieved their current prominence in marine benthic biotas by ever-increasing diversity throughout the Phanerozoic with a shallow trend in a roughly exponential pattern (Miller & Sepkoski 1988; Alroy 2010b).

This genuine pattern is arguably primarily a true biological signal not significantly impacted by sampling biases or the 'Pull of the Recent' effect (Jablonski et al. 2003; Mondal & Harries 2015). However, this seemingly peaceful long-term trend does not imply that bivalve diversity was a bed of roses (Escarguel et al. 2011) and the diversity dynamics within the bivalves remain poorly investigated. Indeed, although most higher taxa are affected by major radiations and extinctions, they have peaked in diversity at different times (Benton 1987; Harper et al. 2020). For example, Paleozoic ocean floors were dominated by trilobites, brachiopods, and crinoids, whereas Cenozoic communities were dominated by scleractinian corals and mollusks (Sepkoski 1981; Alroy 2010b; Muscente et al. 2018; Rojas et al. 2021). Because richness patterns are determined by group-specific characteristics (organisms being adapted to specific environmental and biotic niches) one can logically expect changes in global taxonomic dominance as earth–life systems evolve through time.

Temporal shifts in global taxonomic composition through deep time have been exemplified by the pioneer work of Sepkoksi (1981) who categorized marine animals into the so-called Cambrian, Paleozoic, and Modern ‘evolutionary faunas’ on the basis of shared family richness within metazoan classes. This categorization has served as a benchmark for macroevolutionary research at the Phanerozoic scale in order to understand biodiversity dynamics and critical steps in the evolution of life (Sepkoski 1984; Benton 1987; Alroy 2004; Peters 2008; Bush & Bambach 2011; Brayard et al. 2017; Muscente et al. 2018; Rojas et al. 2021; Rojas 2022). Also, this pattern appears resilient to taxonomic resolution and methods of sampling and counting taxa (Alroy 2010b; Rojas et al. 2021). This concept (marine diversity is highly structured with higher taxa organized into mega-assemblages that successively dominated the oceans) has also been successfully applied to specific

taxonomic groups such as trilobites (Adrain et al. 1998; Bault et al. 2022) and even to terrestrial organisms such as plants and mammals (Niklas et al. 1983; Figueirido et al. 2012; Cleal & Cascales-Miñana 2014).

In addition to such diversity analyses, the study of concomitant ecological changes, either globally or within groups, provides crucial and complementary information (Valentine 1969; Bambach et al. 2007; Bush & Bambach 2011; McGhee et al. 2013). Identification of life modes of taxa based on their morphofunctional traits led to the quantification of their 'ecospace' through time and/or space, typically by examining the three components of mobility, feeding habit and tiering (Bambach 1993; Bambach et al. 2007; Bush et al. 2007; Novack-Gottshall 2007). Recent studies pave the way for a comprehensive analysis of bivalve ecospace and Mondal & Harries (2016) showed that i) bivalves have only occupied a third of their hypothetically available ecological cubes, ii) the major phase of increase in the range of ecological types occurred during the Ordovician, and iii) mass extinctions had a very limited impact on ecospace utilization despite their impacts on bivalve taxonomic richness. However, it remains unclear whether ecological diversity plays any role in driving taxonomic diversification overall and/or among subgroups.

Despite being both a model system for macroevolution in deep time (op. cit.) and nowadays important goods and services (Smaal et al. 2019) impacted by human-scale global warming (Rato et al. 2022; Kruft Welton et al. 2024), how marine bivalve communities (and all organisms in general) respond to varying magnitudes and rates of biotic and/or environmental perturbations across temporal scales remain little understood despite being a crucial concern (Masanja et al. 2023). Typically, the quantitative long-term changes in the dominance of major taxonomic groups within bivalves are currently unknown. Therefore, the goal of this study is to expand the knowledge on diversity dynamics of marine Bivalvia at a macroevolutionary scale during the entire Phanerozoic by evaluating (for the first time) the presence of evolutionary faunas within this key group, and to determine if taxonomic richness

within this class can be described by just a few factors despite complex environmental and biotic changes through deep time. Then, this study reviews the potential biotic and/or abiotic triggers of these documented large-scale variations in taxonomic composition within the marine bivalves.

2.2.2. Material and methods

2.2.2.1. Data

Fossil occurrence data of Phanerozoic bivalves are derived from Payne & Heim (2020), who downloaded them from the international Paleobiology Database (PBDB; https://paleobiodb.org/) and post-processed them (for example by appending body size data; for details, see Payne & Heim 2020). This dataset is further filtered by removing non-marine taxa, by elevating subgenera to genus rank, by considering only occurrences resolved to a single geological stage and at the genus taxonomic rank, and by focusing on the Ordovician–Neogene chronostratigraphic interval (ca. 485 to 2.6 Ma; Cohen et al. 2013). In addition, taxonomic assignments of genera across orders and families are revised and updated to be consistent throughout the dataset and to match published syntheses (Bouchet et al. 2010; Huber 2010, 2015) and international open access databases (e.g., MolluscaBase, https://molluscabase.org; WoRMS, https://www.marinespecies.org). The final dataset contains 71,729 occurrences composed of 30 orders, 196 families and 1119 genera (see Appendices.).

2.2.2.2. Evolutionary faunas and biodiversity

Global paleobiodiversity of bivalves at the genus rank and over time is assessed through taxonomic richness, which is estimated by means of the classical presence-based ‘total diversity’ (range-through diversity including single-interval taxa within time bins) and boundary-crosser diversity (range-through diversity common among successive pairs of time bins) (for further details, see Foote 2000 and Alroy 2010a). For comparison global diversity is

also estimated with sample-standardized methods such as the coverage-based rarefaction (= shareholder quorum sampling) and corrected first-order jackknife (Alroy 2010a, 2020). In addition, genus total diversity is estimated for each bivalve family independently.

Evolutionary faunas can be considered as taxonomic groups having relative high diversity simultaneously through successive time intervals (Sepkoski 1981). Here, such major temporally correlated richness assemblages of taxa, or bivalve evolutionary faunas (BEFs), are identified by a factor analysis (FA; see Sepkoski 1981; Cleal & Cascales-Miñana 2014) on the genus total diversity within bivalve families among geological stages. Each resulting, distinct and selected factor defines a BEF whose historical diversity is rescaled to the global total diversity according to its proportion of explained variance in the FA model. Similarly to Sepkoski (1981) the taxonomic composition of each BEF is determined by the score of each family on the corresponding factor, and a family can contribute to several factors (i.e., evolutionary faunas). Furthermore, the pervasiveness of the FA-based BEFs is corroborated by a hierarchical cluster analysis (HCA with Pearson's correlation and complete agglomeration method; Legendre & Legendre 2012) on the within-family genus total richness among time bins.

2.2.2.3. Ecospace

To gain additional insights on the identified evolutionary faunas, which are diversity-based assemblages/communities, their ecological diversity is investigated by examining their ecospace (Bambach et al 2007; Bush et al. 2007; Novack-Gottshall 2007). The ecological characteristics of each bivalve family that are used to define their ecospace are derived from the comprehensive work of Mondal & Harries (2016) who recognized specifically for bivalves three 'ecological categories' and sixteen 'life habits' leading to a theoretical, discrete three-dimensional ecospace composed of 140 'cubes' (ecological guilds; Aberhan 1994): i) tiering (from T1-erect epifaunal to T7-deep infaunal borer); ii) feeding (from F1-suspension filter-

feeding to F4-other strategies); and iii) motility (from M1-cemented to M5-fully motile and fast) (for details, see Mondal & Harries 2016).

Several analyses are performed on these ecological data by merging them with the occurrence data at the genus rank. First, the proportion of life habits actually occupied by all bivalves, independently of evolutionary faunas, is reconstructed through time for each of the three ecological categories. Similarly, the proportion of documented life habits among genera is compiled globally for each BEF separately. Finally, occupancy of the 3D theoretical ecospace is reconstructed for each BEF separately and then compared. The two latter results are further refined to include only the major contributing families of each BEF that are selected by having a factor score higher than 0.1 in the FA.

2.2.3. Results

2.2.3.1. Evolutionary Faunas

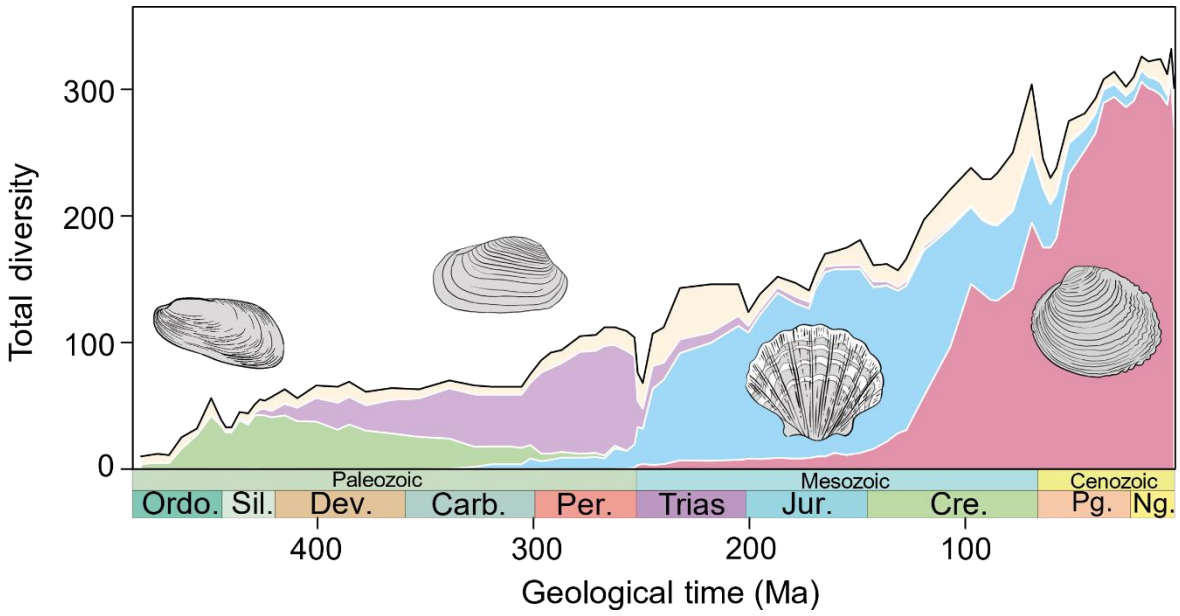


Figure 10 : Paleobiodiversity (genus richness) of bivalves through the Phanerozoic, with their cumulated four evolutionary faunas. The top bold line shows the global total diversity; the green area represents the Ordovician–Devonian fauna (OrDe BEF), the purple the Carboniferous–Permian fauna (CarPe BEF), the blue the Triassic–early Cretaceous fauna (TriJu BEF), and the red the late Cretaceous–Neogene fauna (CreNeo BEF); the top light yellow area corresponds to the residuals of the four-phase model in the factor analysis. Each fauna is illustrated by one taxon of its major family (left to right: Modiomorphidae, Grammysiidae, Pectinidae, and Veneridae).

Factor analysis on genus richness within the 196 bivalve families over the 85 geological stages considered (Ordovician–Neogene; ca. 485 to 2.6 Ma) produces four major eigenvectors, which explain more than 85% of the original variance (suppl. Fig. D). These factors clearly aggregate in clusters of adjacent time units (Figs D, E, F) and, therefore, constitute four major bivalve evolutionary faunas (BEFs), which follow one another over time (Fig. 10): i) an early Paleozoic fauna (OrDe-BEF) from the Tremadocian to the Famennian (Ordovician–Devonian); ii) a late Paleozoic fauna (CarPe-BEF) from the Tournaisian to the Changhsingian (Carboniferous–Permian); iii) a Triassic–early Cretaceous fauna (TriJu-BEF) from the Induan to the Aptian; and iv) a late Cretaceous–Cenozoic fauna (CreNeo-BEF) from the Albian to the Piacenzian.

Interestingly, among the three transitions between the four BEFs, two patterns can be distinguished. On the one hand, two transitions are long-term gradual, protracted replacements taking several million years during the mid-Paleozoic and the mid-Cretaceous. On the other hand, one transition is very sharp, almost instantaneous at the geological timescale, at the Permian/Triassic boundary. Also, importantly, all four BEFs existed before becoming the dominant component of bivalve communities. For example, regarding the third TriJu-BEF, it became predominant in the Triassic, but started diversifying in the Carboniferous and, similarly, in the Cenozoic while another BEF became dominant it still persisted with its families depauperating but without going extinct (Figs 10, 11).

Each BEF is defined by multiple families having high diversity conjointly in time, and a family can contribute sometimes to more than one factor as reflected by its scores on them (Table C). Also, the biodiversity over time of the major contributing families (Fig. 11) clearly shows that most of them extend in time far behind the evolutionary fauna to which they contribute the most. This pattern directly reflects the long-term gradual replacement of each BEF and underlines that BEFs are defined by the temporary dominance of specific families, but not directly by their appearance or disappearance (for example, the Cardiidae are typical

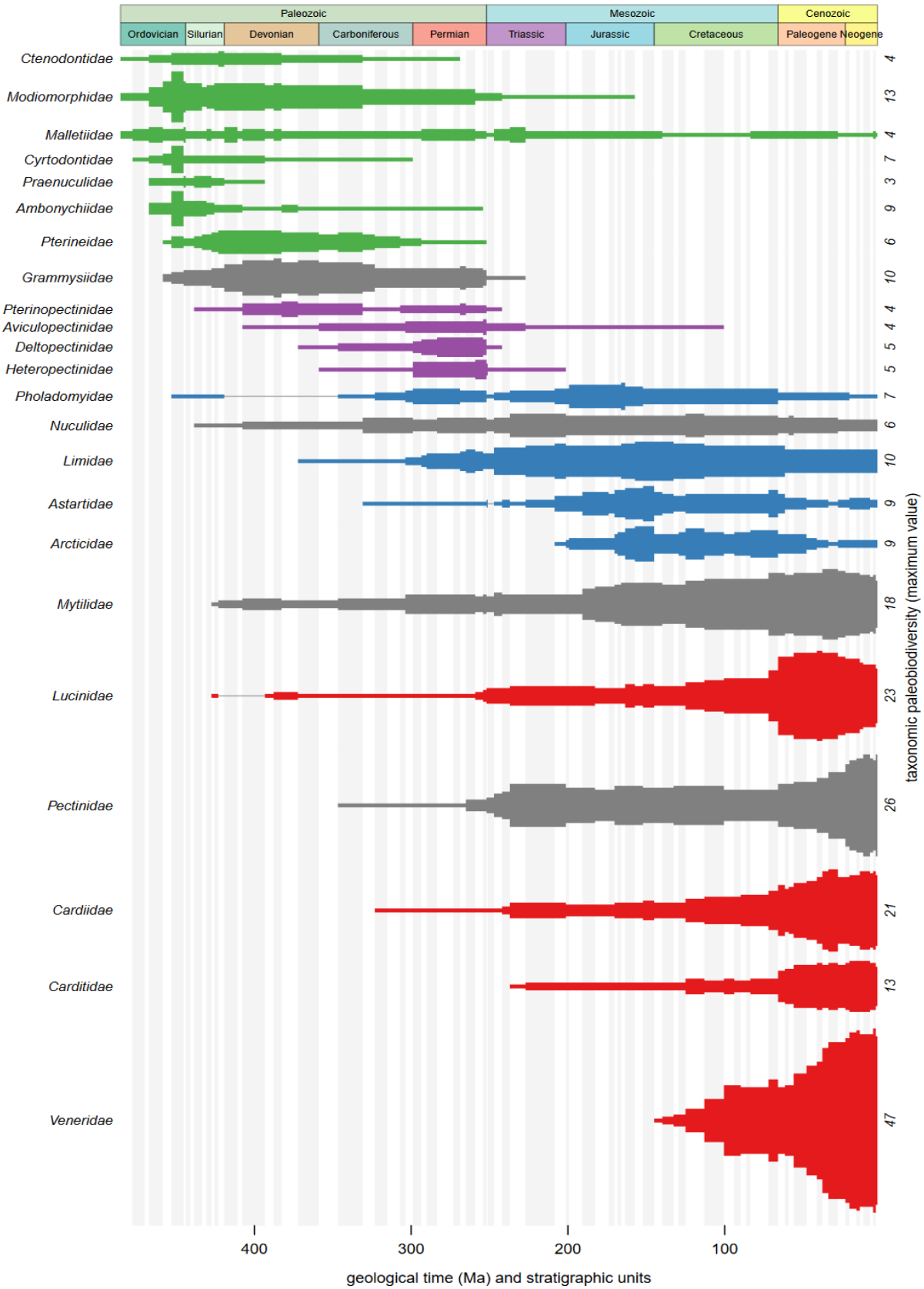


Figure 11 : Genus richness of the major contributing families for each bivalve evolutionary fauna (ordered by appearance and colored by BEF affinity; grey indicates families contributing to several BEFs; thickness is proportional to genus richness).

of the last late Cretaceous–Cenozoic BEF, but they already existed in the Paleozoic with a few genera; Fig. 11).

In terms of genus richness, the major contributing families (Fig. 11; Table C) to the OrDe-BEF are the Modiomorphidae, Malletiidae, Ctenodontidae, Pterineidae, Ambonychiidae, Cyrtodontidae, and Praenuculidae, as well as the Grammysiidae shared with the following CarPe-BEF. Next, the CarPe-BEF is dominated by the Deltopectinidae, Heteropectinidae, Aviculopectinidae, and Pterinopectinidae, as well as the Nuculidae shared with the following TriJu-BEF. Then, the major contributing families of the TriJu-BEF are the Limidae, Astartidae, Pholadomyidae, and Arcticidae, as well as the Mytilidae and Pectinidae shared with the last BEF. Finally, the CreNeo-BEF is largely dominated by the Veneridae, and in a lesser extent by the Lucinidae, Cardiidae, and Carditidae. Usually the most contributing families of each BEF belong to different orders, except for the CarPe-BEF dominated by the order Pectinida.

2.2.3.2. Ecospace

The bivalve theoretical 3D ecospace (tiering, motility, and feeding) and the relative proportion of their life habits documented by the genera of the major contributing families in each of the four BEFs are reported on Figures 12 and 13 (for the detailed time series, see suppl Fig. F,G,H and I). In terms of qualitative ecospace occupancy (Fig. 12), the early Paleozoic ('OrDe') BEF records 19 cubes, concentrated around semi-infaunal habits, and also characterized by the absence of borers. In terms of quantitative proportion of life habits (Fig. 13), bivalve genera of the OrDe-BEF are mainly semi-infaunal (39%) and shallow burrower (35%), with only two other tiering habits present (surface epifaunal and deep burrower). Therefore, during this fauna most bivalve forms are found within the sediments. Also, they are essentially suspension feeder (70%) with a small proportion of deposit feeder (15%). Regarding motility, this fauna is almost equally composed by slow motile (48%) and byssally-attached bivalves (45%).

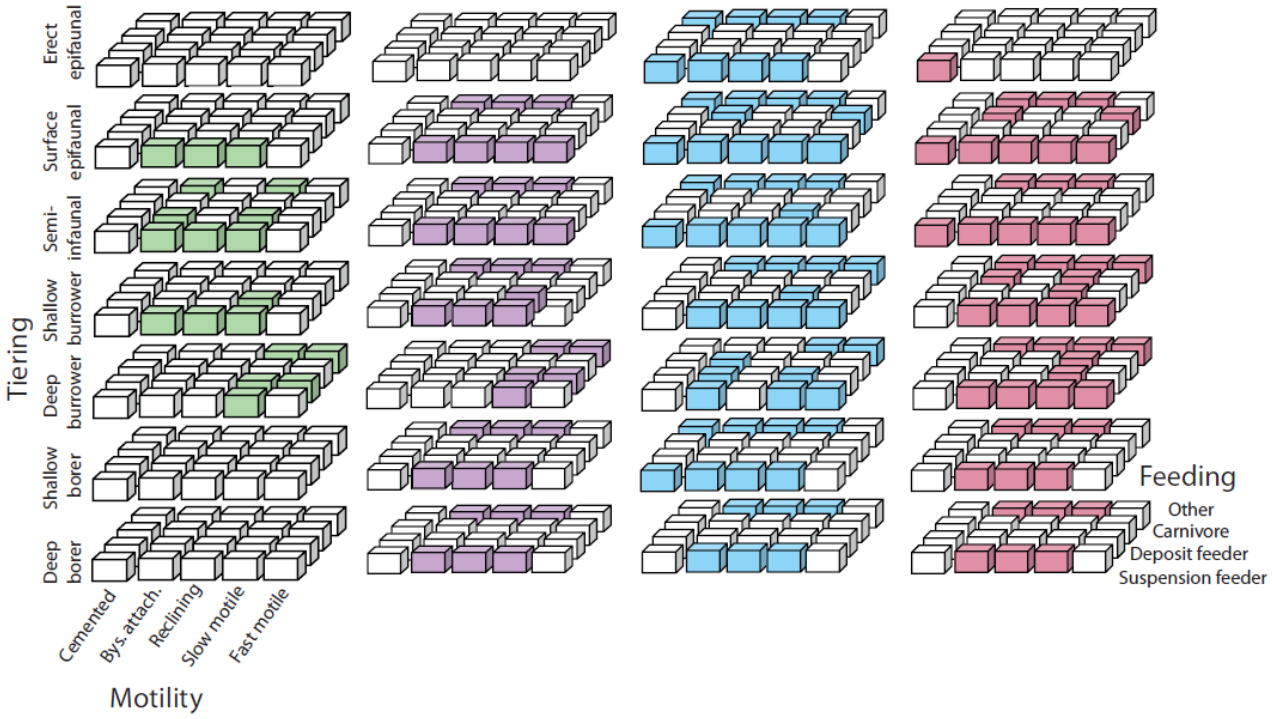


Figure 12: Ecospace (tiering, feeding habit and motility) occupied by the major contributing families for each of the four bivalve evolutionary faunas.

The late Paleozoic ('CarPe') BEF is characterized by the same dominant life habits (essentially suspension feeder, surface epifaunal or semi-infaunal, and slow motile or byssally-attached forms) than the previous OrDe-BEF. However, there is a marked shift towards surface epifaunal bivalve genera reaching a much higher proportion at the expense of shallow burrower genera. Also, the ecospace of this CarPe-BEF clearly expands with the addition of both shallow and deep borers, as well as carnivorous bivalves to the detriment of deposit feeders. This increase in ecological diversity of bivalves is well expressed by the ecospace reaching an occupancy of 38 cubes.

The Triassic–early Cretaceous ('TriJu') BEF has an ecospace qualitatively similar to the previous CarPe-BEF except the anecdotic appearance of erected forms. However, the proportion of deep burrower slightly increases and of semi-infaunal forms slightly decreases. The major ecospace modification is in motility habits with cemented forms appearing (11%) and recliners expanding (17%) to the detriment of byssally-attached forms. Interestingly, the

TriJu-BEF reaches an ecospace occupancy of 60 cubes and is the most ecologically diverse BEF of the Phanerozoic.

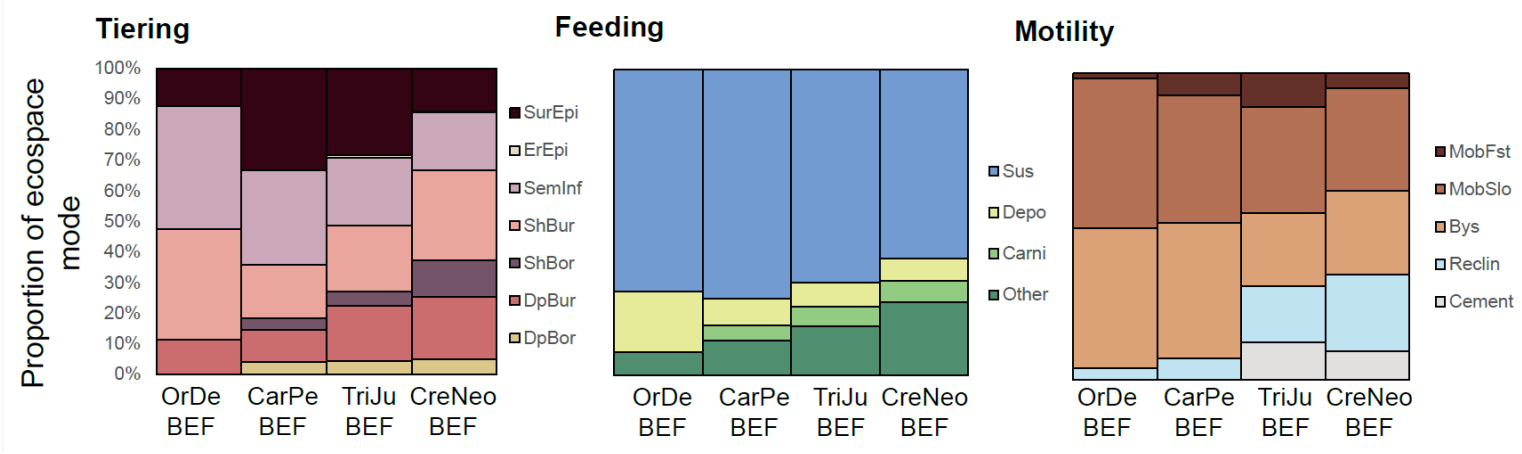


Figure 13: Relative dominance of bivalve genera regarding their ecological guilds (tiering, feeding habit and motility) for the four bivalve evolutionary faunas.

Finally, the late Cretaceous–Neogene ('CreNeo') BEF is dominated by infaunal forms, especially with an increased proportion of shallow burrower (28%) and borer (11%) forms to the detriment of surface epifaunal forms (13%). In contrast to the previous TriJu-BEF, the CreNeo-BEF shows an increase of peculiar feeding habits (e.g., chemo- and photosymbiosis, parasitism) to the detriment of suspension feeders, and the proportion of recliners still increases (24%). However, this most recent BEF occupies 52 ecological cubes that is less than the previous BEF, whereas the global taxonomic richness of bivalves still expands at the same time (Fig. 10).

In addition to the aforementioned differences in ecological habits of the four BEFs, the bivalve ecospace shows global trends through time in increasing disparity coupled with increasing evenness in the proportion among the occupied life habits, especially by increasing importance of recliners to the detriment of byssally-attached forms, as well as by deeper infaunalization (Figs 12,) as already noted by Mondal & Harries (2016). Thus,

changes in ecospace of bivalves are gradual and long-term trends at the scale of the entire Phanerozoic.

2.2.4. Discussion

2.2.4.1. Bivalve evolutionary faunas (BEFs)

Marine bivalves clearly show four major evolutionary faunas (EFs) that pass in deep time throughout the Phanerozoic when ordinating their within-family genus richness (Figs 10, 11, suppl. Fig. D, E, F). Several studies (Miller & Sepkoski 1988; Jablonski et al. 2003; Alroy 2010b) previously highlighted that overall the global diversity of bivalves shows a trend of ever-increasing taxonomic richness throughout the Phanerozoic (Figs 10, suppl. Fig.J). However, this study is the first to highlight that this seemingly peaceful trend is not a bed of roses and rather more complex as underlined here by the identification of four successive bivalve evolutionary faunas (BEFs). Since the milestone study of Sepkoski (1981) on evolutionary faunas, his picture of deep time biodiversity composed by three successive Great Evolutionary Faunas (Cambrian, Paleozoic, and Modern; Sepkoski 1981, Fig. 14) is probably among the most popular and referenced in paleontology (Rojas 2022). This innovative study launched subsequent works to understand underlying processes (Sepkoski 1984; Benton 1987; Alroy 2004; Peters 2008; Bush & Bambach 2011; Brayard et al. 2017; Rojas 2022) and their patterns have been recently re-evaluated and corroborated by means of modern network-based analysis (Muscente et al. 2018; Rojas et al. 2021). Also, the concept has been successfully applied at a higher taxonomic resolution on trilobites (Adrain et al. 1998; Bault et al. 2022; Serra et al. 2023), conodonts (Ginot & Goudemand 2020), mammals (Figueirido et al. 2012; Morales et al. 2015), and plants (Niklas et al. 1983; Cleal & Cascales-Miñana 2014; Capel et al. 2021).

The bivalve EFs (based on within-family genus richness) revealed here match in time Sepkoski's EFs based on within-class family richness of marine invertebrates (Fig. 14): i)

Sepkoski's Modern fauna (Mesozoic–Cenozoic) corresponds to both TriJu- and CreNeo-BEFs; and ii) Sepkoski's Paleozoic fauna to both OrDe- and CarPe-BEFs. Although the oldest Cambrian fauna cannot be recovered by the current study, which includes bivalve occurrence data since the Ordovician, residuals of the FA underlines that the four-factor solution do not fully explain diversity during the Early Ordovician suppl. Fig. C), thus suggesting likely remnants of a potential Cambrian EF also for bivalves. Besides, the early Paleozoic is known to show a drastic change from small, surface crawler bivalves (on microbial mat floors) with a cosmopolitan Cambrian distribution to Ordovician bivalves restricted to Gondwana and principally infaunal in siliciclastic sediments (Fang 2006; Cope & Kříž 2013). The Ordovician radiation of bivalves is associated to the evolution of the feeding gill, which allowed development of more effective feeding strategies (Cope & Babin 1999). Furthermore, unlike several other clades originating in the Cambrian, taxonomic diversity and functional disparity of bivalves were disconnected with the belated acquisition of key anatomical novelties in the Early Ordovician (Fang 2006; Zhou et al. 2023).

Interestingly, the recent re-evaluation of Sepkoski's EFs by Rojas et al. (2021) on benthic marine invertebrates at the genus level by network analysis corroborates the Cambrian and Paleozoic mega-assemblages, but also further refines the Modern fauna into two EFs with a protracted transition during the mid-Cretaceous. This last pattern perfectly corresponds to the TriJu- and CreNeo-BEFs and their transition as documented here only for bivalves (Fig. 10). In addition, similarly to other global studies on evolutionary faunas (Sepkoski 1981; Rojas et al. 2021), all BEFs appeared/emerged tens of millions years before becoming dominant. Last but not least, the current study focusing on bivalves highlights an additional transition during the mid-Paleozoic (among the OrDe- and CarPe-BEFs around the Devonian/Carboniferous boundary) not documented by previous studies on marine invertebrates. Overall, these results support that global paleobiodiversity of marine bivalves experienced a four-phase model during the Phanerozoic (Fig. 10).

The macroevolutionary implications of such evolutionary faunas (non-random shifts in dominance of mega-assemblages/communities sequentially through deep time) has long been debated (Sepkoski 1981, 1984; Benton 1987; Alroy 2004; Peters 2008; Bush & Bambach 2011) and they result from both long-term ecological changes and major (abrupt) geological events (Rojas et al. 2021). This holds also for the bivalve evolutionary faunas, which result from the complex interplay of multiple factors at various temporal and geographic scales in the oceans. Indeed, the OrDe-BEF diversified during the large-scale, long-term early Paleozoic radiation of life covering the 'Cambrian Explosion' and 'Great Ordovician Biodiversification Event' (Servais et al. 2023). Next, the three major biotic transitions among the Phanerozoic BEFs vary in timing and potential causative drivers: two protracted and gradual shifts during the mid-Paleozoic and mid-Cretaceous, and one abrupt change at the Permian/Triassic boundary (PTB).

2.2.4.2. The sharp PTB transition among BEFs

Regarding abrupt events at a geological timescale, mass extinctions are traditionally recognized to play a fundamental role in the Phanerozoic evolution of life and overall diversity dynamics (Raup & Sepkoski 1982; Van Valen 1984; Hallam & Wignall 1997; Brayard et al. 2009; Bond & Grasby 2017). The biotic transition documented here between the CarPe- and TriJu-BEFs coincides with the most severe biotic crisis of the Phanerozoic (Bambach et al. 2004; Bambach 2006; Erwin 2006; Benton 2008; Stanley 2016) at the Permian/Triassic boundary (PTB). This event was triggered by a number of physical environmental shocks (global climate warming, acid rain, ocean acidification and marine anoxia) leading to a complex recovery of marine ecosystems over several million years that paved the way for the transition from Paleozoic to Mesozoic evolutionary faunas (Wignall & Twitchett, 1996; Hallam & Wignall, 1997; Benton & Twitchet 2003; Knoll et al. 2007; Chen & Benton 2012; Joachimski et al. 2012; Burgess & Bowring 2015; Song et al. 2018; Friesenbichler et al. 2021; Feng et al. 2022; Huang et al. 2023). Regarding bivalves, this

crisis is already known to have deeply impacted their biodiversity (Fig. 10; Miller & Sepkoski, 1988; Fraiser & Bottjer, 2007; Mondal & Harries 2015; Huang et al. 2014) and leading to a multiphase recovery (Hautmann et al. 2013; Hofmann et al. 2015; Song et al. 2018). Besides, this long-term recovery is visible in the FA model showing high residuals during the Early Triassic (suppl. Fig. C & suppl. Table C). This pattern is congruent with the studies of Sepkoski (1981) and Rojas et al. (2021) who already noted that the Triassic recovery was concomitant with unusual communities as can be expected in this case given that ecosystems fully recovered only in the Middle Triassic (Bottjer et al. 2008; Chen & Benton, 2012).

Interestingly, despite having a clear impact on global diversity and EFs of bivalves, the PTB did not drastically change their ecological habits. Except a higher proportion of cemented forms, the ecospace occupancy of the TriJu-BEF remains close to the previous CarPe-BEF and in the continuity of the global Phanerozoic trends (Figs 12, 13, suppl Fig F, G, H, I). Although the infaunal ecological structure was resilient and already well established in the early Smithian (Feng et al. 2022), marine level-bottom communities (including bivalves) shows an initial Early Triassic biotic-based lag phase that is followed by a hyperbolic diversity increase during the early Middle Triassic (Friesenbichler et al. 2021). Therefore, at a macroevolutionary scale, it appears that the PTB strongly impacted global bivalve diversity with the extinction of major families (Fig. 11), but the clade fully recovered with other families by occupying almost the same ecospace. This pattern of decoupling between taxonomic and ecological recoveries has also been already recognized for the entire marine ecosystems (Song et al. 2018).

Noteworthy, mass extinctions as short-term events did not governed directly the other BEF transitions, which are protracted shifts through several millions years. This stands in contrast with global taxonomic richness, which dropped sharply also for most other Big Five extinctions (Figs 10, suppl. Fig. J; Miller & Sepkoski 1988; Mondal & Harries 2015). However,

these extinctions remain at the genus level whereas most bivalve families do not disappear except a few at the PTB (Fig. 11). For example, the famous Cretaceous/Tertiary mass extinction with its meteorite impact, massive magmatic output, and disappearance of dinosaurs and ammonites (MacLeod et al. 1997), sharply affected bivalves with extinction of some families (suppl. Fig J), but not enough to affect the CreNeo-BEF community structure with the most characteristic families being already diverse before the event and continuing to expand after, such as the Veneridae (Fig. 11). Also, Lockwood (2005) demonstrated an

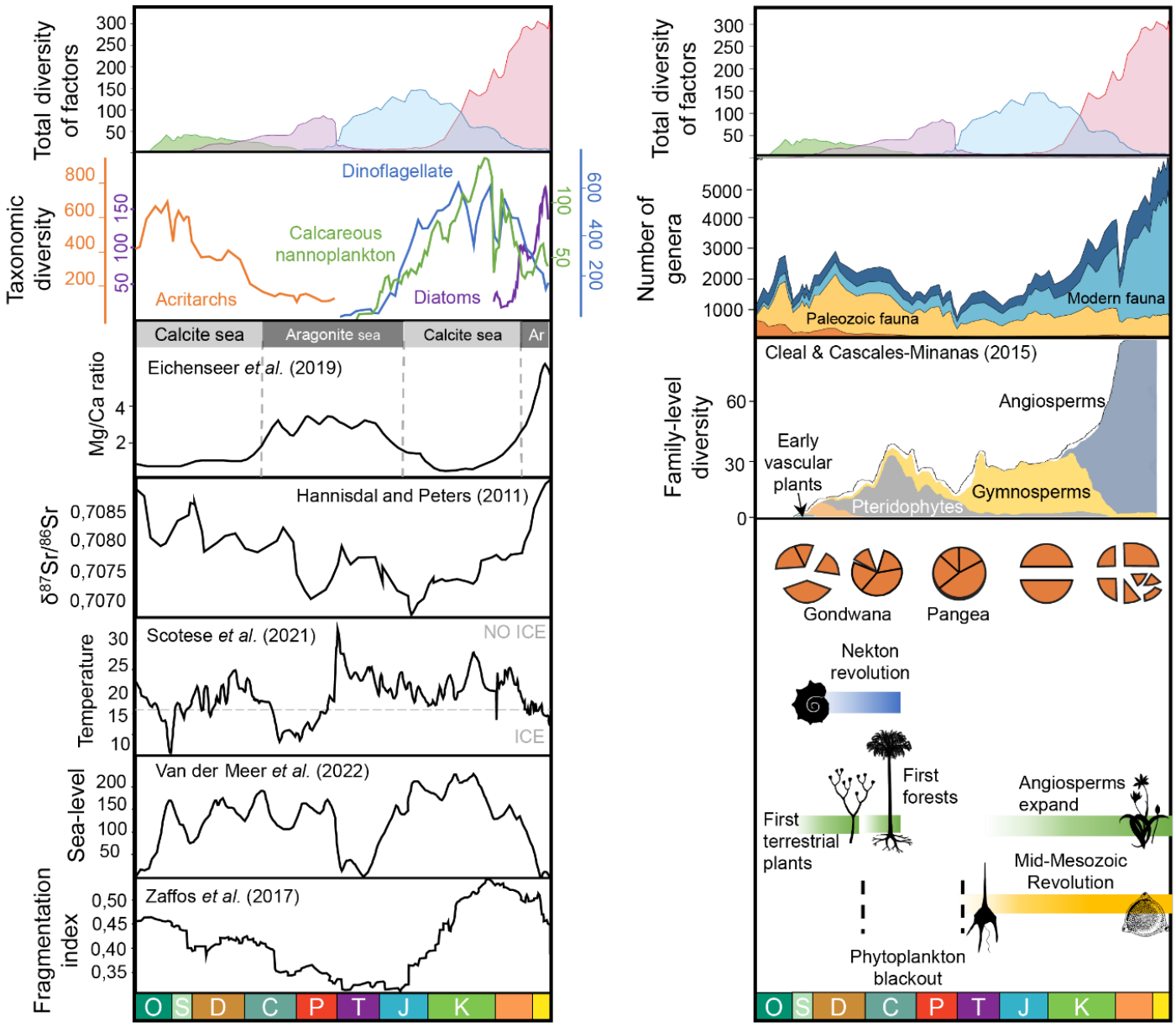


Figure 14 : Comparison of bivalve evolutionary faunas with global environmental proxies and major ecological changes (for details and references, see discussion).

absence of size-selective extinction among these veneroids despite a drop in richness. In addition, similarly to the PTB, this mass extinction event did not drastically change the ecospace of bivalves (Figs 12, 13; Mondal & Harries 2016); a pattern also documented for bivalves at the Triassic/Jurassic boundary mass extinction (Ros et al. 2011; Abdelhady et al. 2023). Therefore those global mass extinction events affected BEFs only once exceptionally at the Permian/Triassic boundary and, thus, are not a pervasive background driver of the evolutionary history of bivalve benthic marine communities. This result highlights that marine bivalves constitute a highly resilient structured group when facing biotic and environmental changes at a macroecological scale. Although bivalves have always recovered from mass extinctions, the Permian/Triassic mass extinction has effectively reset their diversification process and overturned the balance of their groups, suggesting that the current global crisis can still permanently alter the biosphere's taxonomic composition even for such a resilient class.

Nevertheless, the impact of the Permian/Triassic boundary on the bivalve ecospace is more complex. For example, during the Early Triassic in western USA Hautmann et al. (2013) recognized two bivalve subclasses (Pteriomorphia and Heteroconchia), which differ in their evolutionary contexts: on the one hand, chiefly sessile, epifaunal to semi-infaunal pteriomorphs nearly exclusively composed of genera that survived the end-Permian mass extinction; and on the other hand, burrowing heteroconchs highly dominated by genera that newly evolved in the Early Triassic. They hypothesized that this contrasting evolutionary background probably reflects differential effects of the end-Permian mass extinction event on these two subclasses, possibly related to differences in filter feeding efficiency and shell mineralogy. Similar patterns have been observed for the end-Triassic mass extinction, where higher extinction levels of infaunal heteroconchs have been attributed to less efficient filter feeding than epifaunal bivalves (McRoberts & Newton 1995) and their completely aragonitic

shell mineralogy (Hautmann et al. 2008). However, this cannot be evaluated with the ecospace used in this study and related (Mondal & Harries 2016).

Last but not least, the Permian/Triassic boundary is also well-known to witness a switch in the dominance of brachiopods and bivalves in marine benthic biotas that was interpreted as 'ships that pass in the night' (Gould & Calloway 1980; Fraiser & Bottjer 2007) or as biotic competitive replacement (Thayer 1985; Clapham 2015; Liow et al. 2015). Recent analyses demonstrated that brachiopods and bivalves were not actual competitors over macroevolutionary timescales, with extinction events and environmental stresses shaping their divergent fates (Guo et al. 2023). This interpretation of non competitive replacement seems to hold also within the bivalves themselves between the CarPe- and TriJu-BEFs as suggested by the sudden extinction of many typical Paleozoic families, by typical Mesozoic families already present before, and by the presence of families shared by both evolutionary faunas (Figs 11, suppl. Fig J).

2.2.4.3. The gradual mid-Paleozoic and mid-Cretaceous transitions among BEFs

Are the BEFs fuelled by plankton evolution and continental fragmentation?

The evolution of marine organisms in deep time is highly influenced by multiple interconnected factors (Tappan 1968; Vermeij 1977, 1995; Leckie et al. 2002; Alroy 2010c; Saupe et al. 2019; Bush & Payne 2021; Antell & Saupe 2021; Salles et al. 2023; Payne et al. 2024), both abiotic such as bolide impacts (Alvarez et al. 1980), continental configuration/plate tectonics (Valentine & Moores 1970; Zaffos et al. 2017; Pohl et al. 2022), volcanism (Courtillot & Renne 2003), global climate/temperature (Valentine 1968; Crame 2001; Willig et al. 2003; Mayhew et al. 2012), sea level changes and continental flooding (Hallam & Wignall 1997; Hannisdal & Peters 2011), ocean circulation and oxygenation/marine anoxia (Freymueller et al. 2019; Wu et al. 2024), and/or nutrient availability/primary production (Martin 1996; Cárdenas & Harries 2010), and biotic such as competition, diversity dependence and/or predation intensity (Huntley & Kowalewski 2007;

Klompmaker et al. 2017; Rineau et al. 2022; Foote et al. 2024), among many others. These competing paradigms are labeled the 'biotic' Red Queen and the 'abiotic' Court Jester (Benton 2009), and can both translate into patterns that are apparent on extremely long time scales of tens to hundreds of millions of years (Jablonski 2008b). Regarding the Devonian/Carboniferous (OrDe- and CarPe-BEFs) and the Cretaceous (TriJu- and CreNeo-BEFs) transitions, given the nature of their long-term gradual shift they probably result from progressive environmental changes and/or protracted restructuring of marine ecosystems. Among such global changes, few of them particularly coincide with the herein documented within-BEF genus diversity through geological time (Fig. 5): continental fragmentation and plankton stoichiometry.

Indeed, tectonic assembly and breakup of the supercontinent Pangea through the Phanerozoic as reflected by the fragmentation index (Zaffos et al. 2017) parallel the waning and waxing of the BEFs (Fig. 14). Typically, the decreasing trend in diversity of the OrDe-BEF follows the global long-term decreasing continental fragmentation during the Paleozoic, which corresponds to the concomitant assembly of Pangea and a decreasing first-order sea level. Similarly, the spreading of the CreNeo-BEF matches the Pangea breakup (with notably opening of the Atlantic Ocean) and long-term sea level rise of the Mesozoic (Miller et al. 2005; Marcilly et al. 2022). This positive correlation may result from cascading effects of this continental fragmentation, which leads to increased area of coastal habitats, higher sea level and enhanced oceanic circulation, and by increased nutrient fluxes into the seas. These environmental changes are traditionally interpreted as more favorable habitats for bivalves and thus increased diversity and dispersal (Aberhan 1994). However, this interpretation cannot hold for the CarPe- and TriJu-BEFs, which stand in contrast with an opposite, negative correlation, but still a correlation. Therefore, despite this high correlation (either positive or negative) between up and downs of each BEF and continental fragmentation, a direct causal link remains elusive and there are likely cascading environmental and biological

effects leading to these two antisymmetric patterns. Also, the BEF-fragmentation link is not straightforward because flooded continental area and paleocoastline length as recently reconstructed by Kocsis & Scotese (2021) do not correlate with the herein documented BEFs.

Similarly to continental fragmentation, the diversities of the phytoplankton through time mirror both positively with the OrDe- and CreNeo-BEFs and negatively with the CarPe- and TriJu-BEFs (Fig. 14). Indeed, diversity of the OrDe- and CreNeo-BEFs closely follows the phytoplankton diversity as represented by the acritarchs in the Paleozoic (see Kroeck et al. 2022), and the calcareous nannoplankton, dinoflagellates and diatoms as a whole in the Mesozoic–Cenozoic (see Falkowski et al. 2004). Given that bivalves are mostly suspension feeders (Gosling 2015; Mondal & Harries 2016), macroevolution of this plankton may have likely fueled directly the biodiversification and collapse of marine organisms (Signor & Vermeij 1994; Martin 1996; Antell & Saupe 2021; Martin & Cárdenas 2022; Kroeck et al. 2022) such as bivalves by a cascade effect by being their main nutrient supply (Vermeij 2010), and particularly those involved in the OrDe- and CreNeo-BEFs. Interestingly, phytoplankton itself can be fueled by the aforementioned continental fragmentation via nutrients runoff (Martin 2003; Katz et al. 2004; Cárdenas & Harries 2010): continental fragmentation impacts coastline length and so the main habitat of mollusks, implies changes in sea-level and continental weathering and so the continental inputs, which in turn are nutrients for the planktic component of the oceans, and finally these nutrients and plankton are the main food supply of bivalves. Noteworthy, if one assumes that the BEFs are correlated to plankton evolution either positively or negatively (Fig. 14; OrDe- and CreNeo-BEFs vs. CarPe- and TriJu-BEFs), one can infer that the bivalve families contributing to these two BEFs belong to two major ecological guilds, adapted to different nutrient sources and/or filtering abilities. However, this hypothesis cannot yet be evaluated from the fossilized shells alone and remain to be assessed on modern faunas.

Current anthropogenic climate change has brought to the fore the long-recognized role of global climate in driving change in taxonomic richness (Mayhew et al. 2008; Malanoski et al. 2024): biodiversity indeed tracks temperature over deep time when accounting for sampling effort and time series autocorrelation (Mayhew et al. 2012). Regarding marine bivalves, despite a clear temperature-driven latitudinal gradient of diversity in modern oceans (Jablonski et al. 2000; Valentine & Jablonski 2010), their slowly ever-increasing global richness through deep time hardly correlates with the highly fluctuating and cyclical climate changes (Fig. 14) as exemplified by Milankovitch cycles (Bennett 1990). Furthermore, there is no obvious correspondence between the BEFs transitions and the alternance of icehouse and greenhouse intervals (compare Fig. 10 with Song et al. 2019 and Scotese et al. 2021). Therefore, the Phanerozoic BEFs are not directly driven by temperature changes in contrast to Cenozoic mammals (see Figueirido et al. 2012).

Last but not least, because bivalves are shell constructors, ocean chemistry via acidification can be expected to influence their macroevolution by impacting biomineralization (Ries 2010), and the Phanerozoic actually records a long-term alternance of ‘calcite’ and ‘aragonite’ seas (Stanley & Hardie 1998). For example, the increase in calcifying plankton during the Cretaceous is hypothesized to have induced a change from an aragonitic to a calcite sea (Eichenseer et al. 2019) and helps calcite bivalves to reduce the cost of creating their shells. However, this link is not so straightforward because this abiotic forcing may have changed through time (Eichenseer et al. 2019), the shell chemistry of all bivalves is not fully documented, and transitions among BEFs do not closely match changes in aragonite/calcite seas (similarly to climate changes). However, a partial influence cannot be excluded. For example, the detailed study of Hautmann (2006) clearly documented these contrasted patterns among bivalves: in the ‘calcite sea’ of the Jurassic and Cretaceous, the most diverse and abundant families of epifaunal bivalves had largely calcitic shells while some of them acquired this shell mineralogy earlier (e.g. Inoceramidae); however, other families

replaced aragonite by calcite in their shell at the beginning of the Jurassic (e.g. Ostreidae) without changes in morphology and life habit. Finally, the proportions of marine bivalve genera categorized by shell mineralogy over the Phanerozoic (Kidwell 2005) shows no obvious correlation with the four BEFs documented here.

The mid-Paleozoic BEFs transition

The mid-Paleozoic shows the transition from the OrDe-BEF to the CarPe-BEF (Figs 10, 11). The OrDe-BEF clearly coincides with, and contains bivalve families, which diversified during the Great Ordovician Biodiversification Event (GOBE; Webby et al. 2004; Servais et al. 2010) and lasted in the Silurian; most of these families persisted later on but with reduced genus richness. The CarPe-BEF contains families that originated successively since the Silurian, but diversified slowly since the Carboniferous to reach their highest diversity in the Permian. Therefore, the transition among these two BEFs is gradual and protracted, mostly during the entire Devonian with the decline of the OrDe-BEF and rising of the CarPe-BEF, which reached dominance at the Devonian/Carboniferous boundary (Figs 10, suppl. Fig C). The long-term gradual aspect of this transition is well illustrated by, and due to changes in, the relative genus richness of their contributing families but not by their actual appearance or disappearance (Fig. 11). These patterns all point towards slow environmental and/or biotic changes in marine (eco)systems as potential triggers.

Regarding the dominance and decline of the OrDe-BEF, it strikingly and perfectly parallels the paleobiodiversity of acritarchs (Fig. 14; see Kroeck et al. 2022), which are the dominant component of the phytoplankton in the Paleozoic (Martin & Servais 2020). Because early Paleozoic bivalves are mainly suspension feeders, one can hypothesize that the evolution of this phytoplankton likely fueled and drove directly the OrDe-BEF, as suggested by other studies for marine invertebrates (see Martin 1996, 2003; Martin & Servais 2020; Kroeck et al. 2022). Therefore, it suggests that the bivalve families typical of this evolutionary

fauna are direct consumers of this type of phytoplankton; an hypothesis that cannot yet be evaluated by bivalve shell morphologies.

Regarding the CarPe-BEF, unlike the previous older BEF, its rising is associated with the decreasing acritarch diversity (Fig. 14). Furthermore, the time interval (Carboniferous–Permian) of this BEF dominance is associated with a seemingly depauperate plankton diversity known as the 'Phytoplankton Blackout' (Riegel 2008), which is characterized by the non-preservation of the plankton at that time. Importantly, this ‘blackout’ underlines not an actual diversity decline but rather a fundamental change in plankton stoichiometry (Servais et al. 2016; Martin & Servais 2020), which for bivalves means a change in the type of nutrients available in marine food webs. Therefore, one can hypothesize that this gradual change in phytoplankton quality likely enabled the diversification of different bivalve families more adapted to this different food sources and leading to the CarPe-BEF.

Interestingly, the CarPe-BEF is associated with a major change in the ecological tiering of bivalves by a wider occupation of the sediment: the proportion of shallow burrower and erected epifaunal forms are highly reduced in favor of surface epifaunal and (shallow and deep) borer forms (Fig. 13). Noteworthy, this switch from an initial phase dominated by semi-infaunal forms to a post-Devonian phase dominated by surface epifaunal forms in bivalves Paleozoic ecological history was already underlined by Mondal & Harries (2016), who also noted that the root of this change in relative dominance was likely initiated in the Silurian, thus reflecting the gradual transition observed here in the BEFs. In contrast, the CarPe-BEF also records an increased ecospace disparity in feeding with the development of carnivorous forms, but without affecting the dominant proportion of suspension feeders. Therefore, the documented switch both in bivalve evolutionary faunas and phytoplankton stoichiometry around the Devonian/Carboniferous boundary suggests the presence in bivalves of several ecological guilds within the so-called ‘suspension feeders’ that filter-feed on different nutrients.

Noteworthy, if one can hypothesize that the Phytoplankton Blackout is the main trigger of the switch in bivalve evolutionary faunas during the mid-Paleozoic, this time interval is also known to witness major biotic and environmental changes, which may be also related to plankton evolution such as the 'Devonian Nekton Revolution' (Klug et al. 2010), which likely impacted marine food webs. By the way, terrestrial plants also show evolutionary floras concomitant to the BEFs: Cleal & Cascales-Miñana (2014) documented the Rhyniophytic and Eophytic floras before the Devonian/Carboniferous boundary and the Paleophytic flora after. This change in the terrestrial biosphere is thought to have impacted also the marine biosphere by enhanced soil formation and weathering and so increased nutrient fluxes and eutrophic conditions into the oceans (Algeo & Scheckler 1998). Therefore, even if the terrestrial–marine teleconnections remain debated (D'Antonio et al. 2019; Dahl & Arens 2020; Elrick et al. 2022), the Paleozoic BEFs and their gradual transition as documented here underline and reflect large-scale, gradual, interconnected and cascading abiotic and ecosystem changes, which are global and not necessarily restricted to marine benthic organisms.

The mid-Cretaceous BEFs transition

The mid-Cretaceous shows the transition from the TriJu-BEF to the CreNeo-BEF (Figs 10, 11). The TriJu-BEF clearly results from, and contains bivalve families, which diversified during the Early Triassic recovery following the abrupt PTB mass extinction; noteworthy most of these families persisted in the Cenozoic but with reduced genus richness. The CreNeo-BEF contains families that originated successively throughout the Paleozoic and Mesozoic, but diversified slowly during the Cretaceous and more importantly during the Cenozoic without being affected by the Cretaceous/Tertiary mass extinction. Therefore, similarly to the mid-Paleozoic, the transition among these two BEFs is gradual and protracted during most of the Cretaceous, lasting tens of millions years, and is due to changes in the relative genus richness of their contributing families but not by their actual appearance or disappearance,

therefore suggesting that the triggers are likely slow environmental and/or biotic changes in marine (eco)systems.

Interestingly, this mid-Cretaceous transition can be framed by changes in both plankton stoichiometry and continental fragmentation similarly to the mid-Paleozoic transition albeit with an opposite pattern. The TriJu-BEF is still associated with the Pangea supercontinent and with a gap in the phytoplankton fossil record, whereas spreading of the CreNeo-BEF matches the Pangea breakup (with opening of the Atlantic Ocean) and long-term sea level rise of the Mesozoic (Miller et al. 2005; Marcilly et al. 2022), as well as the radiation of the modern eukaryotic phytoplankton represented by dinoflagellates, coccolithophores, and diatoms (Falkowski et al. 2004). Noteworthy, the community structure and ecological function of contemporary marine ecosystems are critically dependent on eukaryotic phytoplankton, which is responsible for the majority of the flux of organic matter to higher trophic levels and oceans (Falkowski et al. 2004). Therefore, the documented long-term Mesozoic rise to prominence in pelagic ecosystems of eukaryotic algae such as phaeophytes (Choi et al. 2024), dinoflagellates, coccolithophores, and diatoms (Falkowski et al. 2004), likely fueled the diversification of metazoan diversity in marine ecosystems (Martin 2003; Martin & Quigg 2012) including marine bivalves. However, the correlation between the phytoplankton and BEF diversities is less stringent with a lag in their rising diversity (dinoflagellates diversified before the CreNeo-BEF) and the Cenozoic dropdown of dinoflagellates is not reflected in the diversity of bivalves (Fig. 14).

Nonetheless, this time interval is already known to record a long-term (tens of million years) major change in ecosystems, the so-called 'Mesozoic Marine Revolution' (MMR; Vermeij 1977, 1987) during which the pace and intensity of biotic interactions (predation, competition and substrate disturbance by grazing and bioturbation) increased and had a marked effect on benthic marine communities, including an increased infaunalization of bivalves (Vermeij 1977; Buatois et al. 2022). Although the exact timing and details of this

ecosystem (r)evolution is debated (Harper & Skelton 1993; Buatois et al. 2016; Harper 2022), it is clearly an accumulation of multiple, gradual and interconnected environmental and biotic changes, which roughly coincide with the observed gradual shift in bivalve evolutionary faunas. Indeed, the adaptive radiation of bivalves during the Mesozoic–Cenozoic gave rise to many new infaunal superfamilies, all siphon-feeding groups, which opened the way for the occupation of many new infaunal ways of life that had been inaccessible to Paleozoic bivalves (Stanley 1968). However, this infaunalization initiated before the BEF transition (Fig. 14) and may result instead from a morphofunctional innovation. Last but not least, during the Mesozoic bivalves evolved not only toward infaunal forms but also toward erected forms and even became a major reef-building component in the Cretaceous (Kiessling 2009).

2.2.5. Conclusion

This study demonstrates that, despite a previously known pattern of long-term, weakly fluctuating biodiversity increasing throughout the Phanerozoic, there is a more complex pattern of faunal dynamics within the marine bivalves. A factor analysis of their within-family genus richness shows for the first time that most of their temporal variation can be partitioned into four successive taxonomic assemblages of concomitant richness (the so-called evolutionary faunas) (Fig. 10): i) an early Paleozoic fauna from the Tremadocian to the Famennian (Ordovician–Devonian); ii) a late Paleozoic fauna from the Tournaisian to the Changhsingian (Carboniferous–Permian); iii) a Triassic–early Cretaceous fauna from the Induan to the Aptian; and iv) a late Cretaceous–Cenozoic fauna from the Albian to the Piacenzian. Noteworthy, the major contributing families of each BEF (Table C) usually appeared and/or disappeared largely outside their time of dominance and often do not share times of origination and extinction (Fig. 9). Furthermore, similarly to the global richness, these four BEFs do not seem to be coupled to changes in the bivalve ecospace, which shows gradual changes throughout the studied time interval.

Interestingly, only one transition among the BEFs is abrupt and coincides with a mass extinction, namely at the Permian/Triassic boundary. The two other BEF transitions during the mid-Paleozoic and mid-Cretaceous are long-term gradual changes over several millions years. Regarding these BEFs, their waxing and waning are mostly correlated to long-term sustained trends in both continental fragmentation and phytoplankton stoichiometry, either toward or against diversity of acritarchs/dinoflagellates and Pangea breakup/assembly over the last 500 Myr. Because marine bivalves are mainly suspension feeders, this correlation between bivalves and phytoplankton – both positive and negative – suggests that marine bivalves can be subdivided into two suspension filter-feeding guilds not reflected in their shell morphology. Strikingly, there is no obvious correlation between the BEFs ups and downs and climate changes (temperature) and/or Mg/Ca seas. Therefore, marine bivalves clearly show four major ships that pass in deep time throughout the Phanerozoic, are mostly fueled by the quality/type of available nutrient resources, and are very resilient and not drastically perturbated by climate changes and/or short-term (a)biotic events, except once by the greatest mass extinction at the Permian/Triassic boundary. As such, marine bivalve evolutionary faunas fully reflect the major large-scale changes of ecosystems in deep time, from the GOBE, over the Devonian Nekton Revolution and Phytoplankton Blackout, and to the Mesozoic Marine Revolution.

Currently, a more precise understanding of processes trigerring the four BEFs are elusive and awaits more details on (living) bivalves and their ecology/anatomy (such as larval traits, thermal tolerance, precise diet, etc.) as well as their phylogeny, i.e. intrinsic traits, which can drive shifts in dominance among major bivalve niches. In our opinion, the major driver of these four BEFs rely on intrinsic parameters too poorly documented for fossils and even for living bivalves. For example, Huntley et al. (2021) in their review of bivalve parasitism through the Phanerozoic noted that escalation in parasite–host bivalve interactions seems to have occurred in both the middle Paleozoic and the late Mesozoic to Cenozoic, therefore at

times of gradual transition among the BEFs. Therefore, although some authors argued that evolutionary faunas are 'only' patterns summarizing coincidental peaks in diversity trajectories (Alroy 2010b), the four BEFs highlighted here fully reflect global changes of earth-life systems in deep time, even if their causes remain to be fully appreciated.

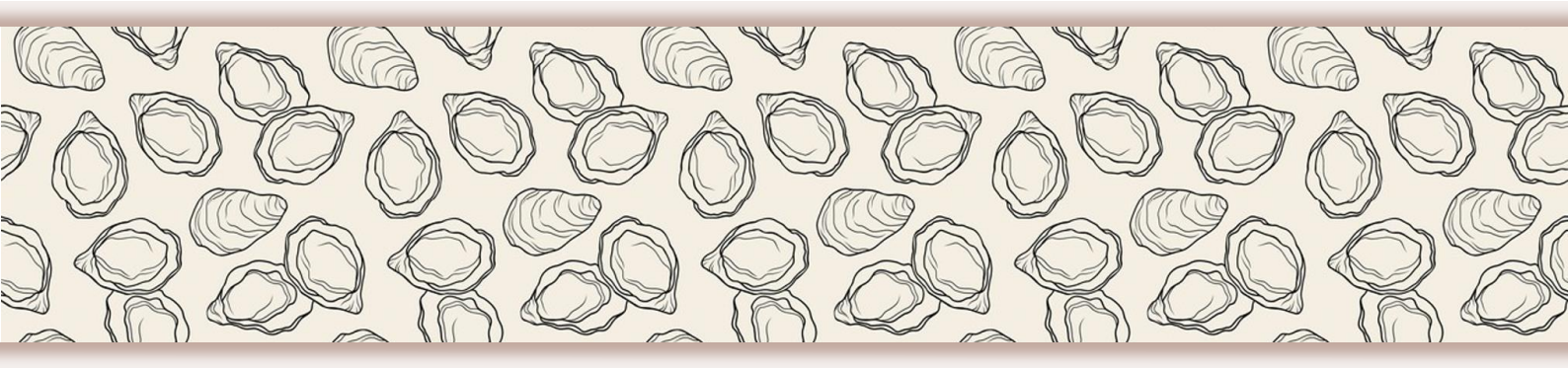
3. From the global diversity analysis, to the exploration of the body size and range size through time

Chapter 2 focuses on the largo sensu diversity of bivalves during the Phanerozoic. This long time span was accompanied by major events that affected all groups on Earth; from radiation events to mass extinctions, bivalves proved sufficiently resilient to be the second most diverse group in the oceans today. The taxa show an increase in taxonomic richness until the Neogene. However, this rise is not linear; four evolutionary faunas have been highlighted by examining the evolutionary dynamics within the families comprising the diversity. Coupling the results with the study of ecospace evolution, the significant difference between the evolutionary faunas can be explained essentially by environmental factors. Fragmentation or continental assembly regulates coastal availability. In addition, Wilson's cycle also controls sediment supply in coastal environments, as well as climate. Together, they are key factors in the proliferation of plankton, the basis of the food chain, particularly for filter-feeding organisms such as bivalves. In addition, major ecological changes in bivalves occur in parallel with other ecological changes, including the Marine Mesozoic Revolution, the Phytoplankton Blackout and the emergence of evolutionary floras. This cascade of effects is responsible for the evolutionary dynamics of the taxa studied, meaning that the role of temperature is only minor in this context.

However, temperature is now known to play a major role in biological factors, particularly body size. It is a crucial ecological and evolutionary factor that can influence the survival of taxa, their reproduction and their interaction with the environment. Previous

studies have shown that changes in the body size of organisms can be linked to environmental factors like temperature, resource availability and predation pressure. Consequently, analysing the body size of bivalves would shed further light on the implicit role of climate change on genera, and highlight possible large-scale patterns. At the same time, for benthic organisms, the issue of body size is considerable and directly influences their biogeographical distribution through larval growth time. Both of these aspects are key to understanding the ecological success of bivalves over time. The distribution of genera in different environments or regions can reveal trends in ecological preferences and adaptations to climatic variations over the Phanerozoic. The combined study of biogeographical distribution and body size offers a new framework for understanding these taxa.

Thus, moving from a study of bivalve diversity to a more detailed morpho-biogeographical analysis, focusing on their body size and distribution, makes it possible to establish new connections with the evolutionary history of organisms. The question will no longer be how environmental conditions - and a fortiori temperature - have modified the dynamics of bivalves, but how bivalves react to temperature variations to maintain themselves in the environment.



3

Bivalve body-size and geographical range variability: a long-term view on temperature effects

Contents

Abstract

The relationship between body size and the geographical range of marine organisms are two essential parameters to understanding the evolution of species, as well as their ecology and ecosystems. This study investigates the patterns of temperature-related body size evolution and the impact of temperature variations on the geographical distribution of bivalve species over geological time. Using fossil records available on paleobiological databases, size, and geographical trends have been reconstructed from the Ordovician to Neogene at a genus level. A correlation has been made with paleotemperature proxies to explore how climatic fluctuations have driven size and range expansion, contraction, or shift. In order to do this, the median latitudinal range and the median volume of each species are calculated for all the Phanerozoic stages included in our analysis.

Our results confirm that periods of global warming were generally associated with reductions in body size, supporting Bergmann's rule, which suggests smaller body sizes in warmer climates. Conversely, cooler periods coincided with larger body sizes and expanded geographical ranges, indicating that temperature played a critical role in shaping bivalves' body size and biogeography. Furthermore, we noted that genera with larger body sizes tend to inhabit wider ranges, possibly due to their enhanced ecological adaptability and ability to withstand environmental changes.

This research corroborates the crucial role of temperature as a primary driver of macroecology patterns in marine invertebrates. It offers valuable insights into how forthcoming climate change might impact bivalve species' body size and distribution. Our findings enhance our understanding of the long-term dynamics of marine biodiversity and the evolutionary strategies organisms adopt to adapt to climatic changes.

Keywords : Body-size ; geographic range size ; climate change

3.1. Introduction

The geographic range is a crucial concept in biogeography (Brown et al. 1996; Quintero et al. 2015), defining the spatial area where a species is present at a specific time. Examining fossil data at large scales allows for the reconstruction of paleo-ranges, shedding light on potential biogeographical changes based on the fossil record. Various intrinsic and extrinsic factors influence the extent of the occupied area, leading to expansion, reduction, or fragmentation of the geographical range (Brown et al. 1996; Gaston, 2008; Gaston & Fuller, 2009). The geographic range of an organism depends on biotic factors (e.g., thermal tolerance, dispersal ability) and abiotic/environmental factors (e.g., temperature, salinity), all of which are influenced by fluctuations in these factors over time. (Gaston & Spicer 2001). Reciprocally, reconstructing ranges over deep time can help understand a wide array of macroevolutionary and macroecological trends. The spatial arrangement of biodiversity has been a central focus since the early '90s and continues to be instrumental in explaining long-term processes (Wills 1992; Gaston & Blackburn 2000; Gould 2002; Jetz et al. 2014; Guo et al. 2024). Numerous studies have delved into the local and regional distribution of organisms (Stigall 2012; Darroch et al. 2014; Kocsis et al. 2018) as well as the connection between geographic ranges and speciation or extinction rates (Harnik et al. 2012a; Saupe et al. 2015; Jablonski 1986; Payne & Finnegan 2007; Botts et al. 2013).

However, climate is critical in understanding species distribution (Moritz et al. 2008; Parmesan 2006; Beaugrand & Kirby 2018). Because of the recent rise in temperatures (IPCC, 2021), some organisms expand to new areas that may be more climatically suitable for them, but the ability to adapt to the pace of climate changes depends on the species' dispersal capacities (Block & Levine 2021; Thompson & Fronhofer 2019). The geographic range expansion, reduction, or shift during climate variation results from a large number of biological processes.

Body size is important in evolving traits responsible for ecological, reproductive, and physiological performances (Anderson 1994; Brown et al. 2004). Body size is one of the most studied processes involved in geographic range variation. Previous studies have shown a predisposition to size-related demographic collapses (Cardillo et al. 2005; Dirzo et al. 2014; Ripple et al. 2017). In addition, ectotherms rely on climatic variation in their environment to maintain thermal homeostasis for metabolic processes. In this context, the temperature-size rule explains the clinal size patterns in ectotherms and describes the responses to temperature changes (Atkinson 1994; Walters & Hassall 2006). Usually, a smaller size is found in modern species at higher temperatures, potentially due to the thermal sensitivity of growth rates.

Moreover, despite intensively utilizing temperature paleogeographic ranges and temperature-related body size in macroecological research, the link between those three parameters still needs to be discovered. The key question of this paper is: Does a correlation exist between paleogeographic range, body size, and temperature through time? Bivalves are a very diverse class of marine ectotherms distributed worldwide, and their history began more than 500 million years ago (Cope 2000; Parkhaev 2008), making them perfect for this framework. They represent the second most important seafood in human consumption today; bivalves are economically important for many countries all around the globe (National Research Council 2010; NOAA 2022). Because their shells are grown by accretion during their life span, the impact of the environment on the body size is easy to measure. In this paper, we hypothesize (1) that past climate change affects bivalves' body size and paleogeographic ranges, and we question a possible (2) link between body size and range size. Moreover, depending on how climate change influences those parameters, we consider that (3) biogeographic patterns of bivalves are modified, causing profound variations in local communities.

3.2. Material & Methods

3.2.1. Raw data and standardization

Bivalves occurrence data from the Phanerozoic were previously downloaded by Payne & Heim (2020) from the Paleobiology Database (PBDB; https://paleobiodb.org/). To increase taxonomic resolution, subgenera are elevated to genus level for analyses (Foote 2006; Foote & Miller 2013). Taxonomical problems could be high in extracted databases because of the revisions of nomenclature after many of the names were entered. Therefore, global taxonomy is revised based on previously published classifications (e.g., Bouchet et al. 2010; Bieler et al. 2010) and international participative open-access databases (MolluscaBase, https://molluscabase.org; WoRMS, https://www.marinespecies.org). Non-marine taxa are removed for the analysis. Paleo-coordinates were obtained by rotating the present-day coordinates with GPlates v.2.20 software (Müller et al. 2018). Our final framework extends from the Ordovician (485.4 Ma) to the Neogene (3.6 Ma), and the final dataset contains 71,729 occurrences of 1119 genera.

Due to the limited taxonomic diversity and the low stratigraphic resolution, the Cambrian has been removed. The data are binned at the finest temporal resolution allowed by the initial database (stage level), which retains sufficient occurrences in every bin to calculate the variables of interest. Not all areas have equal preservation potential. Some stages are represented by only a few localities, making macroecological analysis challenging. A funnel plot is used to mitigate this spatial sampling bias. Here, this graphical tool plots the maximal latitudinal range per stage against the number of localities included in each stage. A funnel is formed by the confidence intervals of the latitudinal range at 95%. Based on the result, the analysis included only stages with at least 50 localities (suppl. fig A; Darroch & Saupe 2018).

Nevertheless, we accounted for spatial sampling bias by creating a distance matrix between each occurrence to avoid too close localities that could polarize our analysis (for more information about robustness analysis on occurrence and distance data, refers to 4.2.4. and suppl. code B). It is necessary to maintain minimum distances between sites to avoid pseudoreplication and ensure the independence of observations. Consequently, we restricted the analysis to occurrences at least 10 km apart representing the same genus (suppl. code A). Additionally, we selected only genera with at least 10 occurrences in the relevant stage (Sepkoski 1996; Fitzgerald & Carlson 2006; Alroy 2010). Filtering singletons and rare genera permits better reflecting "true" macroecological patterns while minimizing artifacts caused by sampling effort or preservation issues.

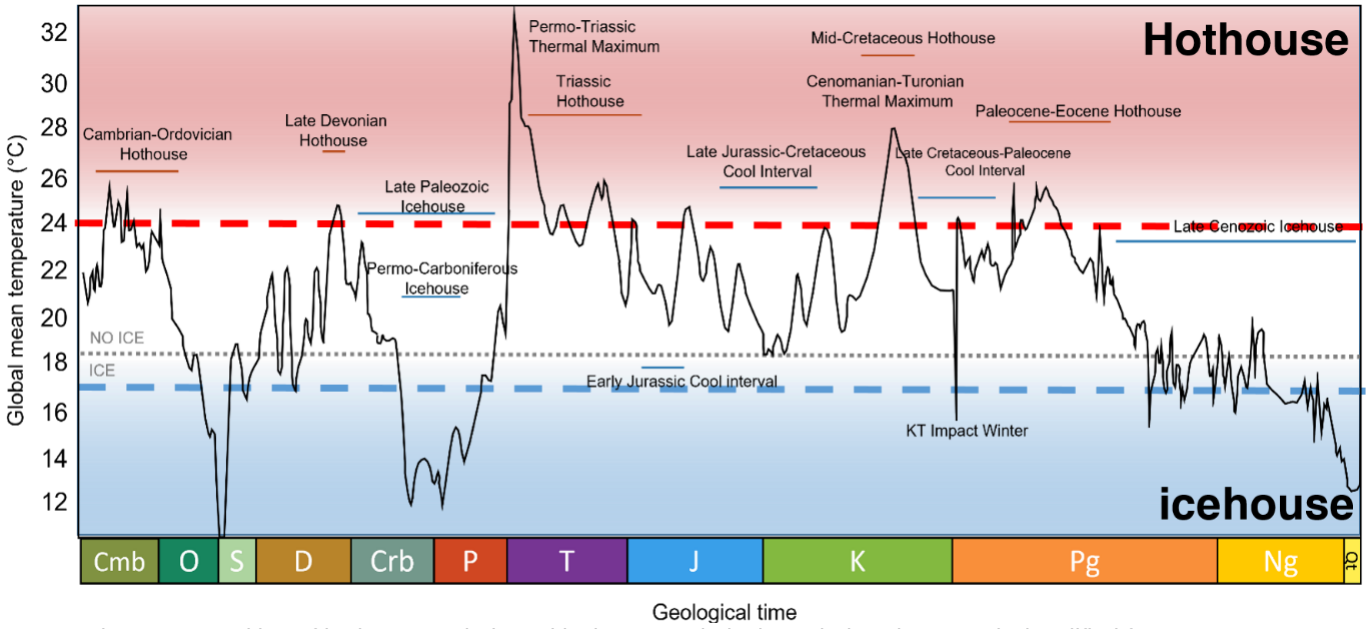


Figure 15. Partition of hothouse periods and icehouse periods through the Phanerozoic (modified form Scotese et al. 2021)

We used various climate partitioning to analyze the data comprehensively (see tab 1). The first part encompasses all Phanerozoic stages, offering a complete overview of climate variations. The second part focuses explicitly on stages showing warming trends, characterized by a positive temperature difference between the current and preceding stages ($0 < \Delta T$; Warming time intervals). Conversely, the third part investigates stages with cooling trends, identified by a negative temperature difference relative to the previous stage ($0 > \Delta T$;

Cooling time intervals). Additionally, we partitioned stages based on absolute temperature values: 'hothouse' periods, where temperatures exceed 23°C, and 'icehouse' periods, where temperatures fall below 17°C, as defined by Scotese (2016, Fig.15 modified). Furthermore, it is intriguing to examine trends within the hothouses and icehouses to comprehend the trends of organisms during warming and cooling in these specific periods.

Tab1. The nine climatic partitioning used in the analysis, and paramaters to consider

Climatic partitioning name		Temperature intervals parameters
Undifferenciate climatic partitioning		All stages are analysed
Warming time intervarls		Only stages with 0 < ΔT
Cooling time intervals		Only stages with 0 ≥ ΔT
Hothouse periods		Stages with temperature > 23°C
	Warming time intervals in hothouse periods	Only stages with 0 < ΔT **and** temperature > 23°C
	Cooling time intervals in hothouse periods	Only stages with 0 ≥ ΔT **and** mean annual temperature > 23°C
Icehouse periods		Stages with temperature < 17°C
	Warming time intervals in icehouse periods	Only stages with 0 < ΔT **and** temperature < 17°C
	Cooling time intervals in icehouse periods	Only stages with 0 ≥ ΔT **and** temperature <17°C

3.2.2. Body size

Body size data for bivalves were previously compiled by Heim et al. (2015) at the genus level. For each time interval, the largest specimen represents its genus to account for the maximum variation in body size possible for these organisms. Furthermore, the errors associated with this variation in body size do not influence the study: it is commonly demonstrated that intraspecific variation is minor compared to interspecific variation—or in the context of the present study, intra- and intergeneric variations (Dommergues et al., 2002; Payne & Heim, 2020). Throughout the analysis, and to maintain continuity with previous

studies, length size (in mm) is used to represent bivalve body size, as defined by Heim and collaborators (2015).

The use of maximum shell length as a proxy for body size is widespread in macroevolutionary and macroecological studies, particularly for mollusks whose accretionary growth produces durable shells that record their ontogenetic history (Kidwell & Bosence, 1991). Because bivalves grow incrementally throughout their life, the largest individuals generally correspond to older, mature specimens, providing a reliable indicator of adult size. This focus on maximum values helps reduce ontogenetic noise and allows for better comparability across taxa and time intervals (Twitchett, 2007; Hunt & Roy, 2006).

However, several potential biases must be acknowledged. At the genus level, taxonomic units may include multiple species with different ecological preferences and body sizes. Aggregating them into a single value can overestimate the average size or mask important environmental and evolutionary variation (Jablonski, 2005). Moreover, genera with broad geographic or stratigraphic ranges might experience body size changes over time that are not captured by a static maximum value. A further limitation concerns preservation and sampling biases. Larger and more robust shells are more likely to fossilize and be recovered, while smaller or thinner specimens may be underrepresented or missing altogether. This introduces a systematic bias toward larger body sizes in fossil datasets (Foote & Raup, 1996; Valentine et al., 2006). In addition, researchers often focus on well-preserved and morphologically distinct specimens, which may further skew the data toward certain taxa or environments.

In their extensive evaluation of such biases, Payne & Heim (2021) emphasized that, although these biases are real, they are unlikely to compromise the validity of large-scale temporal trends in body size evolution when analyzed over broad taxonomic and temporal scales. First, the use of maximum size per genus tends to standardize comparisons, especially when the same methodological approach is applied uniformly across the dataset.

Second, because preservation and sampling biases are relatively consistent through time at the resolution used (stage level), their impact on relative changes in size across intervals is minimized. Furthermore, Payne & Heim demonstrated that the size structure of fossil assemblages remains robust to variation in sampling intensity, provided that the number of occurrences per time bin is sufficient—criteria which are met in the present analysis. Lastly, while genus-level aggregation can obscure species-level variability, it effectively dampens noise caused by short-lived or locally restricted species and facilitates the detection of broader evolutionary patterns (Payne et al., 2009; Heim et al., 2015).

Ideally, such analyses would benefit from the availability of minimum and mean body size estimates per genus, which could provide a more nuanced view of body size evolution. While maximum size captures the upper ecological and developmental limits of a genus, mean size would better reflect central tendencies, potentially revealing shifts in typical ecological strategies or physiological constraints (Roy et al., 2000). Similarly, minimum body size could illuminate evolutionary responses to environmental stress, such as the well-documented Lilliput effect following mass extinctions (Twitchett, 2007; Schaal et al., 2016, Atkinson et al., 2019, Atkinson & Wignall, 2020, Huang et al., 2023). However, obtaining reliable minimum and mean values requires sufficiently large and evenly sampled assemblages per genus and time bin—criteria rarely met in deep-time datasets due to incomplete preservation and sampling biases. As emphasized by Payne & Heim (2021), maximum size is often the most robust and consistently recoverable metric, especially at global scales, making it a pragmatic, though partial, proxy for reconstructing evolutionary patterns in body size.

3.2.3. Geographic range size

This study quantified the geographic range of each genus in each geological stage. Three distinct metrics were computed to comprehensively assess latitudinal range size, convex hull, and maximum great circle distance (suppl Fig. L). The latitudinal range size is the

difference between the highest and lowest observed paleolatitudes. This metric is widely recognized for its utility in characterizing the latitudinal distribution of species, as documented in various studies (e.g., Powell 2005, 2007; Miller & Foote 2013; Finnegan et al. 2016; Balseiro & Halpern 2019; Darroch et al. 2020). The latitudinal range also reflects the breadth of thermal tolerance among species. Specifically, the thermal gradient decreases as one moves toward the poles, leading to the hypothesis that species exhibiting a broader latitudinal range may possess greater thermal tolerance (Jackson 1974; Stanley 2007; Sunday et al. 2012). This relationship underscores the importance of thermal factors in shaping the distribution and survival of various taxa, particularly bivalves, which are the primary focus of this investigation.

Despite the availability of multiple metrics, this study explicitly prioritizes the latitudinal range due to its direct relevance to the effects of temperature on bivalves. A bootstrap was implemented to enhance the robustness of the latitudinal range analysis. During this process, 9 samples are randomly drawn from the database with replacement, and within each resampled dataset, we grouped by time interval and genus to calculate the range. Finally, we obtain the paleolatitudinal range averaged across 1,000 iterations (see suppl. code C). This statistical approach not only strengthens the reliability of the findings but also allows for a more nuanced understanding of the factors influencing the geographic distribution of bivalves and their thermal tolerance.

Finally, these results have been compared to those obtained using the Palaeoverse package (Jones et al. 2023) and are roughly similar. We use functions available on the R package to simplify the R code.

3.2.4. Biogeographic connectedness

We analyzed the biogeographic dynamics of bivalves using the multiple-site β diversity and the biogeographic connectedness (Baselga 2010; 2012; Yan et al. 2023). We

hypothesized that rising temperatures would reduce an organism's geographic range, consequently diminishing biogeographic connectedness. This suggests an inverse relationship between temperature and connectedness. While the multiple-site β diversity measures the variation in taxonomic composition across multiple locations and highlights the dissimilarity between each time-bin (Baselga 2013), biogeographic connectedness is considered a network method that analyzes the biogeographic relationships and spatial cohesion among regions (Sidor et al. 2013; Yan et al. 2023). Following the code provided by Yan et al. (2023), the first biogeographic analysis is performed using a presence-absence matrix of genera per locality for each stage and primarily based on the pairwise Jaccard β-diversity. However, this index does not permit distinguishing common to endemic taxa, but the overall heterogeneity of the taxonomic composition between occupied sites. Multiple-site β diversity ranges from 0 to 1, where low values indicate more similar composition and high values correspond to more different sites.

Moreover, the biogeographic connectedness structure is based on the taxon locality occurrence matrix. It also varies from 0 to 1, with higher values indicating a higher proportion of cosmopolitan taxa and strong connectivity among the regions (Dai & Song 2020). All the analyses were made from the Ordovician to the Neogene. Nevertheless, to match our primary hypothesis that temperature plays a role in the connectedness of bivalve regions, we applied the method to warming and cooling time intervals and hothouses/icehouse intervals.

3.2.5. Correlations across temporal, geographical and taxonomic scales

In this study, we also made a Spearman correlation between the size, range, and biogeographic connectedness, distinguishing data into different geographical areas and separating the occurrences temporally by evolutionary faunas. This approach allows us to examine how the relationships between these variables evolve across different geological periods, considering changes in faunal composition over time. Additionally, we incorporated

a separation by taxonomic order, which helps to find out more about how ecological and biogeographical processes influence species distribution at different taxonomic levels. This dual approach (temporal and taxonomic) provides a more comprehensive view of the underlying mechanisms driving biogeographic diversity variation across varied climatic contexts.

The geographic distinction is made using the midpoint method (Rhode et al. 1993) and considers the north and south hemispheres jointly. This method categorizes genera according to the median latitude of their distribution. Thus, we arbitrarily differentiate between nontropical zones, corresponding to taxa with a midpoint above 30° N or S, and tropical zones with a midpoint below these latitudes. Previous studies have also used this tropical/non-tropical distinction (e.g., Kiessling & Aberhan 2007). This distinction enables us to assess how the relationships between these variables vary between tropical and temperate regions and better understand how ecological and biogeographical processes influence species distribution in different climatic contexts. To make the entire analysis, we 1) computed the midpoint analysis by genera for each stage, then 2) defined tropical/non-tropical genera, and 3) calculated the geographical range, body size, and biogeographic connectedness by latitudinal zone.

In addition, Montariol et al. 2025 (submitted) highlighted four evolutionary faunas with the same database. Evolutionary faunas, characterized by groups with relatively high diversity over multiple time intervals (Sepkoski 1981), are identified through factor analysis (FA) of genus-level diversity within bivalve families across geological stages (Sepkoski 1981; Cleal & Cascales-Miñana 2014). Each factor from this analysis corresponds to a distinct bivalve evolutionary fauna (BEF), with its diversity rescaled to global total diversity based on the explained variance in the FA model. Following Sepkoski (1981), the taxonomic composition of each BEF is determined by the factor scores for each family, acknowledging that a family may contribute to multiple BEFs (more methods in part 2). Thus, distinguishing

evolutionary faunas for our correlations provides a more holistic view and allows a deeper understanding of biogeographical processes and their interaction with environmental changes.

Then, the analysis was performed by considering each bivalve order separately. Each order may exhibit distinct ecological, evolutionary, and biogeographical characteristics that influence their geographic distribution, body size, or biogeographic connectedness. All the Spearman correlations have been computed in R, using the cor.test function in the stats package (version 3.6.2; R core team 2013). The confidence intervals are calculated using the spearman.ci function of the RVAideMemoire (Hervé & Hervé 2020).

3.3. Results.

3.3.1. Size and temperature

Figure 16 reports the correlations between the temperature and the body size. Temperature significantly affected adult body size in global and latitudinal analyses (Fig. 16 A; see more in tab 2). Four of the five climatic partitions with significant results show a reduction in body size trend. The negative correlation is found both in warming and cooling intervals. Despite a global pattern, the overall interaction of temperature on bivalves' body size remains weak most of the time (rhô < 0.2; tab 2). This suggests that while temperature certainly plays a role in shell size variation, it is probably influenced by other factors.

The distinction between genera in the tropical zone and those in the non-tropical zone shows that the responses to changes in temperature are more subtle. Body size increases with temperature during warming periods in the tropical zone (rhô = 0.1, p-value < 0.050), while the trend is reversed for genera in the non-tropical zone (rhô = -0.11, p-value < 0.050). This mirror trend between the two latitudinal regions extends over almost all the other climatic partitionings except for cooling intervals. During these cooling intervals, both tropical and non-tropical bivalves decrease in body size as temperatures increase (tab. 2).

3.3.2. Geographic range size facing temperature

The spearman correlation conducted across the Phanerozoic data revealed no significant correlation between global temperature and bivalve geographic range size when considering all climatic periods combined (Fig. 16 B). This absence of correlation suggests that global temperature do not directly influence the spatial distribution of bivalves on a broad timescale or have particular trends within the class. When considering all climatic periods combined, the Spearman correlation across the Phanerozoic data revealed no significant correlation between global temperature and bivalve geographic range size (Fig. 16 B). This absence of correlation suggests that global temperatures do not directly influence the spatial distribution of bivalves on a broad timescale or have particular trends within the class.

Tab 2. Spearman correlation of the global Phanerozoic analysis of bivalves

		All latitudes		**Non-tropical zone**		**Tropical zone**	
		Rhô	p-value	Rhô	p-value	Rhô	p-value
Undifferenciate climatic scenario	*Body size*	-0.06	**<0.05**	-0.14	**<0.05**	-0.01	0.57
	Latitudinal range	0.01	0.27	-0.11	**<0.05**	0.1	**<0.05**
Warming intervals	*Body size*	0.01	0.7	-0.11	**<0.05**	0.1	**<0.05**
	Latitudinal range	-0.01	0.4	-0.28	**<0.05**	0.33	**<0.05**
Cooling intervals	*Body size*	-0.09	**<0.05**	-0.14	**<0.05**	-0.06	**<0.05**
	Latitudinal range	0.02	0.11	0.03	0.21	-0.01	0.43
Hothouse periods	*Body size*	-0.02	0.38	-0.02	0.68	-0.15	<0.05
	Latitudinal range	0.18	**<0.05**	0.2	**<0.05**	-0.08	**<0.05**
Icehouse periods	*Body size*	-0.02	0.23	-0.11	**<0.05**	0.05	0.06
	Latitudinal range	0.26	**<0.05**	0.1	**<0.05**	0.26	**<0.05**
Warming intervals in hothouse periods	*Body size*	0.16	**<0.05**	0.22	**<0.05**	-0.043	0.41
	Latitudinal range	0.31	**<0.05**	0.03	0.56	0.49	**<0.05**
Warming intervals in icehouse periods	*Body size*	0.03	0.51	-0.11	0.08	0.25	**<0.05**
	Latitudinal range	-0.01	0.83	-0.1	0.09	0.16	**<0.05**
Cooling intervals in hothouse periods	*Body size*	-0.06	0.24	-0.42	**<0.05**	0.16	**<0.05**
	Latitudinal range	0.22	**<0.05**	0.04	0.68	0.22	**<0.05**
Cooling intervals in hothouse periods	*Body size*	-0.05	**<0.05**	-0.13	**<0.05**	0.01	0.72
	Latitudinal range	0.35	**<0.05**	0.23	**<0.05**	0.26	**<0.05**

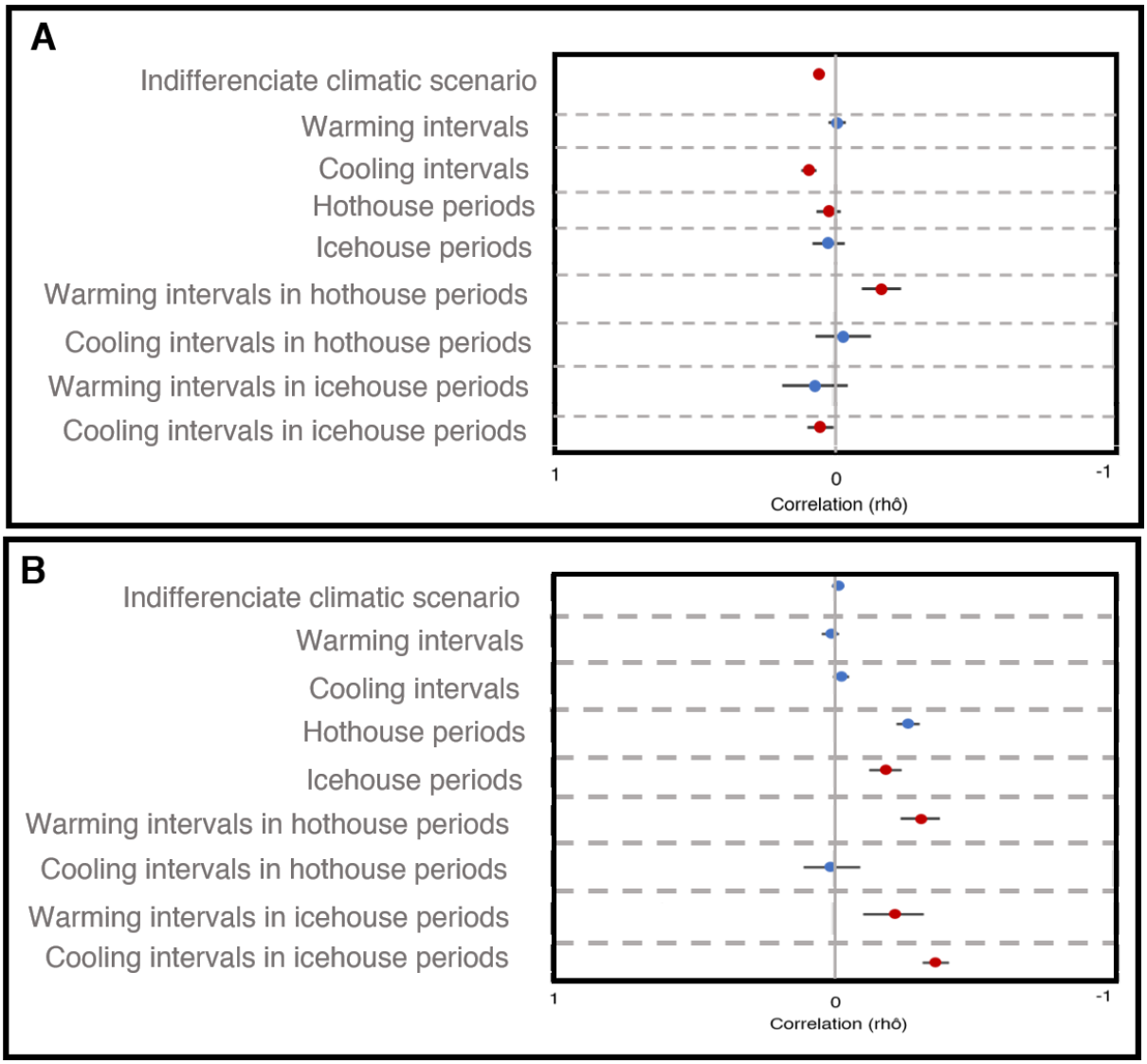


Figure 16. A) Correlation of body size with temperature ; B) Correlation of geographic range with temperature. In red, significan result (p <0.050), in blue non-significant results (p >0.05)

Focusing on the different climatic parts reveals contrasting patterns. During the icehouse periods, a significant positive correlation exists between geographic range and global temperature (R= 0.26, p <0.050). This suggests that higher global temperature values were associated with an expansion of the bivalve geographic range during icehouse intervals. Similarly, during warming phases within hothouse periods and specific warming phases within icehouse periods, a comparable positive correlation was observed (r = 0.31 and r = 0.33, respectively, p-value < 0.050). These findings indicate that bivalves tend to

expand their geographic distribution in response to warming under extreme temperature conditions, highlighting a different sensitivity to climate shifts in these contexts.

To better understand these dynamics, we partitioned the tropical and non-tropical genera. The results highlight notable variability in bivalve range size reactions to temperature changes (Fig. 17). Tropical genera exhibited a consistent increase in range size across all the temperature partitionings, with a significant positive correlation (see tab 2) during warming intervals in icehouse and hothouse periods. This suggests that tropical genera responded uniformly to higher temperatures, expanding their geographic distribution during warming periods, whether in icehouse conditions or during warm phases within hothouse periods (respectively r= 0.26 and r= 0.49, p-values < 0.050). In contrast, non-tropical genera showed a negative correlation between temperature and geographic range size when considering the undifferenciate climatic partitioning ($r = 0.11$, p-value < 0.050; fig 17). However, an expansion in range size was observed in specific climatic partitionings, particularly during warming phases within icehouse and hothouse time intervals. The correlation coefficients during these phases were $r = 0.1$ ($p < 0.050$) and $r = 0.2$ ($p < 0.050$), respectively, indicating a small but significant relationship during these periods of climate change. This suggests that non-tropical genera were less sensitive to long-term temperature fluctuations but responded to higher temperatures during those specific temperature partitionings.

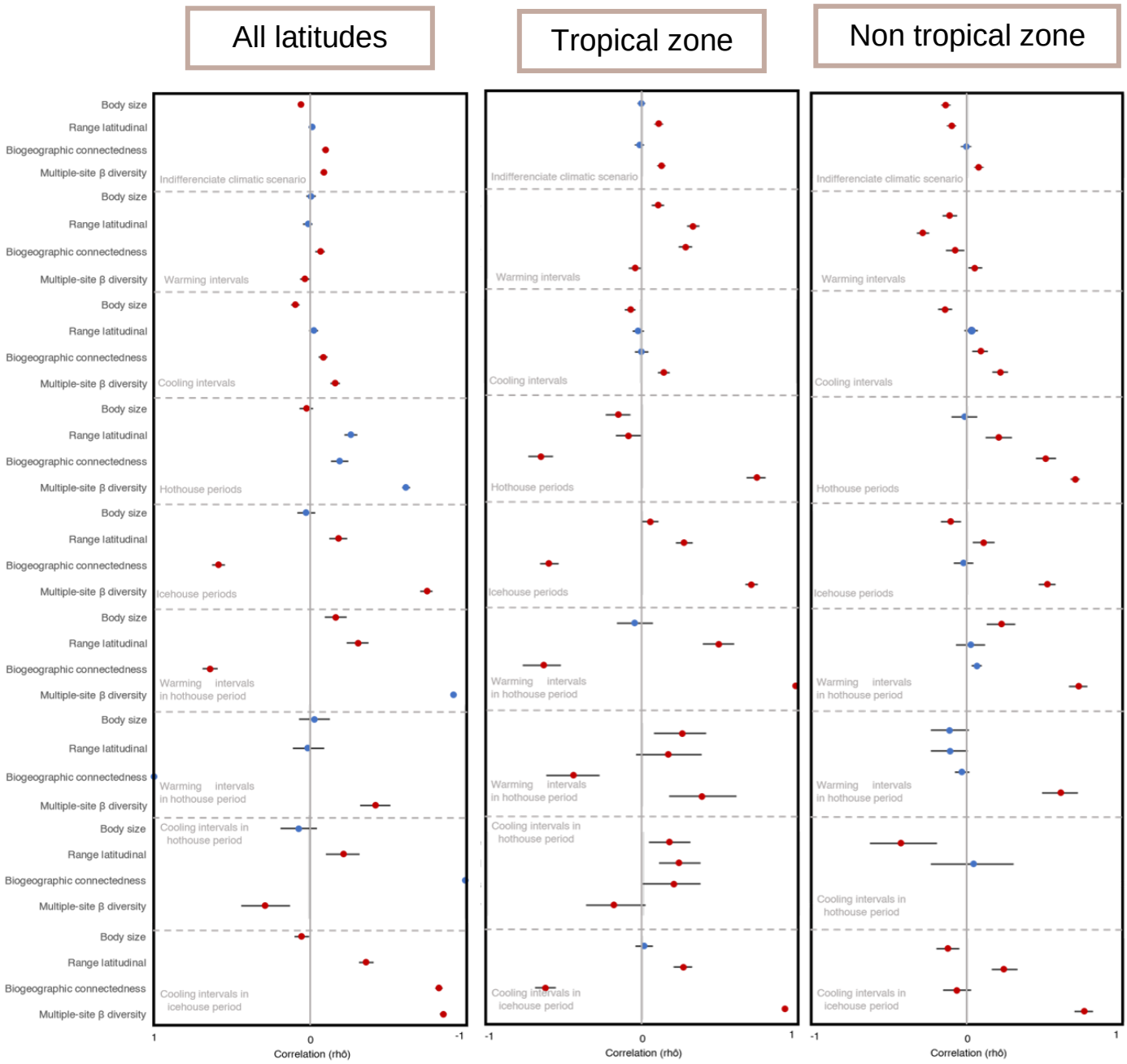


Figure 17: Correlations of morphological and ecological variables with temperature. In red, significant result (p-value < 0.05) ; un blue, non-significant results (p-value > 0.05)

3.3.3. Biogeographic connectedness to climate change

Biogeographic connectedness (BC) and multiple-site β-diversity show a positive correlation with temperature increase (Fig 17). In other words, as temperatures increase, taxa become more cosmopolitan and have a more heterogeneous taxonomic composition in different regions.

For biogeographic connectedness, positive correlations were observed during specific climate conditions. Cooling events within the hothouse and icehouse were linked to increased BC (e.g., icehouse: r = 0.82). These results suggest that bivalve genera were more connected across regions during these extreme cold climatic phases. Conversely, during extremely hot events, the global cosmopolitism of bivalves is negatively correlated with temperature (e.g., warming hothouse and icehouse, respectively, r= -0.6 and r= -1). This correlation is also visible considering the entire icehouse and hothouse periods (icehouse: r= 0.19; hothouse: r= -0.58), which indicate that colder climates promote cosmopolitan genera instead of hot climates, which favor endemism.

Multiple-site beta diversity positively correlated with temperature considering all the undifferentiated climatic partitionings (fig 17) and across various climatic contexts. This phenomenon could be observed during cooling periods ($r = 0.16$, $p < 0.050$), as well as during hothouse and icehouse phases ($r = 0.74$ and $r = 0.6$, respectively), and warming phases within these periods ($r = 0.92$ and $r = 0.42$, fig 17). These results indicate higher spatial species turnover during warming and cooling extremes, reinforcing that environmental shifts drive more significant differentiation in bivalve communities.

Differences in responses emerged between tropical and non-tropical genera. In tropical regions, biogeographic connectedness was generally negatively correlated with temperature (e.g., global r= -0.1; hothouse r= -0.65; icehouse r= -0.59; Table 4 & 5), except during cooling phases within icehouse periods and warming events, where a positive correlation was detected (e.g., cooling hothouse r= 0.19; cooling icehouse r= -0,62; warming r= -0.04). Conversely, multiple-site beta diversity in tropical genera was positively correlated, except during cooling events within icehouse phases and warming, where no significant increase in beta diversity was observed (cooling hothouse r= -0.19; warming r= -0.04). These results are in accordance with more heterogeneous communities at higher temperatures, except in cooling intervals during extreme cold events. In non-tropical regions, BC was

negatively correlated across most, except during hothouse phases, where a positive correlation was identified (r= 0.5). On the other hand, multiple-site beta diversity was positively correlated with temperature across all climatic partitionings, indicating consistent species turnover and differentiation regardless of the climate phase (e.g., hothouse r= 0.69; warming r= 0.05; warming hothouse r= 0.72).

These findings highlight the varying responses of tropical and non-tropical bivalve genera to climatic fluctuations. Tropical regions exhibit more complex patterns of biogeographic connectedness and beta diversity, while non-tropical regions display a more uniform response in terms of similarity/dissimilarity of biogeographic regions.

3.3.4. Evolutionary faunas

3.3.4.1. Global analysis

The relationships between body size, geographic range, biogeographic connectedness, and multiple-site beta diversity with temperature were analyzed for three evolutionary faunas of fossil bivalves (Carboniferous-Permian Bivalve Evolutionary Fauna, Trias-Jurassique Bivalve Evolutionary Fauna, and Cretaceous-Neogene Bivalve Evolutionary Fauna). The Ordovician-Devonian evolutionary fauna was excluded due to insufficient occurrences. Moreover, the evolutionary faunas do not have a result for each temperature partitioning (see suppl. Fig. M, N, and 0). We decided to present the three-shared analysis results here (Fig. 18A).

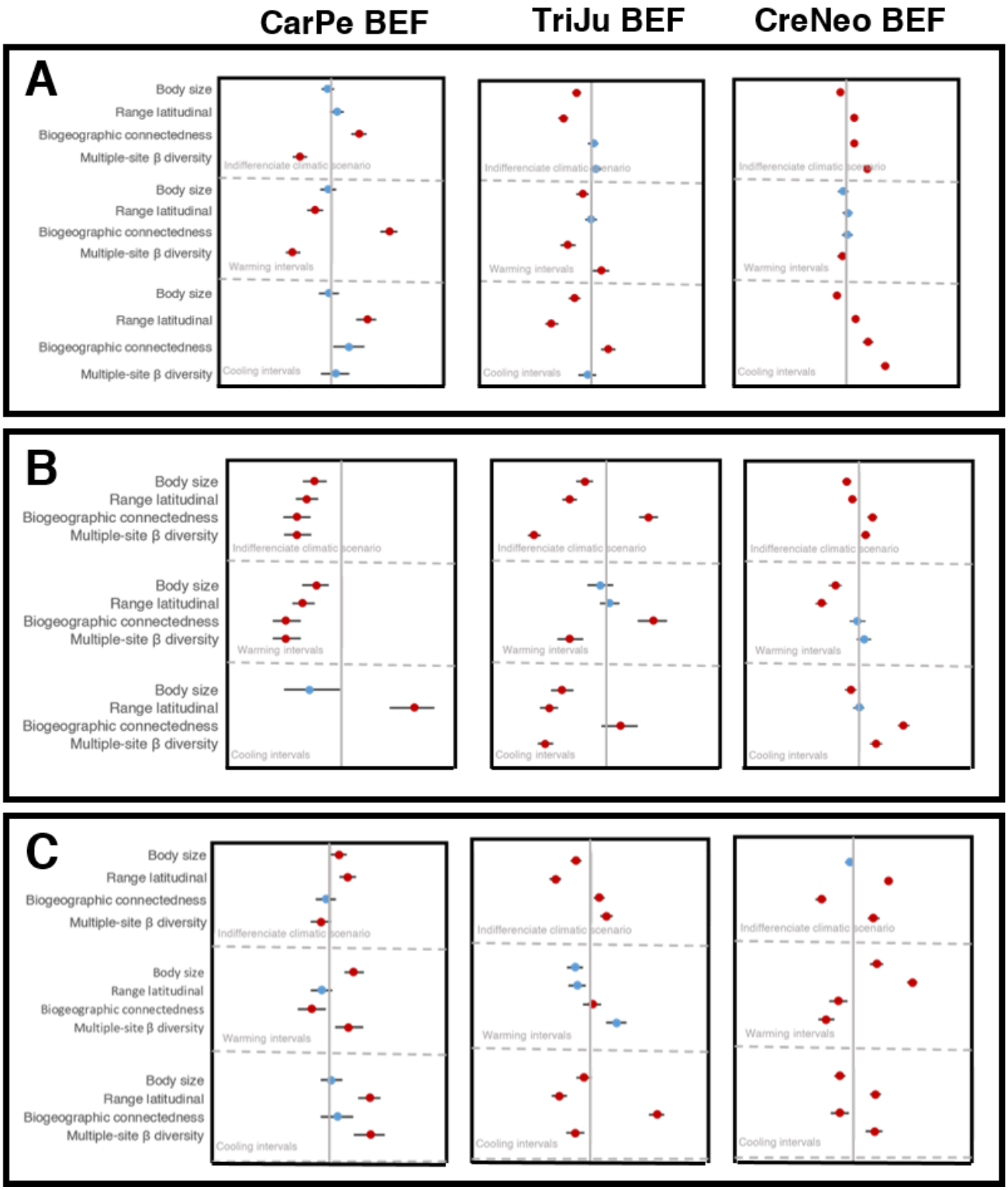


Figure 18: Correlations between morphological and ecological variables of bivalves genus with temperature, for each evolutionary fauna. A) for all latitudes ; B) for non tropical genera ; C) for tropical genera.
In red, significant correlation (p-value < 0.05)

For the CarPe fauna, under the undifferentiated climate partitioning, body size ($r = -0.037$, $p > 0.050$) and geographic range ($r = 0.014$, $p > 0.050$) showed no significant correlations with temperature (Fig. 18A). Biogeographic connectedness was positively correlated ($r = 0.244$, $p < 0.050$). In contrast, multiple-site beta diversity was negatively correlated ($r = -0.284$, $p < 0.050$) (Fig. 18A). Under warming conditions, body size remained uncorrelated with temperature ($r = -0.037$, $p > 0.050$). At the same time, the geographic range showed a significant negative correlation ($r = -0.154$, $p < 0.050$). Biogeographic connectedness exhibited a strong positive correlation ($r = 0.505$, $p < 0.050$), and multiple-site beta diversity remained negatively correlated ($r = -0.286$, $p < 0.050$). During cooling, body size ($r = -0.028$, $p > 0.050$) and multiple-site beta diversity ($r = 0.03$, $p > 0.050$) were not significantly correlated. In contrast, geographic range ($r = 0.313$, $p < 0.050$) and biogeographic connectedness ($r = 0.151$, $p > 0.050$) showed positive correlations (Fig. 18A).

For the TriJu fauna, under the undifferenciate climate partitioning, body size ($r = -0.102$, $p < 0.050$) and geographic range ($r = -0.298$, $p < 0.050$) were negatively correlated with temperature. Biogeographic connectedness ($r = 0.09$, $p > 0.050$) and multiple-site beta diversity ($r = 0.075$, $p > 0.050$) were not significantly correlated (Fig. 18A). During warming, body size remained negatively correlated with temperature ($r = -0.136$, $p < 0.050$). In contrast, the geographic range ($r = 0.047$, $p > 0.050$) showed no significant correlation. Biogeographic connectedness exhibited a negative correlation ($r = -0.217$, $p < 0.050$), while multiple-site beta diversity was weakly but significantly positively correlated ($r = 0.088$, $p < 0.050$) (Fig. 18A). During cooling, both body size ($r = -0.1$, $p < 0.050$) and geographic range ($r = -0.299$, $p < 0.050$) remained negatively correlated with temperature. Biogeographic connectedness showed no significant correlation ($r = 0.212$, $p > 0.050$), while multiple-site beta diversity was weakly negatively correlated ($r = -0.041$, $p < 0.050$) (Fig. 18A).

For the CreNeo fauna, under the undifferenciate climate partitioning, body size ($r = -0.037$, $p < 0.050$) was negatively correlated with temperature. In contrast, geographic range

(r = 0.086, p < 0.050), biogeographic connectedness (r = 0.09, p < 0.050), and multiple-site beta diversity (r = 0.208, p < 0.050) were positively correlated (Fig. 18A). During warming, body size (r = -0.012, p > 0.050), geographic range (r = 0.055, p > 0.050), and biogeographic connectedness (r = 0.056, p > 0.050) were not significantly correlated with temperature. In contrast, multiple-site beta diversity was strongly negatively correlated (r = -0.678, p < 0.050). During cooling, body size (r = -0.055, p < 0.050) was negatively correlated, while geographic range (r = 0.106, p < 0.050), biogeographic connectedness (r = 0.233, p < 0.050), and multiple-site beta diversity (r = 0.377, p < 0.050) were positively correlated (Fig. 18A).

These correlations revealed notable differences among the evolutionary faunas and temperature partitionings. For CarPe fauna, significant correlations were observed under warming, particularly for biogeographic connectedness. TriJu fauna showed consistent negative correlations for body size and geographic range across all partitionings, with variable patterns for biogeographic connectedness and multiple-site beta diversity. CreNeo fauna demonstrated distinct patterns, with stronger positive correlations for geographic range, biogeographic connectedness, and multiple-site beta diversity during cooling conditions.

3.3.4.2. Latitudinal observations

The analysis, separated by tropical and non-tropical genera, revealed distinct patterns across evolutionary faunas (CarPe, TriJu, and CreNeo). For non-tropical genera (Fig. 18 B), significant negative correlations were observed across all faunas in the undifferentiated temperature partitioning. For instance, in CarPe, correlations were -0.234 (p-value < 0.05) for body size and -0.304 (p-value < 0.05) for geographic range. Similarly, TriJu exhibited negative correlations, such as -0.194 (p-value < 0.05) for body size and -0.329 (p-value < 0.05) for geographic range. In CreNeo, values included -0.076 (p-value < 0.05) for body size and -0.023 (p-value < 0.05) for geographic range. In the warming partitioning, CarPe showed

strong negative correlations, with values such as -0.225 (p-value < 0.05) for body size and -0.343 (p-value < 0.05) for geographic range. In TriJu, results included -0.055 (p-value > 0.05) for body size and 0.028 (p-value > 0.05) for geographic range and temperature. For CreNeo, values were consistently negative, including -0.211 (p-value < 0.05) for body size and -0.281 (p-value < 0.05) for geographic range. Under the cooling partitioning, CarPe displayed a mix of weakly significant and non-significant correlations, such as -0.287 (p-value > 0.05) for body size and 0.632 (p-value < 0.05) for geographic range. TriJu revealed mixed results, including -0.394 (p-value < 0.05) for body size and -0.504 (p-value < 0.05) for geographic range. CreNeo exhibited values such as -0.077 (p-value < 0.05) for body size and 0.036 (p-value > 0.05) for geographic.

For tropical genera (fig 20 C), in the indifferentiated climate partitioning, CarPe presented weak positive correlations, such as 0.064 (p-value < 0.05) for body size and 0.138 (p-value < 0.05) for geographic range. TriJu showed mixed trends, with -0.086 (p-value < 0.05) for body size but 0.014 (p-value < 0.05) for biogeographic connectedness. CreNeo exhibited values like 0.017 (p-value > 0.05) for body size and 0.334 (p-value < 0.05) for geographic range. In the warming partitioning, CarPe had predominantly negative correlations, including 0.21 (p-value < 0.05) for body size and -0.067 (p-value > 0.05) for geographic range. TriJu exhibited weak relationships, such as -0.192 (p-value > 0.05) for body size and 0.019 (p-value < 0.05) for biogeographic connectedness. CreNeo displayed mixed results, with values like 0.244 (p-value < 0.05) for body size and 0.445 (p-value < 0.05) for geographic range. In the cooling partitioning, CarPe demonstrated significant positive correlations for geographic range, with values like -0.016 (p-value > 0.05) for body size and 0.343 (p-value < 0.05) for geographic range. TriJu showed alternating patterns, such as -0.061 (p-value > 0.05) for body size and 0.554 (p-value < 0.05) for biogeographic connectedness. CreNeo revealed values such as -0.118 (p-value < 0.05) for body size and 0.225 (p-value < 0.05) for geographic range.

3.3.5. Taxonomical results

3.3.5.1. Global analysis

Across the climatic partitionings, the correlation between body size and temperature exhibited variable strength and significance among different taxa (Tab. 3). In the Indifferentiated climatic partitioning, several taxa, such as Trigoniida, Carditida, and Lucinida, showed significant negative correlations (Rhô ranging from -0.37 to -0.05, p-value < 0.05), indicating that body size tends to decrease with increasing temperatures. Conversely, Pectinida and Mytilida showed weak positive correlations with temperature, though the p-values were significant for Pectinida (Rhô = 0.23, $p < 0.050$). During the Warming intervals, a general trend of negative correlations between body size and temperature was observed in taxa such as Trigoniida (Rhô = -0.25, $p < 0.050$) and Carditida (Rhô = -0.21, $p < 0.050$). At the same time, Mytilida exhibited a weak but positive relationship (Rhô = 0.14, $p = 0.2$). In contrast, the Cooling intervals showed more pronounced negative correlations in Trigoniida (Rhô = -0.55, $p < 0.050$) and Carditida (Rhô = -0.28, $p < 0.050$), with some taxa, like Nuculida, showing significant positive correlations (Rhô = 0.69, $p < 0.050$). Notably, the Hothouse periods also showed significant negative correlations for many taxa, including Trigoniida (Rhô = -0.69, $p < 0.050$) and Carditida (Rhô = -0.41, $p < 0.050$), indicating a possible decrease in body size with increasing temperatures during these periods. During the Icehouse periods, significant positive correlations were found for Pectinida (Rhô = 0.26, $p < 0.050$), but Carditida showed negative correlations (Rhô = -0.23, $p < 0.050$). These variations indicate that the effect of temperature on body size could be taxa-specific and influenced by the climatic conditions of each period.

The latitudinal range and temperature relationship showed more complex patterns across climatic partitionings. In the Indifferentiated climatic partitioning, weak or no significant correlations were observed for most taxa, with Pectinida and Mytilida exhibiting small negative correlations (Rhô = -0.05 to -0.19) but with high p-values indicating non-significance. Notably, Mytilida (Rhô = 0.35, p < 0.050) and Lucinida (Rhô = 0.38, p < 0.050) showed positive correlations, suggesting that these taxa may have expanded their latitudinal range with increasing temperatures. In the Warming intervals, a generally weak or non-significant relationship between latitudinal range and temperature was found, with some taxa such as Carditida (Rhô = 0.02, p = 0.68) and Pectinida (Rhô = -0.02, p = 0.67) showing no clear trend. However, Mytilida displayed a significant positive correlation (Rhô = 0.35, p < 0.050), suggesting some latitudinal expansion during warming conditions. The Cooling intervals revealed more pronounced and statistically significant negative correlations for

Tab 3. Global correlation of each order at all latitudes of the body size and the range size. In bold, significant p-values.

		Pectinida		**Trigoniida**		**Ostreida**		**Carditida**		**Myalinida**		**Cardiida**		**Lucinida**		**Mytilida**	
		Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value
Indifferenciate climatic scenario	*Body size*	-0.23	**<0.05**	-0.58	**<0.05**	-0.19	**<0.05**	-0.1	0.09	-0.12	0.24	-0.25	**<0.05**	0.51	**<0.05**	-0.12	0.17
	Latitudinal range	-0.08	**<0.05**	-0.02	0.77	-0.03	0.52	-0.18	**<0.05**	-0.11	0.28	-0.14	**<0.05**	0.27	**<0.05**	-0.17	**<0.05**
Warming intervals	*Body size*	-0.01	0.98	-0.45	**<0.05**	-0.04	0.58	-0.11	0.19	-0.04	0.76	-0.16	**<0.05**	0.16	0.24	0.12	0.36
	Latitudinal range	-0.19	**<0.05**	0.1	0.37	-0.27	**<0.05**	-0.44	**<0.05**	0.01	0.98	-0.29	**<0.05**	-0.35	**<0.05**	-0.5	**<0.05**
Cooling intervals	*Body size*	-0.33	**<0.05**	-0.73	**<0.05**	-0.22	**<0.05**	-0.11	0.16	0.11	0.53	-0.29	**<0.05**	0.45	**<0.05**	-0.02	0.8
	Latitudinal range	0.03	0.51	-0.29	**<0.05**	0.11	0.15	-0.04	0.53	-0.26	0.11	-0.02	0.68	0.32	**<0.05**	0.25	**<0.05**
Hothouse periods	*Body size*	-0.43	**<0.05**	-0.55	**<0.05**	-0.08	0.46	-0.53	**<0.05**	-0.07	0.61	0.39	**<0.05**	-0.63	**<0.05**	1	**<0.05**
	Latitudinal range	0.4	**<0.05**	0.89	**<0.05**	0.33	**<0.05**	0.62	**<0.05**	0.17	0.23	-0.43	**<0.05**	0.68	**<0.05**	1	**<0.05**
Icehouse periods	*Body size*	0.03	0.57	-0.1	0.7	0.12	0.33	-0.02	0.87	-1	**<0.05**	-0.25	**<0.05**	0.18	**<0.05**	0.5	**<0.05**
	Latitudinal range	-0.03	0.64	-0.92	**<0.05**	0.8	**<0.05**	-0.15	0.28	-1	**<0.05**	0.25	**<0.05**	0.93	**<0.05**	0.19	0.21
Warming intervals in hothouse periods	*Body size*	0.31	**<0.05**	0.9	**<0.05**	0.33	**<0.05**	0.27	0.17	-0.01	0.97	0.39	**<0.05**	0.82	**<0.05**	1	**<0.05**
	Latitudinal range	0.59	**<0.05**	0.62	**<0.05**	0.15	0.24	0.04	0.81	0.22	0.16	-0.43	**<0.05**	-0.36	0.18	1	**<0.05**
Warming intervals in icehouse periods	*Body size*	-0.26	**<0.05**			1	**<0.05**					-1	**<0.05**			1	**<0.05**
	Latitudinal range	-0.01	0.98			1	**<0.05**					-1	**<0.05**			-1	**<0.05**
Cooling intervals in hothouse periods	*Body size*	-0.69	**<0.05**			1	**<0.05**										
	Latitudinal range	0.26	0.11			1	**<0.05**										
Cooling intervals in hothouse periods	*Body size*	0.2	**<0.05**			-0.19	0.15	0.27	0.1	-1	**<0.05**	-0.28	**<0.05**	0.18	0.39	0.56	**<0.05**
	Latitudinal range	0.19	**<0.05**			0.8	**<0.05**	0.04	0.8	-1	**<0.05**	0.51	**<0.05**	0.93	**<0.05**	0.62	**<0.05**

several taxa, particularly Ostreida (Rhô = -0.64, p < 0.050) and Lucinida (Rhô = -0.31, p < 0.050), indicating that colder temperatures might lead to reduced latitudinal ranges in these groups. In contrast, Mytilida showed a positive correlation (Rhô = 0.77, p < 0.050), possibly reflecting a latitudinal range expansion despite cooler conditions. During Hothouse periods, a positive correlation between latitudinal range and temperature was evident in Ostreida (Rhô = 0.73, p < 0.050) and Lucinida (Rhô = 0.45, p < 0.050), with some taxa like Cardiida and Pectinida exhibiting weaker or non-significant correlations. Similarly, in the Icehouse periods, Lucinida (Rhô = 0.58, p < 0.050) and Ostreida (Rhô = 0.76, p < 0.050) showed significant positive correlations, suggesting potential latitudinal range shifts towards the poles during colder intervals. The Warming intervals within Hothouse periods displayed a significant positive correlation between latitudinal range and temperature in Pectinida (Rhô = 0.39, p <

Tab 3. Global correlation of each order at all latitudes of the body size and the range size. In bold, significant p-values. (continued)

Nuculida		**Arcida**		**Modiomorphida**	
Rhô	p-value	Rhô	p-value	Rhô	p-value
0.01	0.98	0.14	**<0.05**	0.01	0.95
-0.31	**<0.05**	-0.26	**<0.05**	0.31	**<0.05**
0.51	**<0.05**	0.1	0.27	0.01	0.95
-0.54	**<0.05**	-0.48	**<0.05**	0.31	<0.05
-0.22	**<0.05**	0.07	0.38		
-0.24	**<0.05**	-0.19	**<0.05**		
-0.68	**<0.05**	-0.44	0.08	0.01	0.95
0.11	0.67	0.17	0.51	0.31	**<0.05**
-0.41	**<0.05**	-0.26	**<0.05**		
0.61	**<0.05**	0.18	0.09		
-0.68	**<0.05**	-0.44	0.08	0.01	0.95
0.12	0.67	0.17	0.51	0.31	**<0.05**
		-0.32	0.07		
		-0.27	0.13		
0	1	0.04	0.75		
0.16	0.46	0.57	**<0.05**		

0.050), but no clear relationship was observed in other taxa. Similarly, the Cooling intervals within Hothouse periods displayed mixed results, with Pectinida showing a significant positive correlation (Rhô = 0.41, p < 0.050) but weaker correlations in other taxa.

3.3.5.2. Latitudinal observations

This study examined the relationship between body size, latitudinal range, and temperature in tropical and non-tropical molluscan orders. Tables 4 and 5 summarize the correlation coefficients (Rhô) and associated p-values for each taxon in both groups, focusing on non-tropical and tropical orders, respectively.

In tropical molluscan orders (Tab. 5), body size was generally weakly correlated with temperature, with several orders showing no significant relationship. For instance, in Pectinida, Lucinida, and Mytilida, the correlations between body size and temperature were either near zero or non-significant (e.g., Rhô = 0.01, p = 0.94 for Pectinida, Rhô = 0.53, p < 0.050 for Mytilida). However, some tropical orders exhibited significant negative correlations, such as Trigoniida (Rhô = -0.27, p < 0.050) and Carditida (Rhô = -0.28, p < 0.050), indicating that these taxa tend to have smaller body sizes in warmer temperatures. In contrast, non-tropical molluscan orders (Tab. 4) displayed more pronounced and varied correlations between body size and temperature. Several orders, such as Trigoniida (Rhô = -0.58, p < 0.050), Carditida (Rhô = -0.25, p < 0.050), and Ostreida (Rhô = -0.19, p < 0.050), exhibited significant negative correlations, suggesting that smaller body sizes are associated with warmer temperatures, similar to some tropical orders. However, Mytilida and Lucinida in non-tropical orders showed positive correlations with body size (Rhô = 0.39, p < 0.050 for Mytilida, Rhô = 0.82, p < 0.050 for Lucinida), indicating that these groups tend to have larger body sizes in warmer environments, which contrasts with the pattern observed in many tropical orders.

Tab 4. Correlation of each order in the non-tropical zones of the body size and the range size. In bold, significant p-values.

		Pectinida		**Trigoniida**		**Ostreida**		**Carditida**		**Myalinida**		**Cardiida**		**Lucinida**		**Mytilida**		**Nuculida**		**Arcida**		**Modiomorphida**	
		Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value
Indifferenciate climatic scenario	*Body size*	-0.23	**<0.05**	-0.58	**<0.05**	-0.19	**<0.05**	-0.1	0.09	-0.12	0.24	-0.25	**<0.05**	0.51	**<0.05**	-0.12	0.17	0.01	0.98	0.14	**<0.05**	0.01	0.95
	Latitudinal range	-0.08	**<0.05**	-0.02	0.77	-0.03	0.52	-0.18	**<0.05**	-0.11	0.28	-0.14	**<0.05**	0.27	**<0.05**	-0.17	**<0.05**	-0.31	**<0.05**	-0.26	**<0.05**	0.31	**<0.05**
Warming intervals	*Body size*	-0.01	0.98	-0.45	**<0.05**	-0.04	0.58	-0.11	0.19	-0.04	0.76	-0.16	**<0.05**	0.16	0.24	0.12	0.36	0.51	**<0.05**	0.1	0.27	0.01	0.95
	Latitudinal range	-0.19	**<0.05**	0.1	0.37	-0.27	**<0.05**	-0.44	**<0.05**	0.01	0.98	-0.29	**<0.05**	-0.35	**<0.05**	-0.5	**<0.05**	-0.54	**<0.05**	-0.48	**<0.05**	0.31	<0.05
Cooling intervals	*Body size*	-0.33	**<0.05**	-0.73	**<0.05**	-0.22	**<0.05**	-0.11	0.16	0.11	0.53	-0.29	**<0.05**	0.45	**<0.05**	-0.02	0.8	-0.22	**<0.05**	0.07	0.38		
	Latitudinal range	0.03	0.51	-0.29	**<0.05**	0.11	0.15	-0.04	0.53	-0.26	0.11	-0.02	0.68	0.32	**<0.05**	0.25	**<0.05**	-0.24	**<0.05**	-0.19	**<0.05**		
Hothouse periods	*Body size*	-0.43	**<0.05**	-0.55	**<0.05**	-0.08	0.46	-0.53	**<0.05**	-0.07	0.61	0.39	**<0.05**	-0.63	**<0.05**	1	**<0.05**	-0.68	**<0.05**	-0.44	0.08	0.01	0.95
	Latitudinal range	0.4	**<0.05**	0.89	**<0.05**	0.33	**<0.05**	0.62	**<0.05**	0.17	0.23	-0.43	**<0.05**	0.68	**<0.05**	1	**<0.05**	0.11	0.67	0.17	0.51	0.31	**<0.05**
Icehouse periods	*Body size*	0.03	0.57	-0.1	0.7	0.12	0.33	-0.02	0.87	-1	**<0.05**	-0.25	**<0.05**	0.18	**<0.05**	0.5	**<0.05**	-0.41	**<0.05**	-0.26	**<0.05**		
	Latitudinal range	-0.03	0.64	-0.92	**<0.05**	0.8	**<0.05**	-0.15	0.28	-1	**<0.05**	0.25	**<0.05**	0.93	**<0.05**	0.19	0.21	0.61	**<0.05**	0.18	0.09		
Warming intervals in hothouse periods	*Body size*	0.31	**<0.05**	0.9	**<0.05**	0.33	**<0.05**	0.27	0.17	-0.01	0.97	0.39	**<0.05**	0.82	**<0.05**	1	**<0.05**	-0.68	**<0.05**	-0.44	0.08	0.01	0.95
	Latitudinal range	0.59	**<0.05**	0.62	**<0.05**	0.15	0.24	0.04	0.81	0.22	0.16	-0.43	**<0.05**	-0.36	0.18	1	**<0.05**	0.12	0.67	0.17	0.51	0.31	**<0.05**
Warming intervals in icehouse periods	*Body size*	-0.26	**<0.05**			1	**<0.05**					-1	**<0.05**			1	**<0.05**			-0.32	0.07		
	Latitudinal range	-0.01	0.98			1	**<0.05**					-1	**<0.05**			-1	**<0.05**			-0.27	0.13		
Cooling intervals in hothouse periods	*Body size*	-0.69	**<0.05**			1	**<0.05**																
	Latitudinal range	0.26	0.11			1	**<0.05**																
Cooling intervals in hothouse periods	*Body size*	0.2	**<0.05**			-0.19	0.15	0.27	0.1	-1	**<0.05**	-0.28	**<0.05**	0.18	0.39	0.56	**<0.05**	0	1	0.04	0.75		
	Latitudinal range	0.19	**<0.05**			0.8	**<0.05**	0.04	0.8	-1	**<0.05**	0.51	**<0.05**	0.93	**<0.05**	0.62	**<0.05**	0.16	0.46	0.57	**<0.05**		

The latitudinal range and temperature relationship showed notable differences between tropical and non-tropical orders. In tropical molluscan orders, the latitudinal range often exhibited significant positive correlations with temperature. For example, Cardiida (Rhô = 0.41, $p < 0.050$) and Arcida (Rhô = 0.55, $p < 0.050$) showed a clear trend of expanding the latitudinal range with increasing temperature. Similarly, Lucinida (Rhô = 0.32, $p < 0.050$) and Nuculida (Rhô = 0.93, $p < 0.050$) also displayed positive correlations, suggesting that warmer temperatures support broader geographical distributions in tropical orders. On the other hand, non-tropical orders exhibited a more mixed pattern. While Lucinida (Rhô = 0.27, $p < 0.050$) and Pectinida (Rhô = -0.08, $p < 0.050$) showed positive correlations between latitudinal range and temperature, Ostreida (Rhô = -0.11, $p = 0.28$) and Carditida (Rhô = -0.31, $p < 0.050$) demonstrated weak or negative correlations, suggesting that warmer temperatures may limit the latitudinal range for some non-tropical taxa. Furthermore, Arcida displayed a significant positive correlation (Rhô = 0.62, $p < 0.050$), suggesting a broader latitudinal range in colder environments.

The comparison between tropical and non-tropical molluscan orders reveals several noteworthy differences in how body size and latitudinal range respond to temperature. The correlations between body size and temperature were generally weak in tropical orders, with only a few orders displaying significant negative correlations. In contrast, non-tropical orders exhibited a wider range of correlations, with negative and positive relationships between body size and temperature, particularly in Lucinida and Mytilida, which showed a positive correlation with temperature. The latitudinal range, however, demonstrated more consistent patterns across tropical orders, with most showing positive correlations with temperature, suggesting that warmer temperatures support broader latitudinal distributions. Non-tropical orders displayed a more mixed pattern, with some taxa showing positive correlations and others showing negative correlations, suggesting that temperature's impact on the latitudinal range may be more complex in this group.

Tab 5. Correlation of each order in the tropical zones of the body size and the range size. In bold, significant p-values.

		Pectinida		**Trigoniida**		**Ostreida**		**Carditida**		**Myalinida**		**Cardiida**		**Lucinida**		**Mytilida**		**Nuculida**		**Arcida**		**Modiomorphida**	
		Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value	Rhô	p-value
Indifferenciate climatic scenario	*Body size*	0.01	0.82	-0.27	**<0.05**	-0.28	**<0.05**	0.01	0.94	0.5	**<0.05**	-0.11	**<0.05**	-0.04	0.59	0.19	**<0.05**	0.53	**<0.05**	0.09	**<0.05**		
	Latitudinal range	0.05	**<0.05**	0.09	0.13	-0.07	**<0.05**	0.2	**<0.05**	0.84	**<0.05**	0.1	**<0.05**	0.58	**<0.05**	0.21	**<0.05**	-0.13	0.16	0.11	**<0.05**		
Warming intervals	*Body size*	0.07	**<0.05**	-0.24	**<0.05**	-0.23	**<0.05**	0.33	**<0.05**	0.55	**<0.05**	-0.17	**<0.05**	-0.23	0.15	0.2	**<0.05**	0.4	**<0.05**	0.07	0.31		
	Latitudinal range	0.26	**<0.05**	0.16	**<0.05**	0.21	**<0.05**	0.49	**<0.05**	0.94	**<0.05**	0.46	**<0.05**	0.88	**<0.05**	0.27	**<0.05**	0.21	0.13	0.28	**<0.05**		
Cooling intervals	*Body size*	-0.05	0.16	-0.44	**<0.05**	-0.24	**<0.05**	-0.09	0.17	0.93	**<0.05**	-0.07	0.17	0.04	0.68	0.45	**<0.05**	0.61	**<0.05**	0.10	0.09		
	Latitudinal range	-0.08	**<0.05**	0.01	0.89	-0.29	**<0.05**	0.06	0.34	0.95	**<0.05**	-0.07	0.15	0.42	<0.05	0.28	**<0.05**	0.01	0.93	-0.03	0.54		
Hothouse periods	*Body size*	-0.21	**<0.05**	-0.77	**<0.05**	0.01	0.96	-0.8	**<0.05**			-0.09	0.73			0.9	**<0.05**			0.32	0.11		
	Latitudinal range	-0.13	0.09	0.27	**<0.05**	-0.11	0.14	-0.28	0.29			-0.88	**<0.05**			-0.45	**<0.05**			-0.55	**<0.05**		
Icehouse periods	*Body size*	0.41	**<0.05**	0.79	**<0.05**	-0.22	**<0.05**	0.11	0.22	1	**<0.05**	-0.1	0.2	0.37	**<0.05**	-0.63	**<0.05**	0.89	**<0.05**	0.11	0.23		
	Latitudinal range	-0.07	0.24	0.84	**<0.05**	0.41	**<0.05**	0.02	0.81	1	**<0.05**	0.28	**<0.05**	0.51	**<0.05**	0.62	**<0.05**	-0.27	0.21	0.25	**<0.05**		
Warming intervals in hothouse periods	*Body size*	-0.24	**<0.05**	-0.79	**<0.05**	0.33	**<0.05**									0.84	**<0.05**			-0.46	**<0.05**		
	Latitudinal range	0.32	**<0.05**	0.93	**<0.05**	0.14	0.25									0.84	**<0.05**			0.78	**<0.05**		
Warming intervals in icehouse periods	*Body size*	0.55	**<0.05**			-0.72	**<0.05**	1	**<0.05**			-0.07	0.77							0.52	**<0.05**		
	Latitudinal range	-0.95	**<0.05**			0.72	**<0.05**	-0.2	0.36			0.85	**<0.05**							0.89	**<0.05**		
Cooling intervals in hothouse periods	*Body size*	0.37	**<0.05**	0.06	0.76	-0.31	**<0.05**																
	Latitudinal range	0.45	**<0.05**	-0.89	**<0.05**	0.19	**<0.05**																
Cooling intervals in hothouse periods	*Body size*	0.34	**<0.05**	0.79	**<0.05**	-0.1	0.18	-0.08	0.4	1	**<0.05**	-0.13	0.14	0.61	**<0.05**	-0.38	**<0.05**	0.89	**<0.05**	-0.15	0.15		
	Latitudinal range	0.08	0.2	0.84	**<0.05**	0.41	<0.05	-0.08	0.39	1	**<0.05**	0.21	**<0.05**	0.61	**<0.05**	0.38	**<0.05**	-0.27	0.21	-0.14	0.16		

Overall, the results indicate that temperature influences body size and latitudinal range in tropical and non-tropical molluscan orders, but the nature of these relationships varies between the two groups. Tropical orders tend to exhibit weaker and more consistent patterns, with body size generally decreasing in warmer temperatures and the latitudinal range expanding in warmer conditions. Non-tropical orders exhibit more variability in these relationships, with negative and positive correlations observed between body size, latitudinal range, and temperature. These differences highlight the complex ecological and evolutionary factors that shape mollusks' geographical and physiological traits in different climatic zones.

3.4. Discussion

The analysis highlights a complex relationship between body size, geographic range, and biogeographic dynamics in response to climatic variations throughout the Phanerozoic. A general trend is found in bivalves, where body size decreases with higher temperatures. Nevertheless, variations in geographic range and biogeographic metrics underline a non-linear trend, depending on latitudes and time.

3.4.1. Temperature-size rule in bivalve

It is widely established that temperature-regulating ectothermic animals generally exhibit smaller body sizes when exposed to warmer temperatures. This is linked to faster metabolic rates, accelerated growth, and earlier maturity, especially in tropical regions compared to colder climates (Forster et al. 2012; Angilletta & Dunham 2003; Audzijonyte et al. 2019). Such organisms tend to have higher metabolic rates and faster life cycles in the tropics, while species in colder regions often exhibit slower growth and greater longevity (Forster et al. 2011). Modern bivalves also show a tendency for increased lifespan and reduced growth with latitude, although no direct confirmation of Bergmann's rule has been demonstrated (Moss et al. 2016; Berke et al. 2013). As a result, organisms are expected to reduce their body size under climate warming, especially if populations shift toward their upper thermal limits. Their survival relies on maintaining metabolic performance during these

optimal temperature ranges, particularly in coping with increased oxygen demands during warming episodes (Atkinson et al. 2006). When oxygen availability fails to meet metabolic needs, growth slows, and mortality rises (Pörtner, 2006a).

Bivalves, in particular, seem to follow a similar pattern of body size reduction with warming temperatures, supporting the Temperature-Size Rule (TSR) of Atkinson (1994). This general trend of decreasing body size aligns with the hypothesis that rising temperatures correlate negatively with body size, especially in non-tropical genera and stable climatic conditions. However, this pattern is not uniform and may vary depending on the temperature conditions, challenging the broader applicability of the TSR. Bivalves may even show body size increases during extreme warming events in particular periods, such as the hothouse or icehouse intervals (Angilletta et al. 2004). These variations suggest that bivalves, while broadly following the TSR, may react differently under specific climatic conditions, depending on the intensity and context of temperature change (Forster et al. 2012). If the hypothesis that bivalves follow the TSR in deep time holds, we expect a general reduction in bivalve body size during warming periods throughout the Phanerozoic. Specifically, we should find negative correlations between temperature and body size, with this pattern being most pronounced under partitions of significant warming. Additionally, taxa with smaller body sizes should dominate during these periods, while larger species would be less abundant. This would support the idea that global warming causes a decrease in body size, particularly in response to stable and long-term temperature increases. At the same time, large taxa would be more vulnerable to extinction during such events.

Our analysis indicates that the global trend of decreasing body size in bivalves throughout the Phanerozoic aligns with the TSR, particularly during warming partitionings where a negative correlation between temperature and body size is observed. This supports the primary hypothesis that body size generally decreases with increasing temperatures, especially in non-tropical genera and stable climatic contexts. However, this pattern does not

hold universally, as bivalves also show instances of body size increase during extreme warming intervals, such as those in the hothouse or icehouse periods. These findings suggest that while the TSR generally applies to bivalves over deep time, exceptions occur under extreme climatic conditions. Furthermore, the mass extinction events in the fossil record demonstrate that smaller species tend to dominate. The disappearance of larger individuals often precedes local and global extinctions; supporting the notion that temperature-driven selective pressures have historically favored smaller body sizes (Peck et al. 2009; Daufresne et al. 2009; Forster et al. 2012). Thus, while the TSR provides a valuable framework, it is important to consider the complexity of environmental factors in shaping bivalve body size over evolutionary timescales.

3.4.2. Range shifts: contrasted patterns

The general pattern observed in many studies suggests that as temperatures rise, species' latitudinal range tends to decrease (Parmesan 2006; Sunday et al. 2025; Hughes 2000; Pörtner 2006a; Chen et al. 2011). This is often linked to a reduction in body size, a phenomenon widely recognized as a response to warmer conditions. Increased temperatures typically reduce the physiological tolerance of many organisms, constraining their distribution to smaller, more temperate zones.

However, bivalves present a different pattern. While body size tends to decrease with higher temperatures, bivalves have been shown to exhibit a remarkable capacity to respond to climate shifts in terms of their latitudinal distribution. Specifically, bivalves often extend their range towards higher latitudes during warming periods. Similarly, during cooling events within extreme climatic events, such as hothouse and icehouse phases, bivalves tend to expand their latitudinal range. This suggests that bivalves have an adaptive behavior that contrasts with the general pattern of range reduction linked to warmer temperatures. For example, Kiessling and Aberhan (2007) demonstrated that during periods of global warming in the Mesozoic, bivalves extended their distribution towards higher latitudes, probably in

response to the increase in marine temperatures. Similarly, Myers et al. (2013) noted a latitudinal expansion of bivalves during the late Cretaceous warming period, explaining this by a greater thermal tolerance of particular species and a reduction in competitive constraints in the new niches colonized. A similar response can be seen in mollusks, particularly after biotic crises, where periods of climatic stress often enable organisms to colonize larger habitats due to reduced competition (Krug & Patzkowsky 2007). The extension of the latitudinal range during periods of warming or cooling within extreme climatic events could be the consequence of the exploitation of new ecological niches released by taxa that are less resilient or that have modified their global distribution range to reach more favorable climatic zones (Dai & Song 2020). In ammonites, similar latitudinal shifts have also been observed. Zacaï et al. (2017) showed that during the T-OAE, certain ammonite lineages were able to expand their ranges poleward, likely exploiting newly favorable habitats created by global warming and sea-level rise. However, in contrast to bivalves, ammonites often show a more pronounced geographic contraction during the peak of anoxic crises, reflecting a tighter coupling between water column oxygenation and distribution.

Suppose this hypothesis of bivalves adapting to climatic fluctuations holds over deep time. In that case, we expect to observe similar patterns of latitudinal range expansion in response to warming or cooling within extreme climatic events (hothouse and icehouse). This would include colonizing new ecological niches left by taxa that are less resilient or have modified their global distribution to adapt to more favorable climatic zones. In other words, bivalves should demonstrate a dynamic ability to expand their range in response to major climatic shifts, even in the face of long-term environmental change.

The evidence found in deep time supports this hypothesis. Studies of bivalve distributions during various evolutionary faunas show patterns consistent with this behavior. For instance, during the TriJu BEF, a contraction in geographical range was observed, likely due to the ecological and climatic upheavals following the Permo-Triassic crisis. During the

post-crisis recovery (during the Trias), the distribution of bivalves was restricted due to significant anoxic conditions and high temperatures (Fraiser & Bottjer 2007; Hautmann et al. 2008). This range restriction is accompanied by a significant increase in biogeographic connectedness as a function of temperature, indicating a parallel event of significant cosmopolitanism (Yan et al. 2023). This trend can be explained by the fact that surviving species can adapt to a limited set of globally homogeneous environmental conditions, resulting in more remarkable taxonomic similarities between regions. In other words, the same species are present over vast geographical areas, but their distribution takes place in restricted environments, leading to a homogenization of faunal assemblages on a global scale (Erwin 1994; Benton & Twichett 2003; Jablonski 1998; Clapham et al. 2009). Conversely, the Creneo BEF displayed an increase in latitudinal range, a reduction in biogeographic connectedness, and an increase in multiple-site β diversity, consistent with climatic fluctuations during the Cenozoic (Rhodes 1992; Jablonski et al. 2006). Overall, the pattern of bivalve range expansion during periods of climatic stress aligns with the hypothesis, showing that bivalves can adapt and modify their distribution in response to major climatic events.

3.4.2. Mechanisms involved in body size and geographic range size changes

By integrating results across evolutionary faunas, taxonomic orders, and climatic contexts, this study provides a comprehensive understanding of bivalve responses to environmental change. These findings underscore the importance of historical contingency, ecological flexibility, and evolutionary constraints in shaping the biodiversity and distribution of marine organisms. They also highlight the critical role of integrating evolutionary and ecological perspectives to predict the long-term impacts of climate change on marine ecosystems and biodiversity. The changes observed in the body size and geographical range of bivalves in response to changes in temperature raise crucial questions about the

nature of these adaptations: do they result from plastic phenotypic responses, enabling organisms to adapt to their environment, or from evolutionary responses, reflecting long-term genetic changes? Results from this study reveal that temperature exerts significant, though often weak, selective pressure on the body size of bivalves, with trends varying across latitudinal, climatic, taxonomic, and evolutionary contexts.

Body size trends generally showed reductions with increasing temperature, consistent with Atkinson's temperature-size rule (Atkinson, 1994), which reflects a physiological optimization of resource allocation between growth and reproduction in warmer environments. However, the strength and direction of correlations varied among evolutionary faunas and bivalve orders, emphasizing the influence of evolutionary history and ecological strategy. For example, the Triassic-Jurassic (TriJu) fauna demonstrated consistent negative correlations between body size and temperature across all partitionings (e.g., $\rho = -0.102$, $p < 0.050$ in undifferentiated conditions), suggesting that these taxa were particularly sensitive to temperature-induced metabolic constraints. In contrast, the Carboniferous-Permian (CarPe) fauna showed no significant correlations in most partitionings, indicating a weaker relationship between body size and temperature. Similarly, Trigoniida and Carditida consistently displayed significant negative correlations with temperature (e.g., Trigoniida $\rho = -0.69$, $p < 0.050$ in hothouse conditions), reflecting a pronounced decrease in body size with warming. In contrast, Mytilida exhibited weak positive correlations in several partitionings (e.g., $\rho = 0.14$, $p = 0.2$ in warming intervals), suggesting a unique tolerance to warmer environments. These taxa-specific and evolutionary patterns align with Cope's rule, as larger-bodied taxa tend to dominate during stable periods, while smaller-bodied taxa become more prominent under environmental stress (Clapham & Payne 2011).

The left wall effect suggests a lower physiological boundary to body size below which further miniaturization is not viable (Gould 2011). This statistical constraint on minimum body size, arising from the fact that body size cannot fall below zero, results in a skewed

distribution where mean size reductions become constrained over time (Jablonski 1997; McShea 1994). Evidence of this effect can be seen in our dataset, where even during extreme warming events, taxa such as Trigoniida did not exhibit reductions beyond a certain threshold, reflecting a hard biological limit to size decrease. This phenomenon is not restricted to bivalves. Similar patterns have been observed in other invertebrate groups, including trilobites, which showed constrained size decreases during Ordovician warming events (Finnegan & Droser 2008; Klug et al. 2015), and ammonites, which demonstrated a shift toward smaller morphotypes during the Toarcian Oceanic Anoxic Event, but never beyond a critical minimum (Piazza et al 2020). Brachiopods also displayed limited body size plasticity during past global warming events, likely due to conservative life history traits and low metabolic rates (Payne et al. 2016). These examples suggest that the left wall effect and ecological and physiological constraints govern how far taxa can reduce their body size in response to warming, with evolutionary history modulating the degree of phenotypic flexibility (Payne et al. 2016).

One other recurring pattern of body size is observed after mass extinctions, and is the so-called Lilliput effect describes a temporary reduction in body size among surviving taxa (Urbanek 1993; Twitchett 2007). This phenomenon has been well documented across several clades and extinction events. For example, bivalves in the aftermath of the end-Permian extinction exhibit notable reductions in body size during the Early Triassic, likely due to low oxygen levels and reduced food availability (Payne 2005; Brayard et al. 2009). These size contractions are generally interpreted as adaptive responses to stressed environmental conditions and are often accompanied by rapid life cycles and opportunistic ecologies (Twitchett 2007). Similarly, ammonoids during the Early Jurassic Toarcian Oceanic Anoxic Event (T-OAE) show marked decreases in average shell size, with genera such as Dactylioceras and Eleganticeras dominated by smaller morphotypes (Ritterbush et al. 2014; Zacaï et al. 2015). These reductions coincide with black shale deposition and widespread

marine hypoxia, and size recovery occurs as oxygen levels stabilize. Brachiopods also provide compelling evidence of Lilliput-like responses following the end-Ordovician and end-Permian events, particularly among deeper water taxa, where reductions in both shell length and thickness are commonly observed (Chen et al. 2019; He et al. 2007).

Despite the ubiquity of this pattern, the Lilliput effect is typically constrained to relatively short geological intervals directly following extinction events and reflects ecological filtering under extreme stress (Harries & Knorr 2009). In contrast, the reported patterns are neither restricted to extinction boundaries nor immediately post-crisis periods. Instead, they reflect long-term correlations between body size and global temperature spanning millions of years. The consistency of size reductions during warming intervals across several taxonomic groups suggests the dominance of sustained physiological constraints over short-term ecological effects. For instance, the order Trigoniida shows strong and significant negative correlations between temperature and body size across multiple climatic regimes, including hothouse and warming intervals. These long-term trends lack the signature rebound in size typically associated with Lilliput dynamics, indicating a more permanent ecological or evolutionary response to elevated temperatures. Furthermore, not all clades responded uniformly to warming. For example, Mytilida showed weak positive correlations with temperature in several partitions, suggesting a unique tolerance or an adaptive advantage in warmer conditions. Such variability points to physiological plasticity, ecological strategy, and evolutionary history in shaping size responses (Olabarria et al. 2016; Fitze et al. 2015).

While the left wall effect may impose a hard physiological limit on minimum body size (Gould, 1991), especially under warming conditions, it does not fully account for the diversity of responses observed. Instead, these patterns appear more consistent with broader macroevolutionary principles, such as Atkinson's temperature–size rule (Atkinson, 1994) and Cope's rule (Hone & Benton 2005), modulated by the constraints of thermal physiology and metabolic scaling (Pörtner 2006b; Forster et al. 2012). The absence of a transient size

collapse followed by recovery (as expected under a classic Lilliput model) suggests that post-extinction ecological filters do not drive our observed trends. Instead, they reflect climate's more continuous and pervasive influence on evolutionary trajectories. This distinction underscores the importance of disentangling short-term crisis responses from long-term physiological constraints in interpreting body size evolution across the Phanerozoic.

Geographic range dynamics also demonstrated variability influenced by climatic and ecological contexts. Warming intervals often facilitated range expansions in tropical genera (e.g., $\rho = 0.31$, $p < 0.050$ in hothouse partitionings), while non-tropical genera exhibited more variable responses, including range contractions under general warming conditions. These findings are consistent with previous studies indicating that rising temperatures generally lead to poleward expansions as organisms preserve their optimal thermal niche (Pinsky et al. 2013; Sunday et al. 2012). Fossil evidence across multiple extinction and warming events supports this observation. For example, marine invertebrates during the Paleocene–Eocene Thermal Maximum (PETM) experienced pronounced poleward shifts and range expansions, especially among warm-adapted taxa (Ivany et al. 2000; Sluijs et al. 2007). Similarly, Jablonski (1993) documented latitudinal range shifts and contractions in molluscs across the Cretaceous–Paleogene (K–Pg) boundary, with warm-water taxa extending into higher latitudes as equatorial conditions expanded. However, not all taxa respond equally. Cooling events are often associated with range fragmentation or contraction in stenothermal taxa, as seen in some brachiopod and trilobite lineages during the Late Ordovician glaciation (Finnegan et al. 2012). The evolutionary faunas analysis highlights a comparable divergence. CarPe taxa showed significant range contractions during warming ($\rho = -0.154$, $p < 0.050$) but expansions during cooling ($\rho = 0.313$, $p < 0.050$), suggesting thermal sensitivity and potentially limited dispersal capabilities. This is reminiscent of post-Devonian faunas, where reef-building groups often failed to expand poleward during warming phases, leading to ecological replacement by more tolerant forms (Bridge et al., 2022; Webb, 2002). In contrast,

TriJu taxa consistently displayed range reductions under all partitionings, which may reflect tighter niche specialization or evolutionary constraints consistent with the reduced range dynamics in some post-Triassic benthic faunas (Foote, 2012). CreNeo taxa demonstrated resilience, with range expansions observed during cooling partitionings ($\rho = 0.106$, $p < 0.050$), likely reflecting broader thermal tolerance and dispersal capability, akin to the geographic flexibility seen in Neogene bivalves such as Mytilus and Lucinoma, which track temperature gradients effectively (Vermeij, 2005b). Taxonomic results further reinforce these macroevolutionary patterns. Lucinida and Mytilida consistently expanded their latitudinal ranges with increasing temperature (e.g., Lucinida $\rho = 0.38$, $p < 0.050$ in warming intervals), suggesting that their symbiotic and opportunistic ecologies may confer advantages under thermal stress, as also proposed by studies of chemosymbiotic bivalves following the end-Cretaceous event (Kaim et al., 2008). At the same time, taxa like Ostreida showed significant range contractions during cooling (e.g., $\rho = -0.64$, $p < 0.050$), consistent with fossil evidence that sessile or reef-associated taxa are particularly vulnerable to environmental fluctuations due to limited dispersal and habitat specificity (Kiessling & Simpson, 2011). These differences emphasize the role of ecological plasticity, habitat preference, and dispersal ability in shaping geographic range responses to climatic changes in the modern biosphere and throughout deep time.

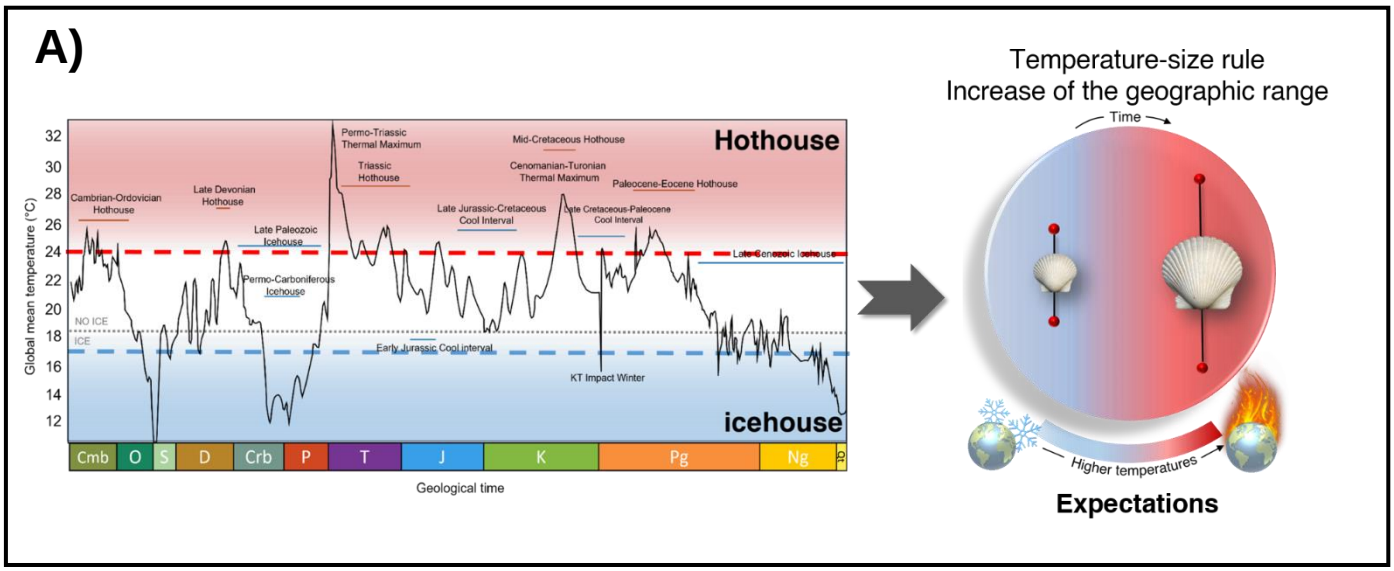
Biogeographic connectedness and beta diversity further elucidate bivalve responses to climatic fluctuations. This study found that connectedness generally increases during cooling intervals, promoting cosmopolitan taxa, while warming partitionings favor endemism, as reflected in reduced connectedness during hothouse intervals. This observation is congruent with previous studies that have linked increased cosmopolitanism to colder climates and decreased connectivity during warming periods (Jablonski 2008b; Yan et al. 2023 ; Zhang et al. 2022). Among evolutionary faunas, CarPe taxa displayed a strong positive correlation with connectedness during warming ($\rho = 0.505$, $p < 0.050$), suggesting

enhanced cosmopolitanism under these conditions. In contrast, TriJu fauna exhibited negative correlations ($\rho = -0.217$, $p < 0.050$), reflecting their limited dispersal ability, while CreNeo taxa showed increasing connectedness during cooling intervals ($\rho = 0.233$, $p < 0.050$), indicative of enhanced spatial cohesion. Taxonomic patterns revealed similar variability; for example, Mytilida and Lucinida consistently displayed positive correlations with connectedness during warming intervals (e.g., Mytilida $\rho = 0.35$, $p < 0.050$), suggesting their ability to maintain spatial cohesion despite thermal stress. However, taxa like Carditida and Trigoniida showed weaker or negative correlations, indicating reduced connectivity in response to warming.

The interplay between body size, range size, and biogeographic connectedness highlights the complexity of bivalve responses to temperature change. Cope's rule provides a framework to understand the general tendency toward larger body sizes during stable periods, while the left wall effect constrains the extent of size reductions during environmental stress (Kingsford & Hughes 2005; Twitchett 2001). Range expansions in tropical genera during warming and the resilience of taxa like Mytilida reflect the advantages of broad thermal tolerance and dispersal capability. Conversely, the vulnerability of TriJu and Trigoniida taxa underscores the challenges faced by groups with narrower ecological niches. These patterns also reveal that evolutionary history and taxonomic identity significantly influence adaptive capacity, as evidenced by the contrasting responses among evolutionary faunas and orders.

3.4.3. Towards latitudinal differenciation

The comparison between the latitudinal results of evolutionary faunas, taxonomic orders, and general patterns reveals both consistencies and divergences in how bivalves



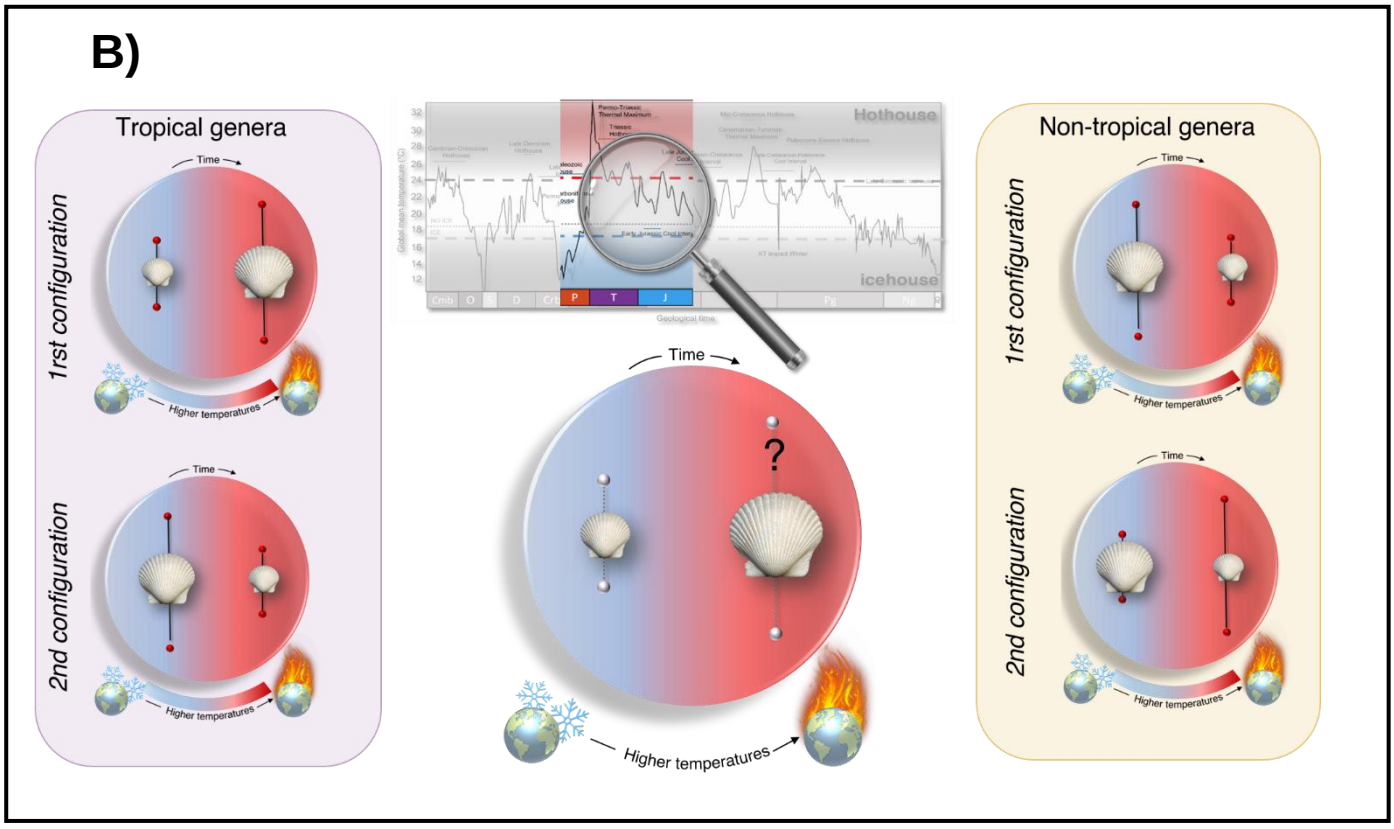


Figure 19: Conceptual figure of the correlation of body size and geographic range with temperature. A) representation of the initial expectation with a constant answer of bivalves to higher temperature(H0) ; B) true variability of the results obtained, depending on the temperature partitioning. Global results show bigger bivalves at higher temperature, following the TSR, but no clear pattern for the geographic range. When focusing on latitudinal zones, some other patterns appears. For non tropical genera, the 1rst configuration correspond to the result obtain during undifferenciate climate and warming intervals ; the 2nd configuration correspond to the result obtain during icehouse periods and cooling intervals in icehouse periods.For tropical genera, the 1rst configuration correspond to the result obtain during undiffirenciate climate, warming intervals, icehouse periods, warming intervals in hothouse and icehouse periods. The 2nd configuration correspond to the result obtain durint hothouse periods.

respond to climate-driven changes in body size and geographic range (Fig. 19). Across all levels, latitude emerges as a key factor influencing these responses, yet the outcomes are shaped by evolutionary history, ecological flexibility, and taxonomic identity. These findings reflect broader trends documented in the scientific literature while illustrating the unique patterns observed in bivalves.

At a global scale, the general pattern shows that body size tends to increase with latitude, consistent with Bergmann's rule (Bergmann 1847), though exceptions among ectotherms are common (Atkinson 1994; Ashton 2002). Such patterns align with studies on other marine taxa, such as gastropods and echinoderms, where body size often increases in colder environments, likely due to metabolic constraints and slower growth rates at low temperatures (Vermeij 2005a; Clarke & Crame 2010). In tropical zones, warming often facilitates range expansions as taxa migrate into temperate areas where ecological niches open due to warming (Tewksbury et al. 2008). Similar trends have been observed in terrestrial and aquatic organisms, including amphibians, reptiles, and freshwater fish (Deutsch et al. 2008; Comte & Olden 2017). Conversely, non-tropical taxa frequently experience range contractions during warming intervals, likely due to narrower thermal tolerances and reduced ability to maintain optimal physiological functions under thermal stress (Sunday et al. 2012). These contractions are often accompanied by reduced body size, reflecting a metabolic trade-off to optimize energy use under high temperatures, a phenomenon also seen in other marine ectotherms, such as mollusks and crustaceans (Pörtner 2002; Cheung et al. 2013).

When considering evolutionary faunas, the global patterns are refined by historical and ecological contexts. The Triassic-Jurassic Bivalve Evolutionary Fauna (TriJu) exhibited consistent range reductions across latitudinal zones, with warming intervals particularly restricting dispersal opportunities. The homogenization of non-tropical communities parallels findings in other fossil records, where global cooling or warming cycles limit species dispersal

and lead to regional clustering of taxa (Kiessling et al. 2003). The Cretaceous-Neogene Bivalve Evolutionary Fauna (CreNeo) demonstrated greater resilience. CreNeo taxa expanded their ranges during cooling periods ($\rho = 0.106$, $p < 0.050$), particularly in tropical zones, reflecting their capacity to occupy new niches in response to cooling, a trend similarly documented in high-latitude echinoderms and gastropods (Krug et al. 2010). Increased biogeographic connectedness ($\rho = 0.233$, $p < 0.050$) during cooling intervals among CreNeo taxa aligns with findings for marine invertebrates, where lower temperatures enhance dispersal by reducing thermal barriers and creating more homogeneous environments (Jablonski et al. 2006; Clarke & Crame 2010). The Carboniferous-Permian Bivalve Evolutionary Fauna (CarPe) displayed intermediate patterns, with significant range contractions during warming ($\rho = -0.154$, $p < 0.050$) and expansions during cooling ($\rho = 0.313$, $p < 0.050$). This highlights the mixed adaptability of CarPe taxa, where thermal tolerance was insufficient to withstand warming but adequate to exploit favorable conditions during cooling. These patterns are consistent with studies of other Paleozoic marine faunas, where temperature changes drove community restructuring and range shifts (Isozaki & Servais 2017).

At the taxonomic level, responses to latitude and temperature show considerable variability among orders. Mytilida and Lucinida consistently exhibited latitudinal range expansions during warming in tropical and non-tropical zones (e.g., Lucinida $\rho = 0.38$, $p < 0.050$ in warming intervals), reflecting their adaptability and dispersal potential. These findings align with studies of modern bivalves, such as mussels and clams, exhibiting strong thermal tolerance and colonization abilities in warming and cooling contexts (Helmuth et al. 2002; Sunday et al. 2012). Conversely, Trigoniida and Carditida exhibited restricted ranges during warming, particularly in non-tropical zones, where range contractions were accompanied by significant reductions in body size (e.g., Trigoniida $\rho = -0.69$, $p < 0.050$ in hothouse conditions). These taxa align with findings from other ectotherms, where limited

dispersal ability and narrower thermal niches contribute to vulnerability under warming partitionings (Angilletta 2009). Ostreida displayed unique patterns, with range expansions in non-tropical zones during cooling, contrasting with range reductions in tropical zones under similar conditions. This divergence highlights the interplay between thermal tolerance and regional ecological conditions, similar to patterns observed in benthic marine taxa like brachiopods and echinoderms during past climatic fluctuations (Valentine & Jablonski 1993; Vermeij 2005a).

Across all levels, a clear distinction emerges between tropical and non-tropical zones. Tropical taxa often benefit from warming, expanding their ranges into higher latitudes and increasing biogeographic connectedness (Yan et al. 2023 ; Zhang et al. 2022). Conversely, non-tropical taxa are more vulnerable to warming, exhibiting reduced ranges and sizes due to physiological stress and limited thermal tolerance (Clapham & Payne 2011). Similar patterns have been documented in other marine groups, where tropical species often display more remarkable thermal plasticity, allowing for poleward migrations (Pinsky et al. 2013). In contrast, non-tropical taxa are more likely to experience range contractions (Sunday et al. 2012). Despite this broad dichotomy, variability among evolutionary faunas and taxonomic orders underscores the complexity of latitudinal responses to temperature changes. For instance, bivalves such as Trigoniida and Pectinida demonstrate contrasting adaptive capacities depending on their ecological niches and evolutionary histories (Stanley 1998). Similarly, the observed trends toward increased biogeographic connectedness during cooling intervals, as taxa expand their ranges and occupy similar ecological niches in more homogeneous environments, are consistent with patterns observed in other marine invertebrates (Jablonski et al. 2006; Clarke & Crame 2010).

The results from this study reinforce findings from the broader literature, demonstrating that a combination of global patterns, evolutionary history, and taxonomic identity shapes latitudinal responses to climate change in bivalves (Fig. 19). These findings

align with broader trends across marine and terrestrial taxa, emphasizing the importance of latitude, thermal tolerance, and ecological flexibility in determining range and size dynamics. Understanding these dynamics is crucial for predicting the impacts of ongoing climate change on marine biodiversity and biogeography.

3.5. Conclusion

This study demonstrates that bivalves adapt their size and geographic distribution in response to temperature, but these adaptations are neither uniform nor consistent across deep time. Instead, the responses are shaped by a complex interplay of latitude, evolutionary history, and taxonomic identity, modulated by ecological and physiological constraints.

Our results confirm that temperature is a key driver influencing bivalve size and range. At a global scale, bivalve body size generally decreases with rising temperatures, consistent with metabolic and physiological constraints under thermal stress. However, this pattern is influenced by latitude: in non-tropical zones, warming often leads to reductions in both size and geographic range. These reductions align with Bergmann's rule in colder environments, where size increases to optimize thermal efficiency but deviate from the rule under warming conditions as physiological limitations reduce fitness and dispersal capacity. This restricted adaptability is reflected in evolutionary faunas such as the Triassic-Jurassic (TriJu), where range reductions during warming intervals led to homogenized communities in non-tropical zones. Similarly, taxonomic groups such as Trigoniida and Carditida exhibit size reductions and range contractions, highlighting their vulnerability to warming. Bivalves generally expand their geographic ranges during warming in tropical zones, reflecting greater thermal tolerance and ecological plasticity. This poleward expansion parallels trends seen in other marine and terrestrial taxa and is facilitated by the availability of ecological niches in temperate regions. However, excessively high temperatures can impose physiological constraints temporarily preventing this expansion. Tropical taxa, such as Mytilida and Lucinida, exemplify this adaptability, consistently expanding their ranges with rising

temperatures. The evolutionary resilience of tropical taxa is also evident in the Cretaceous-Neogene (CreNeo) fauna, where warming facilitated range expansions and increased biogeographic connectedness.

Over deep time, bivalve responses to temperature have been modulated by evolutionary history and ecological dynamics. Evolutionary faunas reveal distinct trends shaped by the climatic regimes and adaptive capacities of their constituent taxa. For example, the TriJu fauna was constrained by limited thermal tolerance and dispersal ability, while the CreNeo fauna displayed enhanced adaptability and broader ranges under both warming and cooling partitionings. Taxonomic variability further underscores the role of ecological specialization: while some orders, such as Mytilida, demonstrate consistent adaptability, others, such as Trigoniida, are more restricted in their response to temperature.

These findings highlight the modulators of bivalve adaptation: latitude, evolutionary history, taxonomic identity, and ecological flexibility. Latitude remains a critical determinant, with contrasting responses between tropical and non-tropical taxa. Evolutionary history shapes the potential for adaptation, as evidenced by the divergent patterns among faunas. Taxonomic identity further refines these responses, with orders demonstrating a spectrum of adaptability tied to their ecological roles and physiological constraints. Future research should unravel the mechanisms driving these patterns to predict better the consequences of ongoing and future climate change on marine ecosystems.

3.6. Transitioning from the general analysis of bivalves range and body size to the application to two well-known macroecological rules

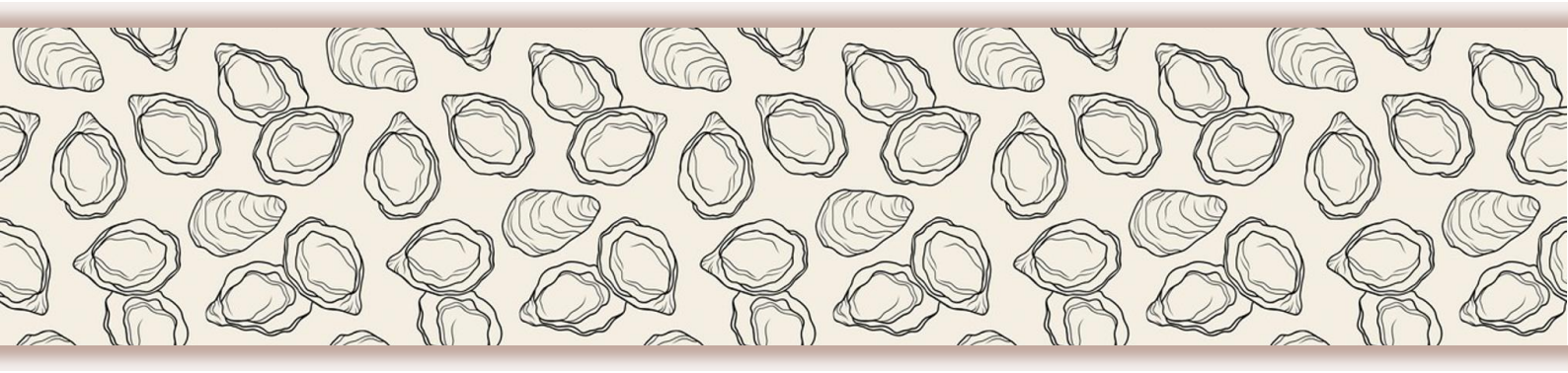
The study of bivalves has revealed general patterns related to size and distribution. The temperature-size rule (TSR), observed in modern species, is also evident in the fossil record. Temperature appears crucial in determining geographic range, and these factors are closely linked to global environmental conditions. However, it is important to note that these correlations are not universally applicable; they depend highly on specific lineages and their evolution over time. The adaptability of organisms is essential for understanding the impact of climate change on biodiversity across different spatial and temporal scales. Furthermore, each taxon's thermal gradient and tolerance play a crucial role in these large-scale responses. Moving beyond a basic empirical description of observed patterns, it is essential to delve into the underlying mechanisms by integrating them into a broader theoretical framework. This is where macroecological principles, such as Rapoport's and Bergmann's rules, prove invaluable for interpreting macroecological trends and universal ecological pressure data.

The connections between organisms and their environment serve as a conceptual basis for understanding the consistent patterns seen in nature. They allow us to link phenomena observed across various spatial and temporal scales and are especially pertinent to studying body size and species distribution. Specifically, Rapoport's and Bergmann's rules provide valuable insights into how organisms respond to environmental changes, particularly concerning temperature and latitudinal gradients.

Rapoport's rule, proposed by biologist Eduardo Rapoport in 1982, suggests that species residing in higher latitudes generally have broader ranges than those in tropical regions. This could be attributed to the greater climatic variability in temperate and polar zones, which compels species to adapt to a broader range of environmental conditions,

thereby expanding their geographic range. Applying this rule to studying bivalves could offer valuable insights into the connection between their geographical distribution and temperature gradients over time, especially in past and future climate change. Integrating this principle enables exploration into whether bivalves from temperate regions have developed greater ecological tolerance than tropical species, potentially resulting in broader geographical distributions. Meanwhile, Bergmann's rule, formulated in 1847 by biologist Karl Bergmann, posits that in warm-blooded animals, species inhabiting colder environments tend to be larger than those living in warmer climates. Although initially developed for homeothermic vertebrates, this principle has been more broadly applied, including in marine ectotherms such as bivalves. Several studies suggest that body size may increase in marine environments with latitude, possibly in response to reduced metabolism in colder waters or thermoregulatory advantages associated with larger body size. In the context of bivalve studies, examining whether species size increases with latitude according to Bergmann's rule could unveil compelling trends related to the morphological evolution of these organisms in response to climate change.

By applying these two macroecological principles to the study of bivalves, we can develop strong hypotheses about the connections between temperature gradients, body size, and range extent. These principles provide a valuable framework for interpreting the intricate patterns observed in the geographical distribution and morphology of bivalves while paving the way for a more comprehensive understanding of their response to historical and current environmental changes. Embracing a macroecological approach enables us to move beyond simply observing variations in size and geographic distribution and delve into more fundamental questions about how bivalves adapt to ecological and climatic gradients. Utilizing Rapoport's and Bergmann's rules allows us to understand the underlying mechanisms that shape bivalve biogeography and to evaluate how these trends might forecast their behavior in future climate change partitionings.



4

Latitudinal patterns of body size and biogeographic distribution as a function of temperature

Contents

Abstract

The study of latitudinal patterns in body size and biogeographic distribution is a central focus in macroecology, particularly in relation to temperature gradients. The two most well-known frameworks for understanding these patterns are Bergmann's rule, which predicts an increase in body size with latitude, and Rapoport's rule, which suggests that species at higher latitudes have larger geographical ranges (Bergmann 1847; Stevens 1989 ; Fig.20). While these rules were initially proposed for terrestrial endotherms, they have since been extended to ectotherms, including marine organisms like bivalves. However, the applicability of these rules in marine systems, particularly for ectotherms, remains debated due to the complex interaction of abiotic and biotic factors that drive size and distribution patterns (Roy et al. 1998; Berke et al. 2013).

This section will explore how temperature affects both body size and biogeographic distribution in bivalves, highlighting the complexity of these relationships in deep time. Analyzing fossil records, we aim to assess whether the classical macroecological rules hold true in marine bivalves or if they require modification to accommodate the unique ecological and evolutionary dynamics of ectothermic organisms.

Key-words : Bergmann rule, Rapoport rule, latitudinal range, body size

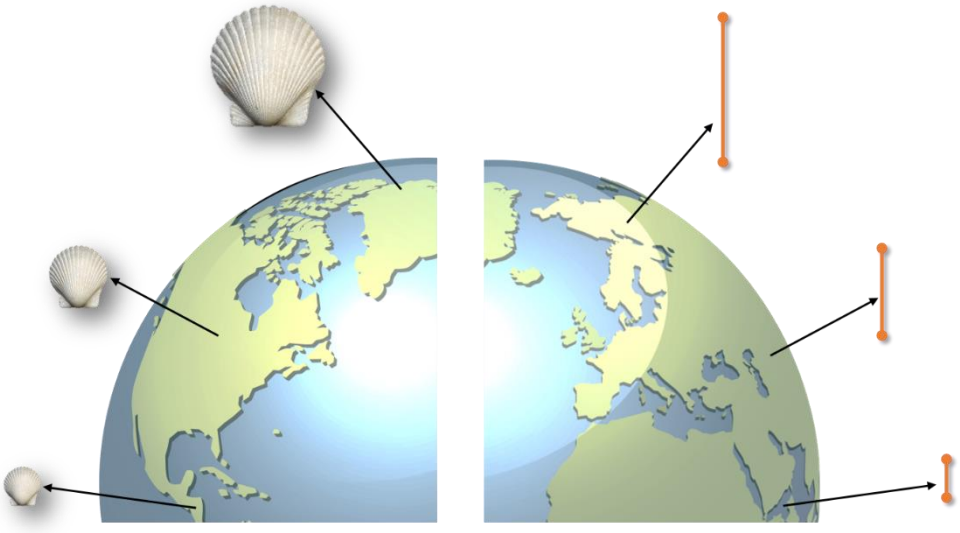


Figure 20: Schematic representation of two latitudinal macroecological rule. On the left, Bergmann's rule and on the right Rapoport's rule

4.1. Introduction

Bivalves represent one of the most diverse and abundant animal groups in both marine and freshwater environments. Their evolutionary history spans over 500 million years, covering the entire Phanerozoic. Extending from the Cambrian to the present, this time interval was punctuated by major abiotic events with periods of warming and cooling, as well as drastic changes in sea levels and continental configurations (Erwin 1994; Raup & Sepkoski 1982). This extensive temporal range makes bivalves valuable indicators of biodiversity changes, species distribution, and morphological adaptations in response to environmental shifts (Stanley 1970; Valentine et al. 1991). In particular, studying the variations in body size and geographic ranges of bivalves over geological epochs provides a unique opportunity to test established ecological rules within a paleontological context (Hunt & Roy 2006).

Ecogeographical ‘rules’ have historically been described to the distribution patterns of fauna and flora influenced by environmental factors (McDowall 2008). Two key concepts, Bergmann's rule and Rapoport's rule, are particularly relevant to the study the evolution of body-size and geographic range during profound climatic changes. They remain central questions in biogeography studies (Blackburn et al. 1999 ; Lomolino et al. 2006) In the middle of the 19th century, Bergman (1847) proposed for the first time an explanation of physiological, ecological and evolution of size distribution. Originally, the rule has been developed as a interspecific geographic trend on mammal. He noticed that large-bodied homeothermic species could be favoured in colder climates due to their heat conservation by a lower surface-to-volume ratio. Conversely, smaller species would tend to occupy warmer environment. Similarly, Rapoport’s rule suggests that species living at higher latitudes have broader geographic ranges, possibly due to the more pronounced climatic variations at these latitudes, which favor species with wider ecological tolerances (Stevens 1989).

To date, most studies on body size and distribution in bivalves have been conducted within a limited paleobiological context, focusing on specific periods or geographical areas (Jablonski 1997; Hunt et al. 2005). While some research has examined general trends in the morphological and ecological traits of fossil bivalves, a comprehensive analysis of these phenomena across the entire, Phanerozoic remains lacking (Roy et al. 2000). Furthermore, the adaptive responses of bivalves to major climatic events during the Phanerozoic are not yet fully understood. Addressing this gap is crucial for better understanding long-term biodiversity dynamics.

This paper aims to investigate how Bergmann's and Rapoport's rules apply to bivalves over the Phanerozoic, by analysing changes in body size and species ranges across geological epochs. We hypothesize that during glacial periods, bivalves exhibit larger body sizes, in line with Bergmann's rule, and that species at higher latitudes have broader geographic ranges, consistent with Rapoport's rule. Through a comparative approach based on global fossil datasets, this study will test the validity of these two rules in a paleontological and paleogeographic framework, thereby providing new insights into the evolutionary processes driving the distribution and adaptation of bivalves (Harnik et al. 2012a; Valentine & Jablonski 2015).

4.2. Material and methods

4.2.1. Data source

The data for this study were derived from the comprehensive fossil dataset compiled by Payne & Heim (2020). This dataset includes extensive records on marine invertebrates, particularly bivalves, spanning the entire Phanerozoic Eon (over 500 million years), with detailed information on body size, geographic distribution, and taxonomic occurrences. The dataset is primarily based on the PaleoDB. It includes spatial and temporal data for fossil occurrences, with geographic coordinates (latitude and longitude) for each entry and

taxonomic resolution at the species level, enabling detailed biogeographic and evolutionary analyses.

To ensure the robustness of the analyses, only species with a well-documented fossil record and multiple occurrences in distinct geographic localities per geological stage were included (more in section 4.2.4 ; see suppl. code B). Specifically, genera with at least three distinct fossil localities per geological stage were retained, allowing for reliable calculation of geographic ranges and body size estimates. Fossils lacking precise geographic coordinates or those assigned only to broader taxonomic levels (e.g., family or order) were excluded from the analysis to maintain consistency in genus-level resolution. The temporal framework was structured around the geological stages of the Phanerozoic, from the Ordovician (541 Ma) to the present day. Each geological stage represents a well-defined time interval, which provides a consistent temporal unit for paleontological analyses (Gradstein et al. 2012). For each genera, occurrences were assigned to the corresponding geological stage based on the age range provided in the dataset.

For both the body size and distributional analyses, the midpoint of each species' geographic range was calculated for each geological stage. The geographic midpoint was determined by calculating the arithmetic mean of the latitudes and longitudes of all recorded occurrences for a given genus within a particular stage (Jablonski et al. 2013). This approach allows for a simplified representation of a species' range and facilitates inter-stage comparisons while accounting for temporal shifts in biogeography due to plate tectonics and sea level changes (Scotese 2021).

4.2.2. Bergmann's rule analysis

Bergmann's rule, originally developed for terrestrial endotherms, posits that individuals of larger body size are more frequently found in colder climates (i.e., higher latitudes), where a larger body size provides a thermoregulatory advantage by reducing heat loss relative to

body volume (Bergmann 1847; Blackburn et al. 1999). Although primarily applied to modern terrestrial species, this principle has also been extended to marine organisms (Roy et al. 2000). In this study, we test whether bivalves follow this size-latitude gradient across geological time, examining whether larger species tend to occur at higher latitudes during cooler periods of Earth's history.

Body size for each species was quantified using the average shell length reported in the Payne & Heim (2020) dataset. Shell length has been widely used as a proxy for body size in paleontological studies due to its ease of measurement and its consistent relationship with body volume (Kidwell 2005). For each species, a mean body size was calculated for each geological stage by averaging the shell lengths of all fossil specimens associated with that species.

The relationship between species body size and latitude was assessed using linear regression models for each geological stage. The mean latitude of each species' occurrences was used as a proxy for climate, under the assumption that higher latitudes generally correlate with cooler temperatures (fig 21). To account for non-linearity and potential confounding factors, we employed generalized least squares (GLS) models that correct for spatial autocorrelation, ensuring more robust parameter estimates (Dormann et al. 2007). Additionally, we examined whether the relationship between body size and latitude varied across major climatic transitions, particularly between cooling and warming time intervals. Given that temperature fluctuations across these periods were significant, their potential influence on Bergmann's rule was assessed by dividing the dataset into warming and cooling time intervals, using paleoclimate reconstructions (Scotese., 2016 ; detailed in Tab.1).

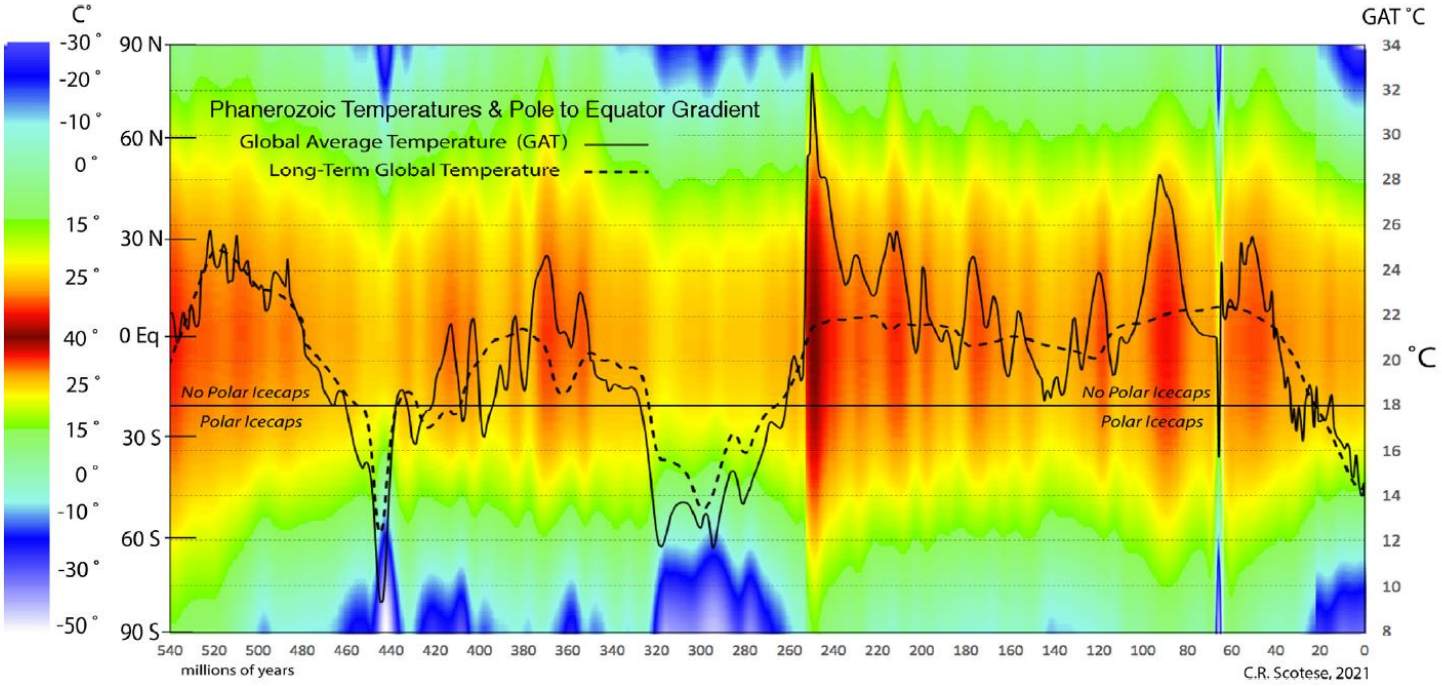


Figure 21: Phanerozoic temperatures and pole-to-equator temperature gradients (Van der Meer et al 2022)

4.2.3. Rapoport's rule analysis

Rapoport's rule proposes that species at higher latitudes tend to have broader geographic ranges than species at lower latitudes, due to the greater climatic variability experienced in polar and temperate regions (Stevens 1989). This rule has been primarily documented in modern ecosystems, but its application to the fossil record, particularly in marine species, remains underexplored (Jablonski 2005). In this study, we test whether bivalves conform to Rapoport's rule across the Phanerozoic, evaluating the relationship between geographic range size and latitude.

For each genus, geographic range size was calculated as the maximum distance between the northernmost and southernmost occurrences (latitudinal range) within each geological stage. This method provides a straightforward measure of geographic range size and has been used in previous studies examining macroecological patterns in the fossil record (Harnik et al. 2012b). Range size was then regressed against the species' latitudinal midpoint to determine if species with higher latitudinal midpoints had larger ranges. To

assess the relationship between geographic range size and latitude, we employed Spearman's rank correlation, which is suitable for non-parametric data and robust to outliers. Additionally, we tested whether the strength of Rapoport's rule varied across climatic epochs by dividing the dataset into warming and cooling time intervals, following the approach used in the Bergmann's rule analysis.

4.2.4. Sensitivity analyses and data validation

4.2.4.1. Filtering the dataset: threshold testing for reliable range and trait estimates

To validate the reliability of macroecological and macroevolutionary patterns derived from the fossil record of bivalves, this study incorporated a structured framework of sensitivity analyses focused on two critical parameters: (1) the minimum number of occurrences per genus per geological stage, and (2) the minimum spatial distance between occurrence localities. These parameters are key to filtering the dataset to reduce noise caused by rare taxa, spatial clustering, and uneven sampling, which are all known to bias range size estimates and trait distributions (Payne & Heim 2020 ; Vilhena & Smith 2013; Puchalski et al. 2008).

To test the effect of these parameters, a wide array of thresholds was applied: occurrence thresholds from 3 to 25 and spatial filtering distances from 100 to 15,000 meters. Range metrics, including latitudinal extent, convex hull area, and maximum great-circle distance (GCD), were recalculated alongside body size estimates for each parameter combination. Summary statistics and ANOVA tests, supplemented by Levene's test and the Kruskal-Wallis test when appropriate, revealed important insights into the sensitivity of these metrics to filtering thresholds (tab.4).

The ANOVA results demonstrated significant differences in trait and spatial metrics across threshold groupings, particularly for mean body size ($F = 7.895$, $p < 0.001$), latitudinal

range ($F = 6.732$, $p < 0.001$), convex hull area ($F = 5.240$, $p = 0.007$), and GCD ($F = 4.112$, $p = 0.012$). However, Levene's test results indicated violations of homogeneity of variance across all variables tested (p-values < 0.05), justifying the use of non-parametric methods. The Kruskal-Wallis test corroborated the ANOVA findings, detecting consistent differences across thresholds in all metrics (H-statistics ranging from 15.782 to 20.135; $p < 0.001$). Further resolution was achieved through Tukey's HSD post hoc tests, which showed that the most substantial differences occurred between the lowest threshold group (e.g., 3 occurrences) and higher threshold groups (notably 10+ and 15+). These differences were especially pronounced in spatial extent metrics (e.g., convex hull area and GCD) and mean body size. The full results are summarized in Table 5, which provides a comparative overview of statistical outputs across all metrics.

These results indicate that while extreme thresholds introduce variance in the estimates, a core range, particularly thresholds between 5 and 15 occurrences, yields relatively stable outcomes. Accordingly, a threshold of 10 occurrences per genus per stage and a 10 km minimum spatial distance is adopted for all core analyses in this thesis. This choice reflects a balance between statistical robustness and data retention. Lower thresholds (e.g., 3 or 5) allow broader sampling but produce inflated variance, especially in spatial metrics, due to limited geographic spread. In contrast, stricter thresholds (20–25) drastically reduce taxonomic coverage, particularly in Paleozoic stages where occurrence data are sparser. The 10-occurrence threshold aligns with standards used in comparable macroevolutionary studies (e.g., Liow et al. 2015; Jones & Close 2024; Close et al. 2018) and minimizes the influence of poorly sampled taxa.

Similarly, both methodological precedent and statistical performance inform the adoption of a 10 km spatial filter. Range size metrics, particularly convex hull area and GCD, are sensitive to spatial clustering. Without a minimum distance filter, taxa represented by tightly clustered localities may yield artificially low range estimates (Jablonski et al. 2006;

Darroch & Saupe 2018). While stricter filters (≥500 m) can effectively reduce spatial redundancy, they often lead to substantial data loss in regions with dense fossil records, such as the Western Interior Seaway. The 10 km threshold thus provides a practical compromise—limiting pseudoreplication without excessively curtailing data coverage.

Tab 4: Summary of statistical tests assessing the effect of filtering thresholds on geographic range and body size metrics

Metric	Test	p-value	Significant?	Notes
Latitudinal Range	ANOVA	**< 0.05**	Yes	Highly significant effect of filters on latitudinal range
	Tukey HSD	**< 0.05**	Yes	All pairwise filter comparisons were significantly different
	Levene's Test	**< 0.05**	Yes	Variance differs significantly between filtering groups
	Kruskal-Wallis	**< 0.05**	Yes	Confirmed non-parametric significance
Convex Hull Area	ANOVA	**< 0.05**	Yes	Strong effect of filtering on area estimates
	Tukey HSD	**< 0.05**	Yes	Significant pairwise differences, especially between low and high thresholds
	Levene's Test	**< 0.05**	Yes	Strong heterogeneity in variances
	Kruskal-Wallis	**< 0.05**	Yes	Very strong non-parametric support
GCD (Max Distance)	ANOVA	**< 0.05**	Yes	Significant variation across filtering levels
	Tukey HSD	**< 0.05**	Yes	Most pairwise differences were statistically significant
	Levene's Test	**< 0.05**	Yes	Indicates differences in dispersion
	Kruskal-Wallis	**< 0.05**	Yes	Confirmed consistent trend in spatial reduction
Body size	ANOVA	**< 0.05**	Yes	Weaker but statistically significant effect
	Tukey HSD	Mixed	Partly	Only comparisons between extreme thresholds showed significance
	Levene's Test	0.087	No	Homogeneity of variance not significantly violated
	Kruskal-Wallis	**< 0.05**	Yes	Borderline significance supports cautious interpretation

The application of these thresholds, supported by a robust suite of statistical tests, ensures methodological transparency and reliability. Lloyd et al. (2012) and Valentine et al. (2006) emphasize that the credibility of macroevolutionary inferences from the fossil record depends critically on data standardization and statistical rigor. The analytical framework employed here, particularly the combination of parametric and non-parametric tests, provides a statistically defensible basis for the patterns reported throughout this thesis. The adopted thresholds reinforce the robustness and interpretability of the macroevolutionary patterns derived from the bivalve fossil record by integrating biological, spatial, and methodological considerations.

Tab 5 : Summary of statistical tests for threshold sensitivity a*nalysis. This table presents the outcomes of ANOVA, Levene's* test, Kruskal-*Wallis test, and Tukey's HSD post hoc compari*sons for each spatial and trait-based metric across different threshold groupings. *p < 0.05, **p < 0.01, ***p < 0.001

Metric	ANOVA F (p)	Levene (p)	Kruskal-Wallis H (p)	Significant Tukey Pairs
Mean Body Size	7.895 (*** **p < 0. 05**)	**p < 0. 05***	20.135 (*** **p < 0. 05**)	3 vs. 10+, 3 vs. 15+
Latitudinal Range	6.732 (*** **p < 0. 05**)	**p < 0. 05***	18.670 (*** **p < 0. 05**)	3 vs. 10+, 5 vs. 15+
Convex Hull Area	5.240 (** **p < 0. 05**)	**p < 0. 05***	16.412 (*** **p < 0. 05**)	3 vs. 10+, 3 vs. 15+
Max Great-Circle Dist.	4.112 (* **p < 0. 05**)	**p < 0. 05***	15.782 (*** **p < 0. 05**)	3 vs. 10+, 5 vs. 15+

4.2.4.2. Spatial weighting: autocorrelation, sensitivity analysis and model validation

In spatial ecological and paleobiogeographic analyses, the specification of the spatial neighborhood structure is critical, as it can substantially influence model estimates and inference (Dormann et al. 2007 ; Dormann 2007). To address this, we conducted a sensitivity analysis on the number of nearest neighbors (K) used to construct spatial weights matrices in our spatial autoregressive (SAR) models. We varied K from 2 to 30 using K-nearest neighbor (KNN) algorithms, a widely used approach for defining spatial contiguity in ecological

applications (suppl. code D). We independently fitted SAR models for each K using two biological response variables: log-transformed body size and latitudinal range size. The corrected Akaike Information Criterion (AICc) was computed for each model to evaluate model fit while adjusting for finite sample sizes (Burnham & Anderson 2002). We plotted AICc values against K to examine model sensitivity to neighborhood configuration (fig 22,Fig 23). The optimal value of K was chosen to minimize the summed AICc of both models, representing a compromise spatial scale that simultaneously optimized performance for both traits.

SAR models were selected due to spatial autocorrelation in both body size and range size distributions, an issue violates the independence assumptions of ordinary least squares (OLS) models (Legendre 1993). Spatial autocorrelation is standard in macroecological and paleobiological datasets, where environmental and evolutionary processes often exhibit geographic structure (Rangel et al. 2010). SAR models explicitly incorporate spatial structure by modeling the influence of neighboring observations via a spatial lag (or error) term, yielding more reliable and unbiased coefficient estimates (Kissling & Carl 2008). Model validation involved comparing SAR to standard OLS models using AIC, coefficient significance, and likelihood-ratio and Wald tests for the spatial lag parameter (ρ). In both body size and range models, SAR consistently outperformed OLS, as evidenced by lower AIC values and statistically significant ρ, confirming the non-random spatial structure of residuals and the appropriateness of SAR models for these data (see suppl. Fig S-W ; Anselin 1988; Dormann et al. 2007). We examined the correlation between the SAR-fitted values and mean paleolatitude using Spearman's rank correlation to assess model robustness further. This served as a post hoc validation of spatial gradients embedded within the fitted values and confirmed that SAR models retained biologically meaningful spatial structure, even after controlling for spatial dependence (suppl. Fig. X-AB).

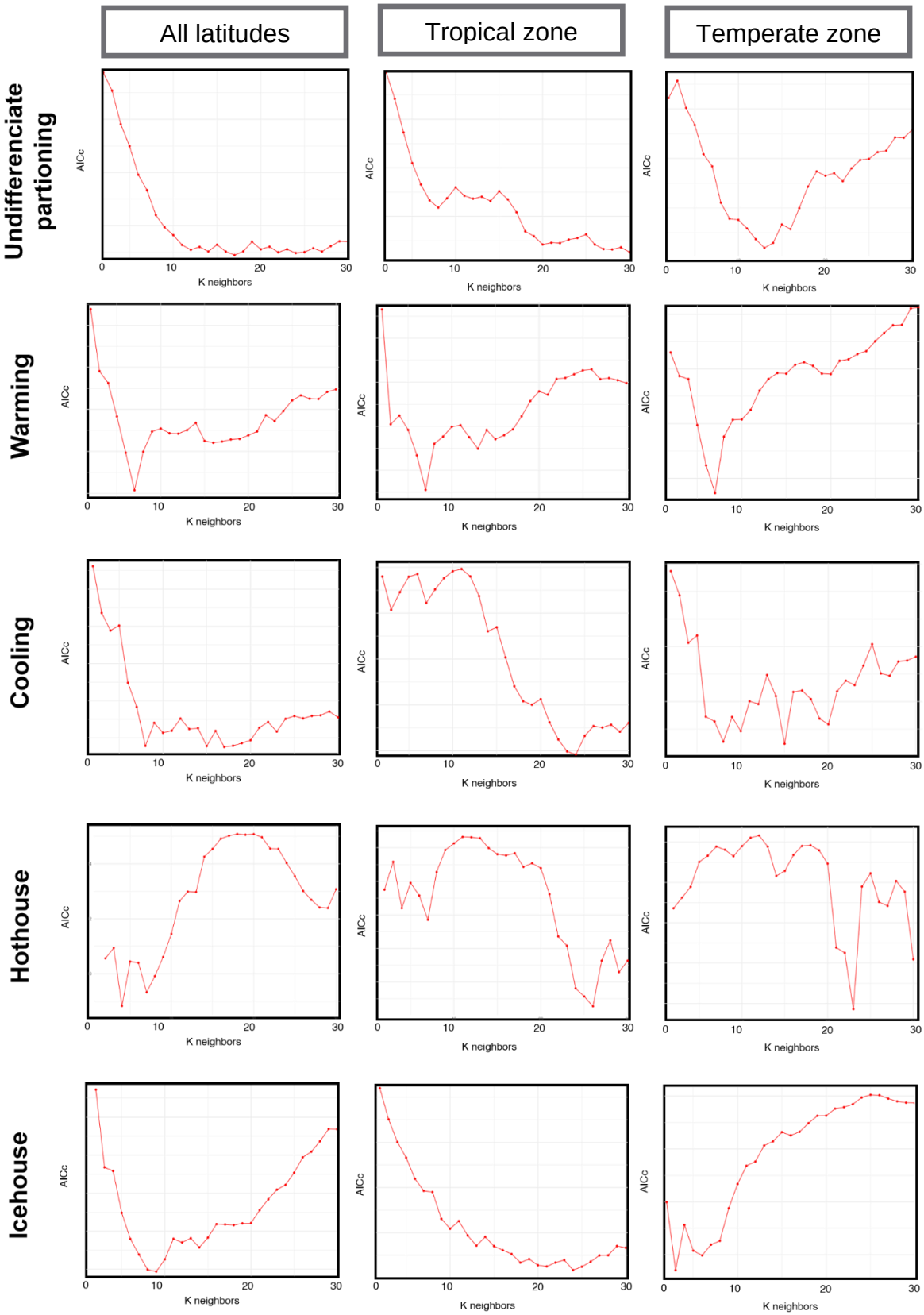


Figure 22: AICc results for each K test sensitivity for the geographic range analysis

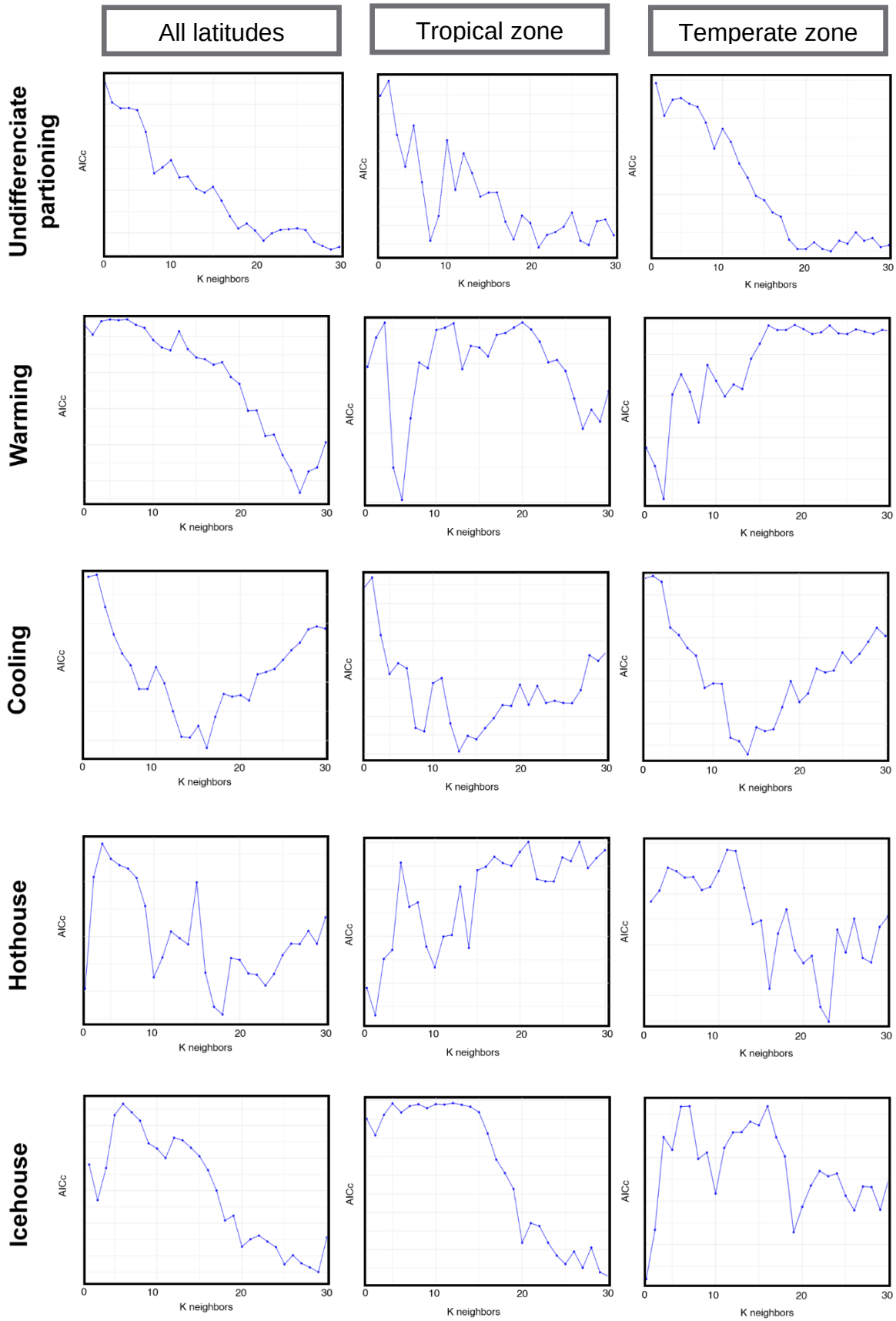


Figure 23: Figure 22: AICc results for each K test sensitivity for the body size analysis

4.3. Results

4.3.1. Global latitudinal patterns

Latitudinal distribution had a clear positive influence on bivalve body size (Fig. 24). The global correlation indicates a significant increase per degree of latitude in overall shell volume (correlation coefficient R = 0.72, p-value < 0.05; Tab. 6). These results are consistent with those found for warming time intervals (R= 0.99, p-value < 0.05) and cooling time intervals (R= 0.65, p-value < 0.05) (Fig. 25; Tab. 6).

Conversely, the latitudinal distribution negatively influenced the latitudinal range of bivalves (Fig. 24), regardless of the range calculation model used (e.g., latitudinal range, convex hull, and great circle distance; suppl. Fig L). Regardless of the climate partitioning, bivalves exhibit a significant negative correlation: the higher the latitude, the lower the latitudinal range (Tab. 6; Fig. 24 ; Fig 25), latitudinal range, convex hull, and great circle distance; suppl. Fig. L).

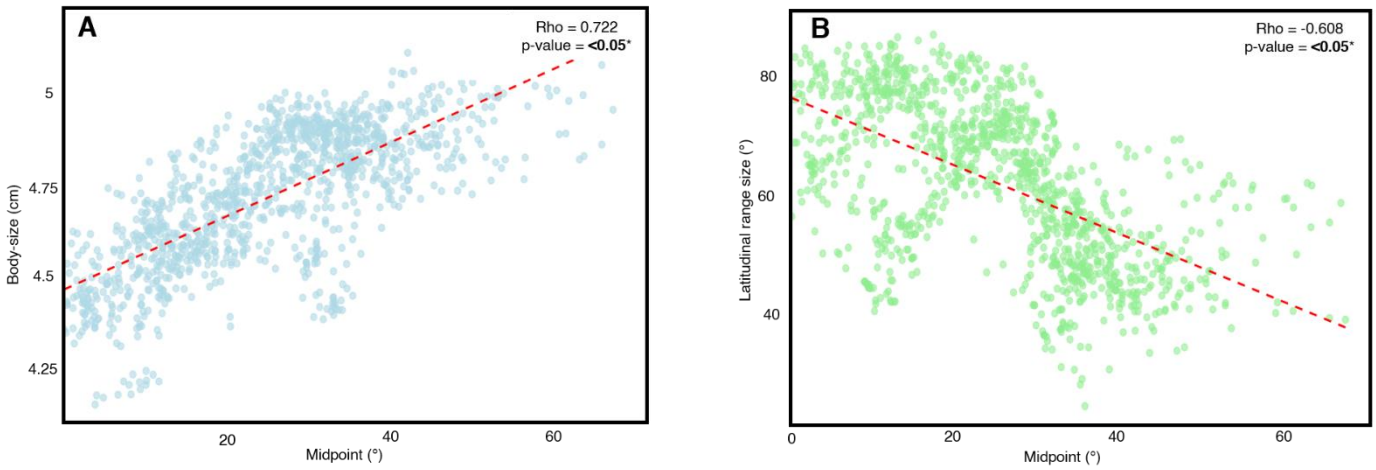


Figure 24: Correlation between body size and latitudinal range size and midpoint of bivalves. (A) correspond to Bergmann's rule and (B) correspond to Rapoport's rule

4.3.2. Evaluating Bergmann's and Rapoport's rules in tropical and temperate regions

Criticism of the two macroecological rules highlights the importance of the study area considered. Most of the studies carried out confirm these rules in temperate regions (> 30° lat), corresponding to the location of the main research areas exploited, particularly at the end of the 20th century (i.e. North America, Western Europe). For this reason, the analysis was subdivided into two categories: the tropical zone (≥ 30° latitude) and the nontropical zone (<30° latitude). In both cases, no significant results were found when considering all the stages in the study (Tab 6).

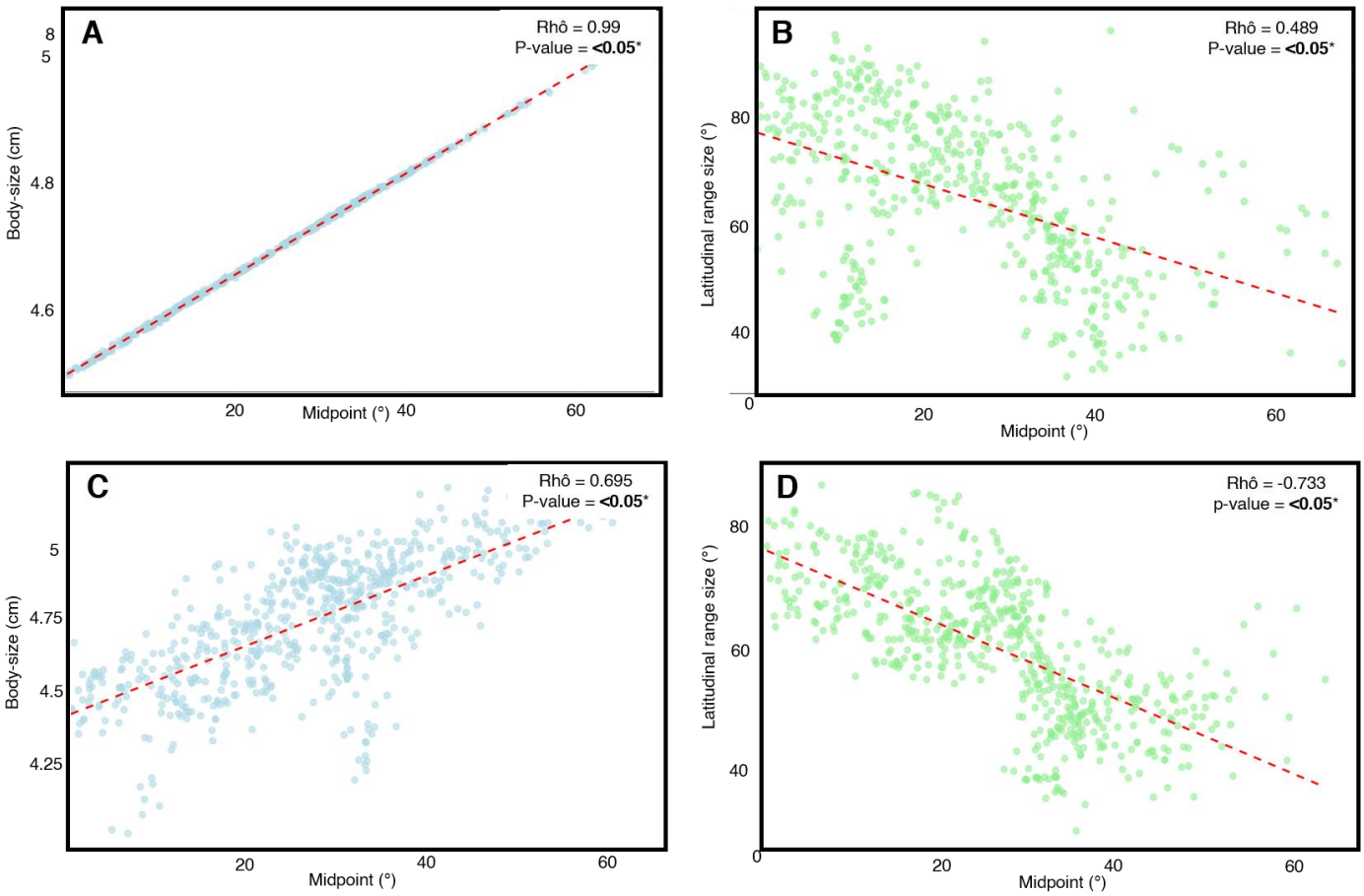
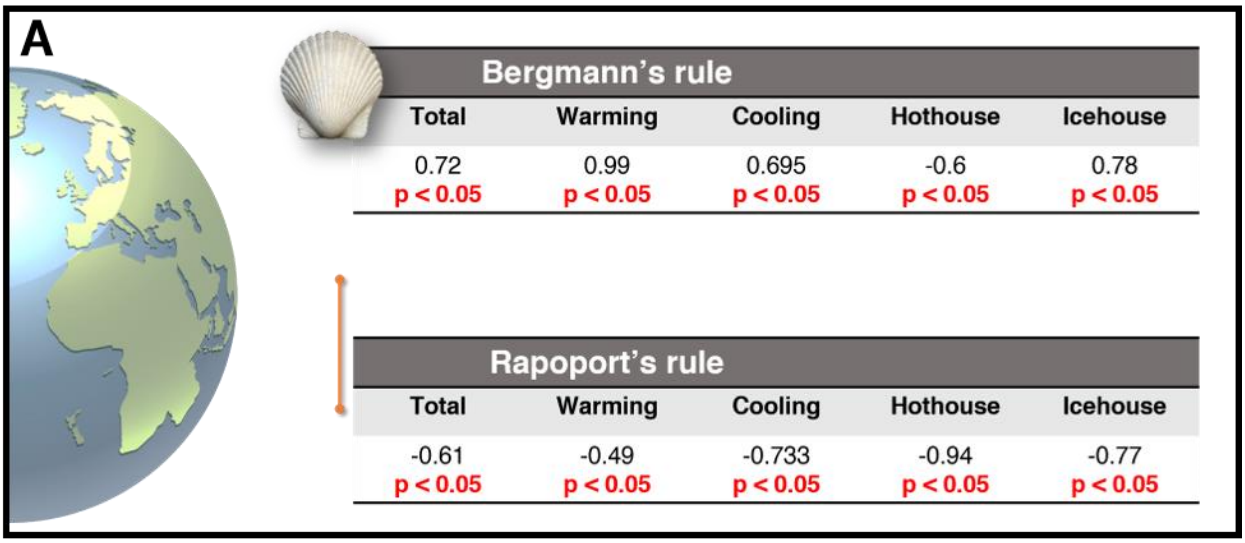


Figure 25: Correlation between body size and latitudinal range and midpoint of bivalves. (A-B) correspond to warming time intervals and (C-D) correspond to cooling time intervals. For more details on thermic periods, see 4.2.

Within the non-tropical zone, Bergmann's rule remained significant under undifferenciate climatic partitioning ($r = 0.78$, $p < 0.05$). This pattern persisted during hothouse ($r = 0.60$, $p < 0.05$) and cooling partitioning ($r = 0.95$, $p < 0.05$), but not during warming partitioning ($r = 0.09$, $p < 0.05$). Rapoport's rule was significantly negative across all partitionings: total ($r = -0.77$, $p < 0.05$), warming ($r = -0.49$, $p < 0.05$), cooling ($r = -0.733$, $p < 0.05$), and hothouse conditions ($r = -0.94$, $p < 0.05$), indicating a robust latitudinal range shift in response to temperature changes (Tab 6).

In contrast, patterns in the tropical zone are weaker and less consistent. Bergmann's rule remained significant overall ($r = 0.94$, $p < 0.05$), during warming ($r = 0.98$, $p < 0.05$), and cooling intervals ($r = 0.87$, $p < 0.05$), with a slightly diminished but still significant signal during hothouse period ($r = 0.83$, $p < 0.05$). Rapoport's rule, however, showed a weaker and mostly non-significant relationship with temperature in tropical zone. While a slight positive correlation was observed under total conditions ($r = 0.10$, $p < 0.05$) and during warming ($r = 0.32$, $p < 0.05$), cooling periods ($r = -0.06$, $p = 0.24$) and hothouse phases ($r = -0.85$, $p < 0.05$) yielded mixed results. Notably, the icehouse phase correlation ($r = -0.30$, $p < 0.05$) was statistically significant but modest.

Tab 6 : Median latitudinal range size and body size of bivalves genera as a function of latitude; A) all latitudes, B) Non-tropical zone and C) Tropical zone



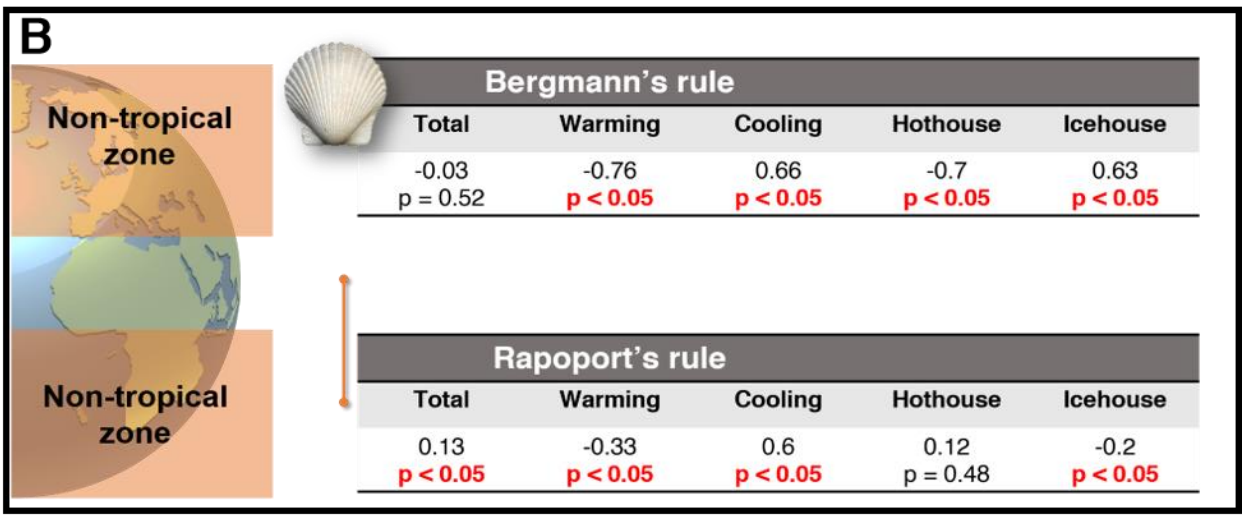
A

Bergmann's rule

Total	Warming	Cooling	Hothouse	Icehouse
0.72 $p < 0.05$	0.99 $p < 0.05$	0.695 $p < 0.05$	-0.6 $p < 0.05$	0.78 $p < 0.05$

Rapoport's rule

Total	Warming	Cooling	Hothouse	Icehouse
-0.61 $p < 0.05$	-0.49 $p < 0.05$	-0.733 $p < 0.05$	-0.94 $p < 0.05$	-0.77 $p < 0.05$



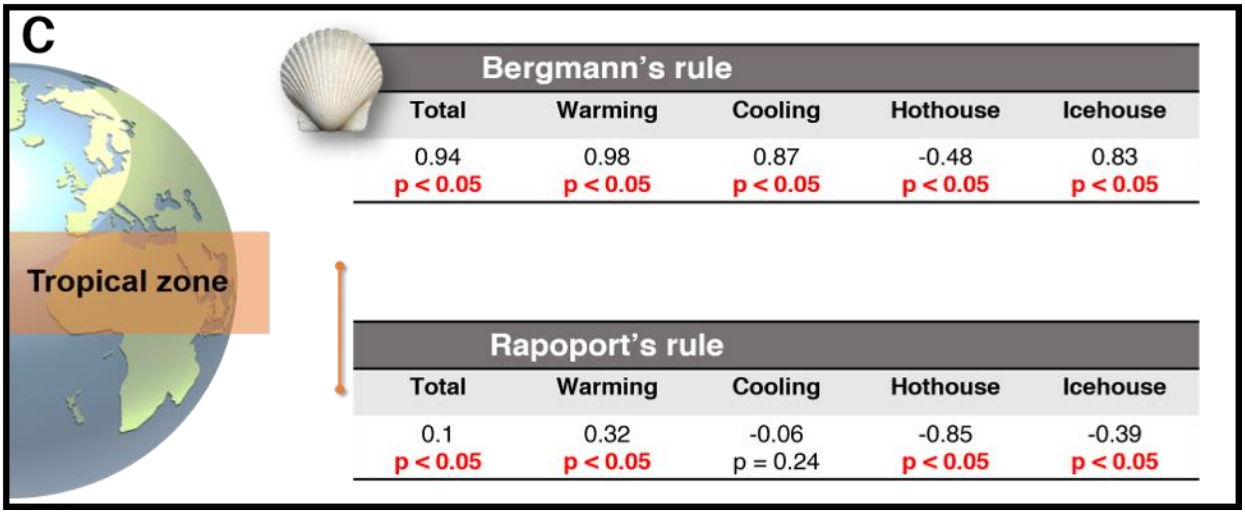
B

Bergmann's rule

Total	Warming	Cooling	Hothouse	Icehouse
-0.03 $p = 0.52$	-0.76 $p < 0.05$	0.66 $p < 0.05$	-0.7 $p < 0.05$	0.63 $p < 0.05$

Rapoport's rule

Total	Warming	Cooling	Hothouse	Icehouse
0.13 $p < 0.05$	-0.33 $p < 0.05$	0.6 $p < 0.05$	0.12 $p = 0.48$	-0.2 $p < 0.05$



C

Bergmann's rule

Total	Warming	Cooling	Hothouse	Icehouse
0.94 $p < 0.05$	0.98 $p < 0.05$	0.87 $p < 0.05$	-0.48 $p < 0.05$	0.83 $p < 0.05$

Rapoport's rule

Total	Warming	Cooling	Hothouse	Icehouse
0.1 $p < 0.05$	0.32 $p < 0.05$	-0.06 $p = 0.24$	-0.85 $p < 0.05$	-0.39 $p < 0.05$

4.4. Discussion

Our analysis provides a concrete insight into the applicability of Bergmann's and Rapoport's rules to an ectothermic marine organism in different latitudinal zones. The present results challenge the traditional understanding of these two macroecological rules.

4.4.1. Bivalves and Bergmann's Rule: Questioning latitudinal expectations

Contrary to earlier suggestions of independence between body size and latitude in bivalves, our results reveal a significant positive correlation, supporting Bergmann's rule. Specifically, larger body sizes were consistently associated with higher latitudes, particularly in non-tropical zones during cooling phases and under hothouse conditions, and more broadly across tropical zones. These findings indicate that bivalves exhibit a latitudinal size gradient, aligning with classical ecogeographical predictions. However, exceptions were observed: in the non-tropical zone, correlations under undifferenciate climatic partitioning ($r = -0.03$, $p = 0.52$) and during warming intervals ($r = -0.76$, $p < 0.05$) did not support Bergmann's rule. The total correlation was non-significant, and the warming partitioning even showed a negative trend. These deviations suggest that the strength and direction of the size-latitude relationship can vary depending on specific climatic contexts, possibly reflecting different ecological or physiological constraints during certain phases.

Earlier studies on ectotherms presented mixed results. Ray (1960) and Lindsey (1966) reported that nearly 75% of ectothermic species followed Bergmann-like trends akin to those observed in mammals. However, subsequent research using more rigorous phylogenetic and statistical methods cast doubt on the universality of this pattern (Felsenstein 1985; Harvey & Pagel 1991; Blackburn et al. 1999; Ashton & Feldman 2003). In invertebrates, the pattern remains complex and often context-dependent. Roy et al. (2000) emphasized that variability in size-latitude relationships depends on the group studied, the region, and methodological differences. For instance, Cushman et al. (1993) observed

increasing body size with latitude in northern European ants, whereas Hawkins (1995) reported no such trend in North American bees. Among butterflies, patterns even vary by hemisphere: body size tends to increase slightly or remain unchanged with latitude in the Northern Hemisphere (Miller 1991; Hawkins & Lawton 1995), but shows a decreasing trend in the Southern Hemisphere (Barlow 1994; Hawkins & Lawton 1995).

Despite this variability, our findings support Bergmann's rule in bivalves at macroevolutionary scales, although not universally. This contrasts with some earlier ecological studies on modern bivalves, which found no clear latitudinal gradient in body size (Roy & Martien 2001; Berke et al. 2013). The strong and significant correlations observed in most scenarios suggest that bivalves tend to follow a predictable pattern of larger body sizes at higher latitudes at least in a palaeontological context. These results highlight the need to consider climatic phase and geographic context when assessing ecogeographic rules and suggest that Bergmann's rule may apply more broadly to marine ectotherms than previously recognized, albeit with important exceptions.

Although Bergmann's rule has been quantified extensively since it was first published, the underlying processes remain little or poorly understood (May 1978; Barlow 1994). As a result, debates about why increased body size might be advantageous for species in cold climates and why these predictions are observed in some groups and not others have provided the basis for number of ideas (Blackburn et al. 1999; Ashton & Feldman 2003; Pincheira-Donoso et al. 2007). Among the most popular hypotheses, the conservation of heat in organisms is the most popular. While a number of studies have compared the morphological characteristics of groups (such as fur or feather density), less attention has been paid to the role of the organisms' thermoregulatory physiology. Furthermore, it has been shown that the body size of bivalves is not directly influenced by the need to maintain heat (Rombouts et al. 2010).

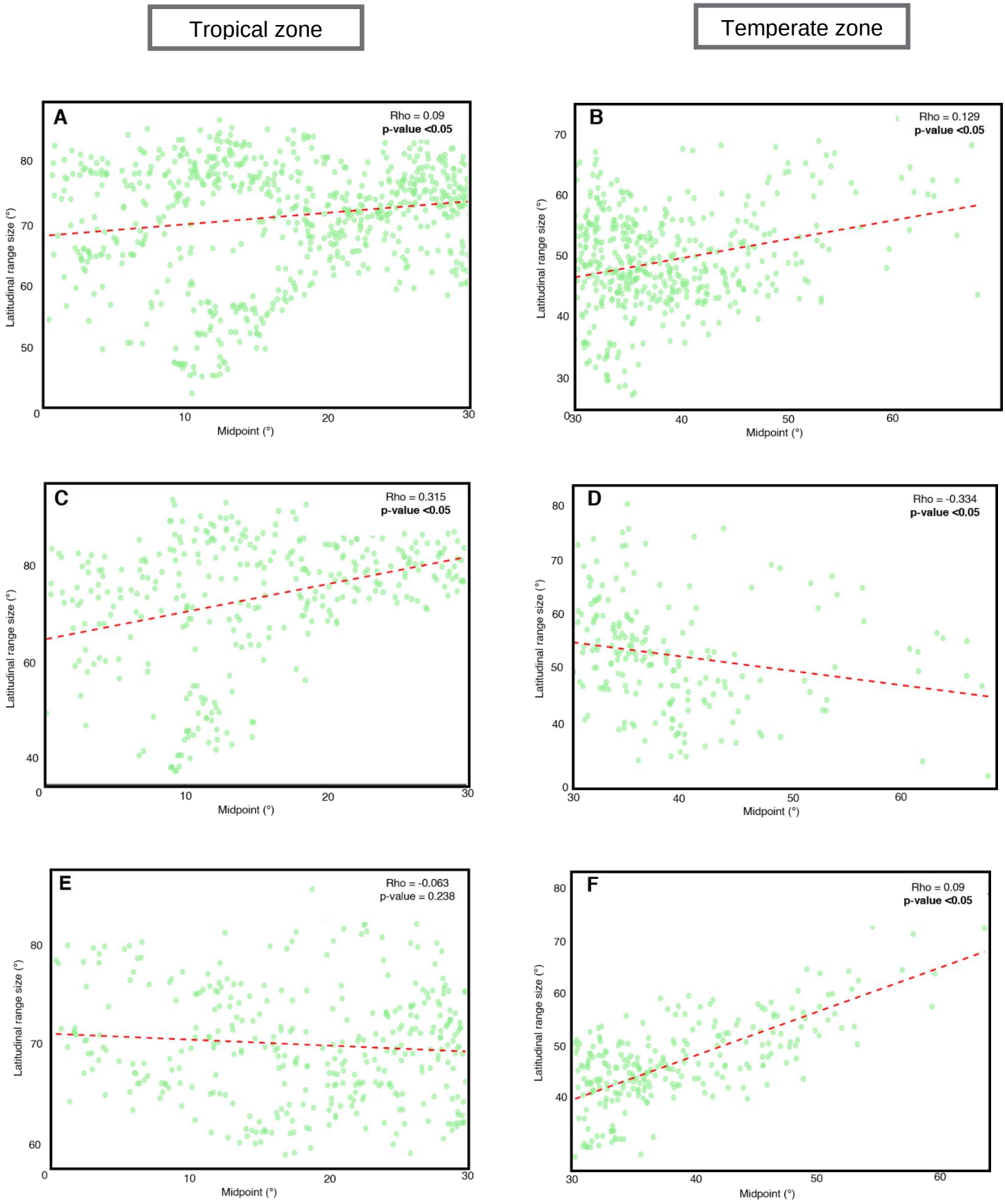


Figure 26: Correlation between latitudinal range size and midpoint of bivalves at different latitudes; (A-B) : all stages are included ; (C-D) : only warming stages are considered ; (E-F) : only cooling stages are considered. The tropical zone extend from 0° to 30° and the non-tropical zone from 30° to 90°

If body size is a function of a species' metabolism, then an increase in body size would allow greater functioning in less energy-rich environments (Wright 1983; Turner & Lennon 1989; Wright et al. 1993; Fraser & Currie 1996). This hypothesis of the availability of environmental energy is true for the latitudinal distribution of mollusc diversity (Roy et al. 1998). In bivalves, some smaller organisms could have an adaptive advantage in colder waters, being more efficient in environments with lower energy production, as is the case in other marine animals (Much & Salinas 2009). Furthermore, following the work of Roy & Matien. (2001) on present-day bivalves, there is a difference between tropical and nontropical zones throughout the Phanerozoic. The temperature gradient as we know it today was established at the end of the Cenozoic, when the Drake Sea opened up and the Antarctic ice cap formed (~34 Ma; Kennet 1977; Barker et al. 2007; Imbrie et al. 1992). The results of the palaeontological analysis are therefore likely to be smoothed by the variety of temperature gradients that have existed since the Ordovician.

More generally, biogeography plays an important role in the latitudinal distribution of bivalve body size (Roy & Martien 2001). Environmental barriers clearly influence molluscs, which are directly dependent on coastal availability. Consequently, body size varies according to latitude, from one province to another (suppl. Fig. AC). This modulation of body size is intrinsically linked to the ability of bivalves to adapt locally and be highly resilient (Schwaner 2023; Cameron 2020). Most of these organisms can adjust their physiology according to specific environmental conditions. This allows them to thrive in a wide variety of ecological niches, without relying entirely on their latitudinal distribution. It also implies a strong relationship with the evolutionary history of each species (Roy et al. 2000), because each region is determined by a set of processes such as speciation or local as well as global extinctions (Ricklefs & Schulter 1993). Every bivalve family becomes relatively independent and can follow Bergmann's law or its converse (Berke et al. 2013).

Whilst temperature or the resources available in a regionally differentiated pattern can have influenced body size, these environmental factors do not play a coherent global role that would allow a universal response within bivalves (Berke et al. 2013). Rather, they are an assemblage of complex evolutionary and ecological trade-offs involving both growth rate and resource metabolism, predation, lifespan, etc. Hence, it is not possible to define a single response. Temperature cannot be excluded from the potential influences on trends in size variation as a function of latitude because this factor is known to play a role in certain life-history traits (Angilletta & Dunham 2003; Atkinson et al. 2006; Dufresne et al. 2009). Another possibility raised is that changes in size within families or genera are affected by many other factors, making it challenging to identify a clear trend with temperature.

Finally, these results raise important questions about the generalisability of Bergmann's rule, particularly for marine ectotherms. This rule, initially described to apply to terrestrial environments where temperature directly affects body size due to thermoregulation (Meiri & Dayan 2003), could not explain trends in marine ectotherms animal such as bivalves because it appears that they are more influenced by ecological, biotic or abiotic factors (Roy et al. 2000; Berke et al. 2013).

4.4.2. Bivalves in a changing climate: Geographic range patterns and their implications

Similar to Bergmann's rule, our analysis reveals a significant relationship between latitude and latitudinal range in bivalves, in line with or in contradiction to Rapoport's rule, depending on context. While Rapoport's rule posits that species at higher latitudes tend to have broader geographic ranges (Stevens, 1989), our data reveal an overall negative correlation between latitude and range size ($r = –0.61$, $p < 0.05$; Fig. 24), indicating that bivalves at lower latitudes typically possess wider latitudinal distributions. This pattern runs counter to Rapoport's predictions and is congruent with earlier observations in other marine groups (Roy et al. 1994; Rhodes et al. 1993; Zacaï et al. 2018; Jones et al. 2002; Connolly et al. 2003). As

suggested by Gaston & Chown (1999b) and Gaston (2003), this inversion may stem from modifications to the climate variability hypothesis (Stevens 1989), where tropical regions, characterized by greater thermal stability, permit broader range sizes when not constrained by geographical barriers. The greater environmental uniformity in tropical marine waters may enable species to disperse more widely, especially when thermal niches are more prevalent across broad latitudinal swaths (Jablonski et al. 2013). Despite their narrower thermal tolerances, this allows "tropical" species to exploit broad geographic ranges during favorable climatic conditions, especially when oceanic circulation and seaway configuration are permissive (Tab.6; Fig. 26; Gaston & Chown 1999a).

However, this general trend exhibits substantial temporal and regional variability. During cooling intervals, the negative correlation becomes particularly pronounced ($r = –0.73$, $p < 0.05$), while in hothouse climates, the trend is even stronger ($r = –0.94$, $p < 0.05$), indicating consistent rejection of Rapoport's rule across different thermal regimes. Conversely, during icehouse periods, no significant correlation was detected ($r = –0.77$, $p = 0.06$), suggesting that extreme climatic conditions may constrain dispersal uniformly across latitudes, reducing variability in range size. Regional and climatic phase analyses clarify this dynamic further. In the tropical zone, significant negative or positive correlations appear (Total: $r = 0.1$, $p < 0.05$; warming: $r = 0.32$, $p < 0.05$; Hothouse $r = -0.85$, $p < 0.05$), indicating that tropical bivalves expand their ranges poleward during warming, consistent with the poleward shift of their thermal niche. This expansion reduces thermal constraints and opens access to higher-latitude habitats, broadening tropical species' ranges. Conversely, during cooling periods, these same taxa face increasing thermal barriers, forcing range contraction toward the equator, potentially fragmenting populations and increasing extinction risk (Harnik et al. 2012b). In the non-tropical zone, the relationship is mirroring what is observed in the tropical zone (Fig. 26). Across all stages, the correlation varies from negative to positive depending on the climatic portioning. While warming shows a positive correlation between

latitudinal range and latitude. This likely reflects competitive displacement and habitat encroachment from expanding tropical taxa, as the thermal envelope favorable to tropical species shifts poleward, reducing the available niche space for non-tropical species (Tomašových et al. 2015). During cooling intervals, bivalves follow an invert trend. The same pattern is observed between Hothouse and Icehouse (Fig 26 ; Tab 6). The environment available essentially limits them. While “tropical” species do not have a high tolerance of thermal or environmental variations, they are capable of long-distance dispersal, as their optimal range corresponds to the most commonly found temperature and environmental range on Earth (Jablonski et al. 2013). Thus, smaller latitudinal extents are expected at the poles than at the equator, not only in bivalves (Jablonski et al. 2013; Tomašových et al. 2015) but also in other tropical animals (Gaston & Gauld 1993; Gaston, 1996).

However, although our results are congruent with Gaston & Chown's (1999a) and Gaston's (2003) hypothesis, climate variability in marine environments has some limitations. It is mainly limited to the ocean surface corresponding to the top 200 m of the thermocline, and seems to be more critical in non tropicals (~35-60° N and S)(Clarke 2009). “Tropical” bivalves tend to extend their geographic range towards higher latitudes during periods of climatic warming. This trend, which runs counter to the global trend in these organisms, is undoubtedly linked to the increase in their preferential thermal zone towards the poles. This also enables the “tropical” genera to colonize new regions, since the availability of habitats increases as the thermal barriers between regions diminish, allowing these organisms to disperse more easily. Conversely, during periods of cooling, “tropical” species find themselves restricted to a zone of lower thermal tolerance (Fig. 23). These contractions in tropical environments engender species that are more specialized and less adapted to climatic variations, which can lead to fragmentation in communities and even to extinction if the species is unable to disperse to more favorable areas (Harnik et al. 2012b). Similarly, during cooling time intervals, bivalves from nontropical zone are favoured, and their

latitudinal extension increases towards cold zones at high latitudes. Bivalves living in the nontropical zone tolerate more climatic fluctuation, enabling them to establish a wider biogeographical range (Tomašových et al. 2015; Addo-Bedaiko et al. 2000). On the other hand, as temperatures warm, the homogenization of environmental conditions may help bivalves in nontropical zone to concentrate on more localized habitats, corresponding to optimized conditions (Tomašových et al. 2015). Moreover, the extension of the tropical zone and the lowering of thermal barriers are increasing competition for nontropicals (Fig. 23).

4.5. Conclusions

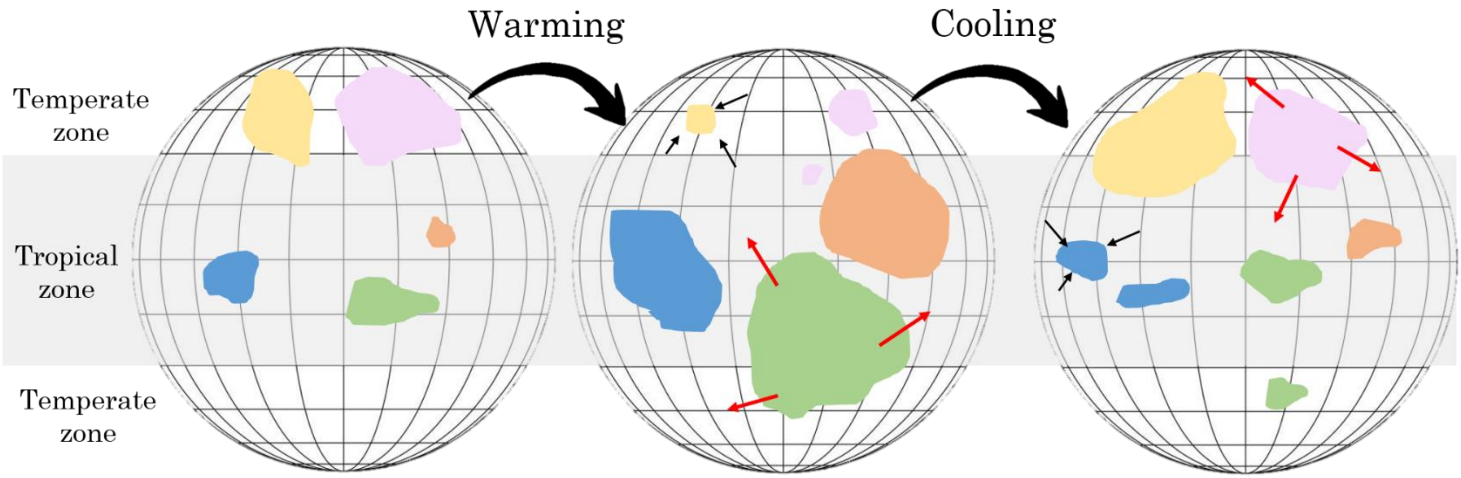


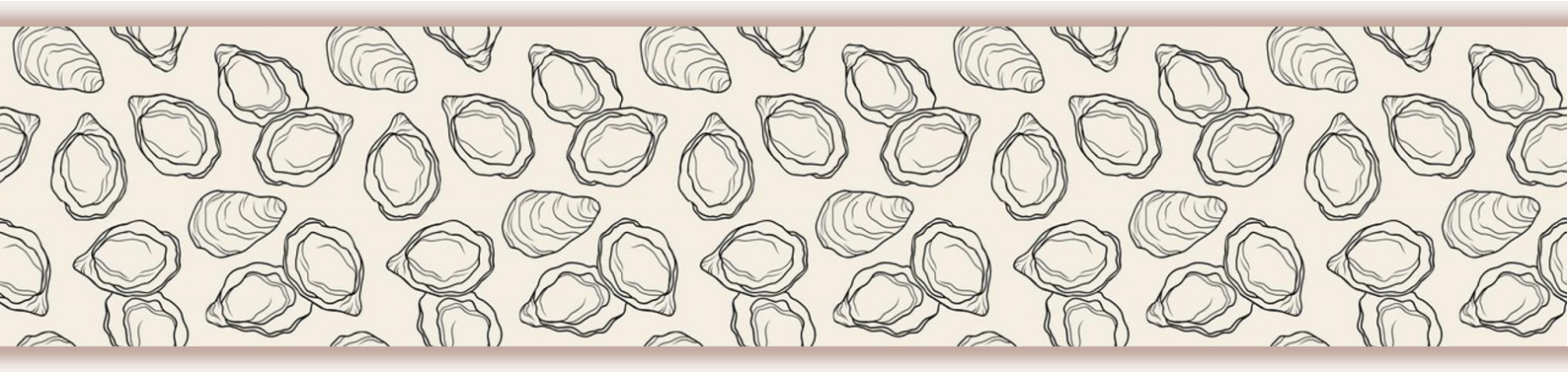
Figure 27: Conceptual diagram of the impact of climate variability on tropical and temperate species range size

This study highlights the dynamic and context-dependent nature of macroecological patterns in marine bivalves across the Phanerozoic. Contrary to longstanding assumptions that body size–latitude and range–latitude relationships are inconsistent or weak in ectotherms, our analysis reveals significant and recurrent patterns, particularly under specific climatic regimes and in regional focus (Lindsey 1966; Ashton & Fedman 2003; Chown & Gaston 2010). While variability remains an important feature of these patterns, our findings demonstrate that both Bergmann's and the inverse of Rapoport's rules are frequently supported, albeit modulated by geography and climate phase (Roy et al. 2001a ; Berke et al. 2013).

In particular, body size tends to increase with latitude (consistent with Bergmann's rule) across the total dataset, during warming, and cooling intervals. Similarly, latitudinal range decreases with increasing latitude (inverting Rapoport's rule), with strong negative correlations in the total dataset, and also during cooling and warming intervals. However, these trends weaken or disappear in the regional zones during certain phases, such as undifferenciate climatic partitioning, or become non-significant altogether during cooling intervals. These divergences emphasize the regionalization of macroecological patterns, shaped by differing evolutionary histories, environmental filters, and biogeographic configurations. The tropical zone, with its broader and more homogeneous thermal envelope, appears particularly conducive to the emergence of clear macroecological signals, while the non-tropical zone presents more complex and often opposing dynamics, possibly due to increased climatic variability and historical contingency.

The partial absence or inversion of classical rules in specific contexts reflects not a failure of these rules, but their conditional validity. Regional differences in speciation and extinction rates (Jablonski et al. 2006), phylogenetic conservatism in size (Berke et al. 2013), and selective extinction dynamics (Smith & Roy 2006) all contribute to shaping these patterns over deep time. Changes in latitudinal range may also be size-selective (Roy et al. 2001b), further complicating the relationship between body size, latitude, and climatic forcing. Moreover, the reciprocal relationship observed with Rapoport's rule — where species in tropical zones exhibit wider ranges than those at higher latitudes — points to the fundamental influence of temperature and climatic stability on range dynamics (Fig. 27). As the thermal envelope shifts poleward during warming, tropical taxa expand while non-tropical ranges contract, and vice versa during cooling, underscoring the climatic sensitivity of biogeographic structure.

The fossil record of marine bivalves offers a uniquely powerful lens through which to test and refine macroecological theory. Rather than dismissing ecogeographical rules as overly simplistic or inconsistent, our findings argue for a more nuanced and climate-aware interpretation, one that accounts for both regional differences and temporal variability. Future research should continue integrating evolutionary, ecological, and environmental dimensions to refine macroecological models, particularly in light of current global climate change and its potential to reshape biodiversity patterns at a planetary scale.



5

Conclusions and perspectives

Contents

This thesis aimed to analyze the spatial, temporal, and morphological dynamics of bivalve biodiversity globally throughout the Phanerozoic era, and to determine their connections with environmental and ecological factors, particularly in global warming. Three main questions were addressed: (1) What are the impacts of climate change on bivalve diversity and ecology? (2) How does climate change affect the size and geographic range of bivalves? (3) What are the biogeographical responses to climate change?

To address these questions, we studied the evolutionary and ecological dynamics of bivalves by analyzing evolutionary faunas and eco spaces and establishing the links between geographic range size, body size, and temperature. In a more in-depth study, we examined these parameters in relation to the latitudinal temperature gradient. The key findings of this work are summarized below and connected to current scientific discussions.

5.1. Paleontological approach to macroecological problems

5.1.1. Comprehensive evolutionary dynamics

Bivalves emphasize that macroecological responses must be clarified, particularly when considering the entire Phanerozoic. Moreover, the lack of studies on their evolutionary dynamics complicates our understanding of these organisms. A study of all genera, using more modern quantification methods, could help identify global biodiversity trends and offer a better analysis of patterns across all marine organisms (Sepkoski 1981). In this respect, the database compiled by Payne and Heim (2020) offers an ideal framework for gathering the taxonomic information essential to diversity studies, the coordinates of occurrences, and the size of each genus.

Diversity analysis shows a significant increase in taxonomic richness throughout the Phanerozoic. The major biotic crises that affected bivalves appear to have been insensitive. These results are congruent with those of Mondal et al. (2015). However, this rise is directly linked to four successive evolutionary faunas (Montariol et al. submitted), raising questions

about the "linearity" of the class' evolution in deep time. Each faunal change occurs parallel to global environmental or ecological changes, mainly driven by continental fragmentation and resource input. The formation or break-up of supercontinents varies the length of coastline available to organisms and contributes to increased ocean sediment supply. This influx favors plankton, conditioning the alternation of evolutionary faunas since the Palaeozoic. Consequently, the large-scale data on bivalves strongly suggest that the classical vision of this group's biodiversity (e.g., Mondal et al. 2015) needs to be deepened to understand all the dynamics involved.

In this context, overall understanding cannot be extracted from an extensive analysis of paleoenvironments and their ecological responses to the life-history traits of mollusks. The data reviewed in chapter two of this dissertation point to changes in the ecospaces of evolutionary faunas. While no direct causality between taxonomic richness and mean temperature has been demonstrated, it cannot be ruled out as a possible secondary factor impacting marine organisms on a global scale.

5.1.2. Does non-correlation with temperature mean non-influence on organisms?

In this work, we considered a direct correlation between mean surface temperature and bivalves' body size and biogeographical distribution parameters. However, temperature often plays an implicit role in physiological and environmental changes. Most of these aspects are difficult or impossible to determine in paleontological studies, particularly when considering factors such as growth or fecundity. Nevertheless, some observations can be made even in the fossil record if we consider the cascade of effect and its feedback on marine organisms. The rich studies on well-sampled present-day or late Cenozoic organisms already highlight the relationship between climate change and organisms (Jablonski 1997; Roy et al. 1998, 2000; Roy & Martien 2001). However, most of these trends are geographically or temporally restricted. Therefore, the comprehensive analysis proposed in chapters 3 and 4 of this

dissertation seems appropriate to highlight the subtle relationship between temperature and organisms through a broad overview and confronting the data with two current macroecological hypotheses.

The findings presented here emphasize the intricate nature of macroecological responses of organisms to a multifaceted factor such as temperature. The question of whether temperature affects the size and biogeographical distribution of bivalves does not have a definitive answer. The outcome depends on the initial environmental conditions and the specific lineages involved. This ambiguity offers a fresh perspective, although not all the intricacies behind these macroecological patterns have been fully uncovered yet.

5.1.3. Broadening the research framework

The methodology used in this research, which examines the size and distribution of bivalves in the context of global warming, could readily be applied to the empirical investigation of other paleontological groups. Echinoderms and ammonites, for instance, present promising opportunities due to their extensive biogeographical range and the abundance of available data in existing literature (Kier 1977; Wignall & Twitchett 1996). Like bivalves, these two groups are marine ectotherms highly sensitive to environmental changes, particularly temperature fluctuations, making them valuable subjects for exploring historical climate influences and extinction dynamics.

Notably, studies of echinoderms, such as crinoids and sea urchins, have revealed significant responses to environmental crises, including the Permian-Triassic extinction event. Twitchett (2006) documented a substantial reduction in organism size during this event, linked to thermal stress and diminished resource availability. Similarly, ammonites, well-studied for their biogeography and morphological variability, exhibited dramatic reactions to past episodes of climate warming (Tissot & Vennin 1996; Ward et al. 2001; Rudwick 2022). For example, certain ammonite genera experienced a reduction in their geographic

range and eventual extinction during periods of rapid warming, attributed to increasing temperatures and the contraction of suitable habitats (Landman et al. 2014). These extinction events underscore the interplay between climatic stressors and the adaptive limitations of marine ectotherms. A comparative analysis incorporating echinoderms and ammonites alongside bivalves could illuminate how species-specific traits, such as mobility or dispersal capacity, influenced survival or extinction under similar climatic pressures. For instance, ammonites, with their greater mobility, may have exhibited different responses to climatic fluctuations compared to the more sessile echinoderms and bivalves. Understanding these dynamics offers valuable insights into the differential extinction risks faced by taxa during historical warming events. Focusing on shorter, specific time intervals could refine these comparative analyses, revealing nuanced patterns of size reduction, range contraction, and extinction thresholds. Such studies would deepen our understanding of the evolutionary and biogeographical dynamics of marine ectotherms and their resilience mechanisms during periods of climatic stress, providing context for contemporary biodiversity crises.

The sclerochronological analysis of bivalves complements morphometric studies and geographic distribution assessments, especially under global warming partitionings. It enables the direct examination of physiological responses to environmental changes over time. While morphometric and spatial analyses reveal trends in size, distribution, and adaptability, sclerochronology reconstructs precise chronologies by analyzing growth streaks in shells. This method provides insight into seasonal temperature variations, resource availability, and stress events that shaped bivalves' life histories (Schöne et al. 2003). Recent sclerochronological studies on fossil bivalves, such as those from the Paleocene-Eocene Thermal Maximum (PETM), highlight their utility in interpreting marine organism responses to rapid warming. Schöne and Gillikin (2013) demonstrated that bivalves from the PETM exhibited reduced growth rates due to elevated temperatures and fluctuating nutrient availability. When paired with evidence of size reduction and geographic range contraction,

such data provide a framework for understanding the mechanisms driving adaptation, resilience, and extinction during periods of environmental upheaval. The sclerochronological study of fossil bivalves also reveals phases of rapid warming followed by sudden cooling, corresponding to oceanographic disturbances or shifts in marine circulation (Surlyk et al. 2010). These insights help unravel the survival dynamics, reproductive strategies, and phenotypic plasticity of bivalve populations in the face of abrupt environmental changes. By integrating data on individual growth and population-level size patterns, researchers can better assess extinction pressures and the factors contributing to survival or collapse.

These analyses contribute to a comprehensive understanding of the evolutionary trajectories and extinction risks of bivalves and other marine ectotherms under global warming partitionings. Such knowledge is crucial for modeling the potential impacts of contemporary climate change on marine ecosystems, particularly in identifying taxa or traits most susceptible to extinction (Ivany & Runnegar, 2010). By synthesizing these approaches, we can develop a more robust framework for predicting and mitigating biodiversity loss in the Anthropocene.

5.2. Link to current macroecological perspectives

This thesis is part of an interdisciplinary effort to integrate paleobiological data into a macroecological perspective. Observing the influence of climate on bivalves in deep time provides several insights into the mechanisms governing evolutionary dynamics, size, and geographic distribution. For example, latitudinal extension is greater in tropical zones than at the poles and, thus, by extension, greater when the thermal gradient increases. When the time interval warms up or cools down, the configuration may be altered according to the latitudinal zone to which the studied organism belongs. One of the main conclusions of this thesis is that body size and range size parameters can be analyzed in both present-day and past models and that temperature is likely to play a role in marine organisms. Our results

confirm the importance of environmental gradients (temperature, primary productivity, water chemistry) in structuring and maintaining environmental communities.

Of course, when applied to a neontological context, our findings offer a renewed understanding of the current biodiversity crisis. The latter is considered one of the most severe biotic crises in Phanerozoic. Although anthropogenic effects directly affect living organisms (such as pollution), the current crisis is also the result of increased global warming and climate instability (Barnosky et al. 2011). The consequences on taxa are already noticeable, affecting their growth, fecundity, and distribution (Bellard et al. 2012). However, the human observation scale does not allow us to measure long-term effects.

A detailed study of bivalves over the entire Phanerozoic can provide forecasts (at least for marine ectotherm organisms) for the current crisis. If current global warming persists, we can expect a reduction in the overall size of taxa. These taxa are likely to have cosmopolitan distributions due to the decrease in temperature gradients and the homogenization of living conditions between low and mid-latitudes. Rising temperatures should lead to a shift from temperate to tropical species, increasing competition in mid-latitudes and leading to the extinction of local endemics.

In the current macroecological debate, paleontological research can contribute a vast amount of information and a better grasp of today's diversity and the dynamics shaping it. It sheds light on patterns on large timescales and could help refine numerical models by incorporating parameters of long-term environmental change. In this way, merging data from present-day statistical models with long-term environmental parameters could make the results more realistic and offer more robust and consistent explanations for past and present macroecological trends (e.g., Leighton 2005). From this point of view, this thesis can contribute directly to anticipating future problems linked to current global warming and the biotic crisis we are experiencing. Bivalves, with their continuous record over the entire Phanerozoic, are an instructive empirical example of how taxa respond to global events,

especially climatic variations. This example also provides many suggestions, notably concerning the variability of biological responses (i.e., body size) and biogeographical distribution (latitudinal gradient, cosmopolitanism, endemism) depending on the environments inhabited and the evolutionary lineages of marine ectothermic organisms.

Macroecology seeks to find general rules for community ecology. When addressing questions of body size and biogeographical range size, the human observation scale becomes restrictive: environmental variables are rarely taken into account in their historical dimension and thus obscure all the variability linked to long-term changes. As introduced at the start of this thesis, spatial and temporal parameters are inextricably linked when establishing realistic projections for present-day taxa. They are crucial to building reliable analyses in the short and long term. By considering all evolutionary dimensions, models will be able to predict the impact of global warming on the biosphere accurately. Ignoring these data could lead to a misestimation of the overall effects and intensity of the diversity crisis. Today, when climate change is a major concern for scientists and society, cross-disciplinary analyses combining neontological and paleontological knowledge are indispensable for implementing conservation strategies. As Machiavelli wrote in his novel: "*To anticipate the future, we need to know the past because the events of this world are always linked to the times that preceded them.*"

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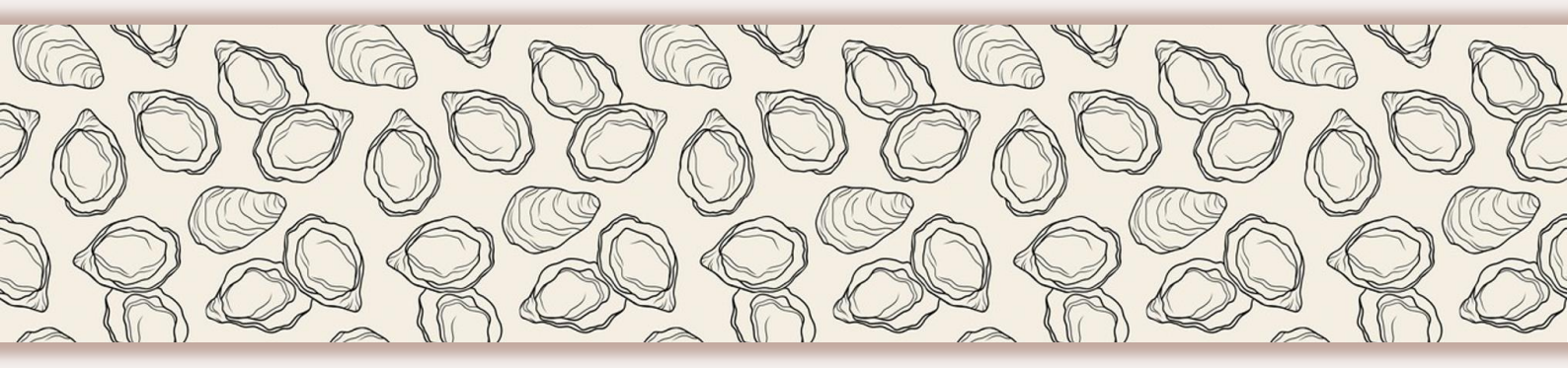


Appendices

- Supplementary table
- Supplementary figures
- R code

Supplementary table A : Extract of the 200 first lines of the cleaned database

occurrence_no	order	family	genus	early_interval	late_interval	max_ma	min_ma	fad	lad	fad_age	lad_age	logsize	logvol	lat	lng	paleolng	paleolat	Series	short	bottom	mid	slc	rely	stage
674952	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,027779	-84,510559	-67,192024	-27,200291	Ordovician	Kat	453	449,1	22	d	Katian
674951	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,027779	-84,510559	-67,192024	-27,200291	Ordovician	Kat	453	449,1	22	d	Katian
674980	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,027779	-84,510559	-67,192024	-27,200291	Ordovician	Kat	453	449,1	22	d	Katian
675084	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	38,870331	-83,91333	-66,968261	-27,6487	Ordovician	Kat	453	449,1	22	d	Katian
675096	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	38,870331	-83,91333	-66,968261	-27,6487	Ordovician	Kat	453	449,1	22	d	Katian
675094	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	38,870331	-83,91333	-66,968261	-27,6487	Ordovician	Kat	453	449,1	22	d	Katian
675117	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	38,870331	-83,91333	-66,968261	-27,6487	Ordovician	Kat	453	449,1	22	d	Katian
675140	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	38,870331	-83,91333	-66,968261	-27,6487	Ordovician	Kat	453	449,1	22	d	Katian
675164	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,328281	-84,067833	-66,681996	-27,249251	Ordovician	Kat	453	449,1	22	d	Katian
675165	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,328281	-84,067833	-66,681996	-27,249251	Ordovician	Kat	453	449,1	22	d	Katian
675173	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,328281	-84,067833	-66,681996	-27,249251	Ordovician	Kat	453	449,1	22	d	Katian
675174	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,328281	-84,067833	-66,681996	-27,249251	Ordovician	Kat	453	449,1	22	d	Katian
675226	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,328281	-84,067833	-66,681996	-27,249251	Ordovician	Kat	453	449,1	22	d	Katian
675705	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675704	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675715	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675724	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675723	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675734	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675746	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675756	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675765	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675764	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675774	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675775	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675784	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675796	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675795	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675828	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675840	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675841	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675851	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675852	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675863	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675864	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675872	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675873	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675879	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675905	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675916	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
675926	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,171928	-84,121933	-66,843057	-27,324834	Ordovician	Kat	453	449,1	22	d	Katian
676149	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,406029	-84,501923	-66,873514	-26,949918	Ordovician	Kat	453	449,1	22	d	Katian
676443	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676456	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676466	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676467	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676475	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676478	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676497	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676505	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian

Supplementary table A : Extract of the 200 first lines of the cleaned database (continued)

occurrence_no	order	family	genus	early_interval	late_interval	max_ma	min_ma	fad	lad	fad_age	lad_age	logsize	logvol	lat	lng	paleolng	paleolat	Series	short	bottom	mid	slc	rely	stage
676514	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676522	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676549	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676563	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676570	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676585	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676612	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676631	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676651	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676652	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676663	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676662	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,296551	-84,404297	-66,906739	-27,079565	Ordovician	Kat	453	449,1	22	d	Katian
676902	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
676901	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
676911	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
676910	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
676921	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
676932	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
676931	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
676943	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
677049	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	39,328281	-84,067833	-66,681996	-27,249251	Ordovician	Kat	453	449,1	22	d	Katian
677059	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,328281	-84,067833	-66,681996	-27,249251	Ordovician	Kat	453	449,1	22	d	Katian
677064	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,328281	-84,067833	-66,681996	-27,249251	Ordovician	Kat	453	449,1	22	d	Katian
677262	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
677263	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
677317	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
677331	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
677356	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
677445	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
677446	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	38,682629	-83,79007	-67,049813	-27,846834	Ordovician	Kat	453	449,1	22	d	Katian
677893	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	39,425072	-84,600731	-66,915586	-26,880764	Ordovician	Kat	453	449,1	22	d	Katian
712787	Nuculanida	Malletiidae	Nuculites	Katian	Katian	453	445,2	485,4	254,17	485,4	252,17	1,48939592	3,75007584	52	-4	-19,159866	-59,746755	Ordovician	Kat	453	449,1	22	d	Katian
718228	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	44	-76	-58,114398	-27,876516	Ordovician	Kat	453	449,1	22	d	Katian
1020642	Cyrtodontida	Cyrtodontidae	Cyrtodontula	Katian	Katian	453	445,2	477,7	303,7	476,8	298,9	1,45591024	3,65489737	61,166668	14,708333	-8,1975359	-33,198736	Ordovician	Kat	453	449,1	22	d	Katian
1020603	Modiomorphida	Modiomorphidae	Modiolopsis	Katian	Katian	453	445,2	485,4	265,1	485,4	259,9	1,59906391	4,06179209	61,166668	14,708333	-8,1975359	-33,198736	Ordovician	Kat	453	449,1	22	d	Katian
1298803	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	45,450001	-73,283333	-55,384165	-27,845507	Ordovician	Kat	453	449,1	22	d	Katian
1298805	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	45,450001	-73,283333	-55,384165	-27,845507	Ordovician	Kat	453	449,1	22	d	Katian
1298562	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	45,794445	-72,859718	-54,888085	-27,728012	Ordovician	Kat	453	449,1	22	d	Katian
1248084	Cyrtodontida	Cyrtodontidae	Cyrtodontula	Katian	Katian	453	445,2	477,7	303,7	476,8	298,9	1,45591024	3,65489737	66,76667	13,466667	-7,6758276	-27,590562	Ordovician	Kat	453	449,1	22	d	Katian
1248093	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	60,055279	10,213889	-11,067439	-33,806942	Ordovician	Kat	453	449,1	22	d	Katian
1248079	Nuculanida	Malletiidae	Nuculites	Katian	Katian	453	445,2	485,4	254,17	485,4	252,17	1,48939592	3,75007584	58,453609	8,755278	-12,47945	-35,135897	Ordovician	Kat	453	449,1	22	d	Katian
1248111	Nuculanida	Malletiidae	Nuculites	Katian	Katian	453	445,2	485,4	254,17	485,4	252,17	1,48939592	3,75007584	60,048889	10,1775	-11,090555	-33,80833	Ordovician	Kat	453	449,1	22	d	Katian
1297264	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	45,740833	-81,608055	-60,239904	-23,982396	Ordovician	Kat	453	449,1	22	d	Katian
1297266	Modiomorphida	Modiomorphidae	Modiolopsis	Katian	Katian	453	445,2	485,4	265,1	485,4	259,9	1,59906391	4,06179209	45,740833	-81,608055	-60,239904	-23,982396	Ordovician	Kat	453	449,1	22	d	Katian
1298501	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	45,740833	-81,608055	-60,239904	-23,982396	Ordovician	Kat	453	449,1	22	d	Katian
1297543	Cyrtodontida	Cyrtodontidae	Cyrtodontula	Katian	Katian	453	445,2	477,7	303,7	476,8	298,9	1,45591024	3,65489737	43,688999	-79,364998	-60,443476	-26,573844	Ordovician	Kat	453	449,1	22	d	Katian
1298391	Cyrtodontida	Cyrtodontidae	Cyrtodontula	Katian	Katian	453	445,2	477,7	303,7	476,8	298,9	1,45591024	3,65489737	46,216667	-72,616669	-54,464445	-27,471455	Ordovician	Kat	453	449,1	22	d	Katian
1298392	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	46,216667	-72,616669	-54,464445	-27,471455	Ordovician	Kat	453	449,1	22	d	Katian
1298393	Myalinida	Ambonychiidae	Ambonychia	Katian	Katian	453	445,2	458,4	410,8	457,5	407,6	1,60108173	4,06752747	46,216667	-72,616669	-54,464445	-27,471455	Ordovician	Kat	453	449,1	22	d	Katian
1298597	Ostreida	Pterineidae	Pterinea	Katian	Katian	453	445,2	453	298,9	452	295,5	1,74888544	4,4876393	45,560001	-73,17778	-55,244774	-27,796774	Ordovician	Kat	453	449,1	22	d	Katian

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis

order	family	Tremadocian	Floian	Dapingian	Darriwilian	Sandbian	Katian	Hirnantian	Rhuddanian	Aeronian	Telychian	Sheinwoodian	Homerian	Gorstian	Ludfordian	Pridoli	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Myalinida	Alatoconchidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiomorphida	Allodesmatidae	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Myalinida	Ambonychiidae	0	0	0	3	3	9	4	4	4	4	4	3	3	2	2	2	2	1	1	1	2	1
Pectinida	Annuliconchidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Anomiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Antillocaprinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Antipleuridae	0	0	0	0	0	0	0	0	0	1	1	1	1	1	4	5	2	1	1	1	1	1
Arcida	Arcidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Arcticidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Astaridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Astartidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myalinida	Atomodesmatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Aviculopectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Modiomorphida	Babinkidae	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Bakevelliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Buchiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraciida	Burmesiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Caprinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Caprotinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Cardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Cardiliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Cardiniidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Nuculida	Cardiolariidae	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cyrtodontida	Cardiolidae	0	0	0	0	0	0	0	0	0	1	1	1	1	2	3	1	1	1	1	1	1	1
Carditida	Carditidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiomorphida	Carydiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0
Pteriida	Cassianellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadida	Ceratomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megalodontida	Ceratomyopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Chaenocardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Chamidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pandorida	Clavagellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Colpomyida	Colpomyidae	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Condylocardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Cooperellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Corbulidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiomorphida	Coxiconchiidae	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Crassatellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
Solemyida	Ctenodontidae	1	1	1	2	2	3	3	3	3	3	3	3	3	3	4	3	3	3	3	3	2	2
Arcida	Cucullaeidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Poromyida	Cuspidariidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Veneroida	Cyamiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinodontida	Cycloconchidae	0	0	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Cymiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Cyrtodontidae	0	1	1	2	3	7	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1
Pectinida	Deltopectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hippuritida	Diceratidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megalodontida	Dicerocardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Dictyoptychidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Dimyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

order	family	Tournaisian	Visean	Serpukhovian	Bashkirian	Moscovian	Kasimovian	Gzhelian	Asselian	Sakmarian	Artinskian	Kungurian	Roadian	Wordian	Capitanian	Wuchiapingian	Changhsingian	Induan	Olenekian	Anisian	Ladinian	Carnian	Norian
Myalinida	Alatoconchidae	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Modiomorphida	Allodesmatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myalinida	Ambonychiidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
Pectinida	Annuliconchidae	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Pectinida	Anomiidae	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	2	2	2	2
Hippuritida	Antillocaprinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Antipleuridae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Arcidae	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
Cardiida	Arcticidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Astaridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Astartidae	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	0	1	2	1	2
Myalinida	Atomodesmatidae	0	0	0	0	0	0	0	1	2	2	2	2	2	2	2	1	1	0	0	0	0	0
Pectinida	Aviculopectinidae	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	4	2	2	2	2	2	1
Modiomorphida	Babinkidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Bakevelliidae	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	3	3	3	3
Pectinida	Buchiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Thraciida	Burmesiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hippuritida	Caprinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Caprotinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Cardiidae	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	4	4
Cardiida	Cardiliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Cardiniidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	2	1
Nuculida	Cardiolariidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cyrtodontida	Cardiolidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Carditidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
Modiomorphida	Carydiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Cassianellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1
Pholadida	Ceratomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Megalodontida	Ceratomyopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Chaenocardiidae	1	1	1	1	1	1	1	3	3	2	2	2	2	1	0	0	0	0	0	0	0	0
Venerida	Chamidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pandorida	Clavagellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Colpomyida	Colpomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Condylocardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Cooperellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Corbulidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiomorphida	Coxiconchiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Crassatellidae	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	1	0	0	0	0	0	0
Solemyida	Ctenodontidae	2	2	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Arcida	Cucullaeidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Poromyida	Cuspidariidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Veneroida	Cyamiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinodontida	Cycloconchidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Cymiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Cyrtodontidae	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Deltopectinidae	1	2	2	2	2	2	2	3	4	4	5	5	5	5	5	4	1	1	1	0	0	0
Hippuritida	Diceratidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megalodontida	Dicerocardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1
Hippuritida	Dictyoptychidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Dimyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

order	family	Rhaetian	Hettangian	Sinemurian	Pliensbachian	Toarcian	Aalenian	Bajocian	Bathonian	Callovian	Oxfordian	Kimmeridgian	Tithonian	Berriasian	Valanginian	Hauterivian	Barremian	Aptian	Albian	Cenomanian	Turonian	Coniacian	Santonian	Campanian	Maastrichtian
Myalinida	Alatoconchidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiomorphida	Allodesmatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myalinida	Ambonychiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Annuliconchidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Anomiidae	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3
Hippuritida	Antillocaprinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Cyrtodontida	Antipleuridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Arcidae	1	1	1	1	1	1	1	2	2	2	2	2	2	3	3	3	3	4	5	5	4	4	5	8
Cardiida	Arcticidae	1	2	3	3	3	3	5	6	6	8	9	9	5	5	5	6	8	6	5	6	6	6	7	7
Carditida	Astaridae	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Carditida	Astartidae	4	4	4	6	6	5	7	7	7	8	8	9	6	5	4	4	5	5	5	5	5	5	5	7
Myalinida	Atomodesmatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Aviculopectinidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Modiomorphida	Babinkidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Bakevelliidae	3	3	3	3	3	3	4	4	4	4	4	3	3	3	2	2	3	3	4	2	2	2	2	3
Pectinida	Buchiidae	0	0	0	1	0	0	0	0	0	1	2	3	2	2	2	2	2	2	2	2	1	1	1	1
Thraciida	Burmesiidae	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Caprinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	4	3	3	3	3	3
Hippuritida	Caprotinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	3	2	2	2	2	2	2	2
Cardiida	Cardiidae	4	3	3	3	3	3	4	4	4	4	4	5	4	4	4	4	6	7	7	7	8	8	8	10
Cardiida	Cardiliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Cardiniidae	2	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculida	Cardiolariidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cyrtodontida	Cardiolidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Carditidae	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	4	3	4	3	3	3	4	4
Modiomorphida	Carydiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Cassianellidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadida	Ceratomyidae	2	2	2	2	2	2	2	3	3	3	3	1	1	1	1	1	1	0	0	0	0	0	0	0
Megalodontida	Ceratomyopsidae	0	0	0	0	1	1	1	1	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Chaenocardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Chamidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pandorida	Clavagellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Colpomyida	Colpomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Condylocardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cardiida	Cooperellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Corbulidae	0	0	0	0	0	0	0	1	1	1	2	2	2	2	2	2	3	2	3	3	3	3	3	6
Modiomorphida	Coxiconchiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Crassatellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	3	3	3	3	3	5	6
Solemyida	Ctenodontidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Cucullaeidae	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Poromyida	Cuspidariidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Veneroida	Cyamiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinodontida	Cycloconchidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Cymiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Cyrtodontidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Deltopectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Diceratidae	0	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	0	0	0	0	0	0	0	0
Megalodontida	Dicerocardiidae	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Dictyoptychidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pectinida	Dimyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

order	family	Danian	Selandian	Thanetian	Ypresian	Lutetian	Bartonian	Priabonian	Rupelian	Chattian	Aquitanian	Burdigalian	Langhian	Serravallian	Tortonian	Messinian	Zanclean	Piacenzian
Myalinida	Alatoconchidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiomorphida	Allodesmatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myalinida	Ambonychiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Annuliconchidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Anomiidae	3	2	2	3	3	3	3	4	5	5	5	4	4	4	4	5	4
Hippuritida	Antillocaprinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Antipleuridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Arcidae	7	7	7	9	10	10	10	10	10	11	11	11	11	10	10	12	11
Cardiida	Arcticidae	5	5	5	5	3	2	2	1	2	2	2	2	2	2	2	2	2
Carditida	Astaridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Astartidae	5	3	3	3	2	2	2	1	2	2	3	3	3	3	2	2	2
Myalinida	Atomodesmatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Aviculopectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiomorphida	Babinkidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Bakevelliidae	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Buchiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraciida	Burmesiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Caprinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Caprotinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Cardiidae	13	11	12	14	15	17	20	21	17	17	18	18	20	20	19	20	18
Cardiida	Cardiliidae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Carditida	Cardiniidae	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
Nuculida	Cardiolariidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Cardiolidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Carditidae	8	9	9	11	11	12	11	12	11	12	13	13	13	13	12	12	10
Modiomorphida	Carydiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Cassianellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadida	Ceratomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megalodontida	Ceratomyopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Chaenocardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Chamidae	1	1	1	1	1	2	2	2	2	2	3	3	3	3	3	3	3
Pandorida	Clavagellidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Colpomyida	Colpomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Condylocardiidae	1	1	1	1	2	2	3	2	2	2	2	2	2	2	2	2	2
Cardiida	Cooperellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Myida	Corbulidae	7	7	7	8	7	5	5	5	4	5	5	5	5	5	4	4	4
Modiomorphida	Coxiconchiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Crassatellidae	5	4	4	5	6	7	7	6	5	5	5	5	5	5	5	5	4
Solemyida	Ctenodontidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Cucullaeidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Poromyida	Cuspidariidae	1	1	2	2	2	2	2	3	3	3	3	3	3	3	2	2	2
Veneroida	Cyamiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Actinodontida	Cycloconchidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Cymiidae	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Cyrtodontidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Deltopectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Diceratidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megalodontida	Dicerocardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Dictyoptychidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Dimyidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

order	family	Tremadocian	Floian	Dapingian	Darriwilian	Sandbian	Katian	Hirnantian	Rhuddanian	Aeronian	Telychian	Sheinwoodian	Homerian	Gorstian	Ludfordian	Pridoli	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Cardiida	Donacidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adapedonta	Edmondiidae	0	0	0	0	1	1	1	1	1	1	1	1	2	2	2	2	2	3	3	3	3	3
Pectinida	Entoliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pectinida	Euchondriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cardiida	Euloxidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Flemingostreidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Frejidae	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Cardiida	Galeommatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastrochaenida	Gastrochaenidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Veneroida	Glauconomidae	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Glossidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Glycymerididae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Grammysiidae	0	0	0	0	2	3	4	4	4	4	4	4	5	5	5	7	7	9	9	10	8	9
Ostreida	Gryphaeidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Halobiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Heteropectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adapedonta	Hiatellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Hippopodiumidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Hippuritidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Hunanopectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Icanotiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myalinida	Inoceramidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Iotrigoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculanida	Isoarcidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Kalenteridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
Cardiida	Kelliellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Laevitrigoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Lahillidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Lasaeidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Laternulidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Leiopectinidae	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Pectinida	Leptochondriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Limatulinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Limidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pectinida	Limipectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Arcida	Limopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiomorphida	Lipanellidae	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Lucinida	Lucinidae	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	2	2	1
Myalinida	Lunulacardiidae	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	2	2	2	2	2	1	0
Pandorida	Lyonsiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Mactridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Mallaeidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Malleidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculanida	Malletiidae	2	3	3	4	3	3	4	2	2	2	2	3	2	2	2	4	2	3	2	3	2	2
Solemyida	Manzanellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Megadesmidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megalodontida	Megalodontidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1
Trigoniida	Megatrigoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Mesodesmatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mytilida	Modiolopsidae	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

order	family	Tournaisian	Visean	Serpukhovian	Bashkirian	Moscovian	Kasimovian	Gzhelian	Asselian	Sakmarian	Artinskian	Kungurian	Roadian	Wordian	Capitanian	Wuchiapingian	Changhsingian	Induan	Olenekian	Anisian	Ladinian	Carnian	Norian	Rhaetian	Hettangian
Cardiida	Donacidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adapedonta	Edmondiidae	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	0	0	2	2	2	2	2	2
Pectinida	Entoliidae	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1
Pectinida	Euchondriidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Cardiida	Euloxidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Flemingostreidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Frejidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Galeommatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastrochaenida	Gastrochaenidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
Veneroida	Glauconomidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Glossidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Arcida	Glycymeridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Grammysiidae	8	8	7	5	5	5	5	5	5	5	5	5	6	5	5	4	1	1	1	1	1	0	0	0
Ostreida	Gryphaeidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	2	2
Ostreida	Halobiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	3	1	1	0
Pectinida	Heteropectinidae	1	1	1	1	1	1	1	4	4	4	4	4	4	4	5	5	3	1	1	1	1	1	1	0
Adapedonta	Hiatellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
Carditida	Hippopodiumidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Hippuritidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Hunanopectinidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Icanotiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myalinida	Inoceramidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Trigoniida	Iotrigoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculanida	Isoarcidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Kalenteridae	0	0	0	0	0	0	0	0	1	1	2	2	2	2	2	2	2	1	2	2	2	1	2	2
Cardiida	Kelliellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Laevitrigoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Cardiida	Lahillidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Lasaeidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Laternulidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	2
Pectinida	Leiopectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Leptochondriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0
Pteriida	Limatulinidae	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
Pectinida	Limidae	1	1	1	1	1	1	2	2	3	4	4	4	5	6	5	4	4	4	7	7	7	8	9	8
Pectinida	Limipectinidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Arcida	Limopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Modiomorphida	Lipanellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lucinida	Lucinidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	3	4	4	4	4	5	5	5	5
Myalinida	Lunulacardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pandorida	Lyonsiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Mactridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Ostreida	Mallaeidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Malleidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2	2	1	1
Nuculanida	Malletiidae	2	2	2	2	2	2	2	2	3	3	3	3	3	3	2	2	1	1	3	3	4	2	2	2
Solemyida	Manzanellidae	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1
Pholadomyida	Megadesmidae	0	0	0	0	0	0	0	2	3	3	3	3	4	3	3	3	0	0	0	0	0	0	0	0
Megalodontida	Megalodontidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	4	3	1
Trigoniida	Megatrigoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Mesodesmatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mytilida	Modiolopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

order	family	Sinemurian	Pliensbachian	Toarcian	Aalenian	Bajocian	Bathonian	Callovian	Oxfordian	Kimmeridgian	Tithonian	Berriasian	Valanginian	Hauterivian	Barremian	Aptian	Albian	Cenomanian	Turonian	Coniacian	Santonian	Campanian	Maastrichtian
Cardiida	Donacidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
Adapedonta	Edmondiidae	2	2	2	2	2	3	3	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2
Pectinida	Entoliidae	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1
Pectinida	Euchondriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Euloxidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Flemingostreidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
Arcida	Frejidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Galeommatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Gastrochaenida	Gastrochaenidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3
Veneroida	Glauconomidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Glossidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
Arcida	Glycymerididae	0	0	0	0	0	1	1	1	1	1	1	1	1	1	3	2	3	3	4	4	4	4
Pholadomyida	Grammysiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Gryphaeidae	3	4	4	4	4	4	4	5	4	3	3	6	6	7	7	9	9	10	10	11	10	9
Ostreida	Halobiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Heteropectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adapedonta	Hiatellidae	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	3
Carditida	Hippopodiumidae	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Hippuritidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	3	3
Pectinida	Hunanopectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Icanotiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1
Myalinida	Inoceramidae	2	2	2	1	1	1	1	1	1	2	1	1	1	1	1	1	0	0	0	0	0	1
Trigoniida	Iotrigoniidae	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
Nuculanida	Isoarcidae	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cardiida	Kalenteridae	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cardiida	Kelliellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Laevitrigoniidae	2	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Cardiida	Lahillidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Venerida	Lasaeidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pholadomyida	Laternulidae	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4	5	5	5	5	5	5
Pectinida	Leiopectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Leptochondriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Limatulinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Limidae	8	8	8	8	8	8	9	9	10	10	10	10	9	9	9	8	8	8	8	8	8	8
Pectinida	Limipectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Limopsidae	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Modiomorphida	Lipanellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lucinida	Lucinidae	5	5	4	4	4	4	4	6	5	6	5	5	5	5	7	8	9	9	9	9	9	13
Myalinida	Lunulacardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pandorida	Lyonsiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Mactridae	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	6	3	3	3	3	5
Ostreida	Mallaeidae	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ostreida	Malleidae	2	3	2	2	3	3	3	3	2	2	1	1	1	1	1	1	2	2	2	2	2	3
Nuculanida	Malletiidae	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	1	1	2	2
Solemyida	Manzanellidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pholadomyida	Megadesmidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megalodontida	Megalodontidae	1	1	2	2	2	2	2	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Megatrigoniidae	0	0	0	0	0	0	0	0	0	1	1	1	1	1	2	2	2	2	2	2	2	2
Venerida	Mesodesmatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Mytilida	Modiolopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

order	family	Danian	Selandian	Thanetian	Ypresian	Lutetian	Bartonian	Priabonian	Rupelian	Chattian	Aquitanian	Burdigalian	Langhian	Serravallian	Tortonian	Messinian	Zanclean	Piacenzian
Cardiida	Donacidae	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adapedonta	Edmondiidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Entoliidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Euchondriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Euloxidae	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0
Ostreida	Flemingostreidae	1	1	1	1	3	3	3	3	3	2	2	2	2	2	2	2	2
Arcida	Frejidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Galeommatidae	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	0
Gastrochaenida	Gastrochaenidae	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Veneroida	Glauconomidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Glossidae	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	2	1
Arcida	Glycymerididae	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Pholadomyida	Grammysiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Gryphaeidae	7	7	7	6	6	6	5	4	4	5	5	4	4	4	3	3	3
Ostreida	Halobiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Heteropectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adapedonta	Hiatellidae	3	3	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Carditida	Hippopodiumidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Hippuritidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Hunanopectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Icanotiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myalinida	Inoceramidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Iotrigoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculanida	Isoarcidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Kalenteridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Kelliellidae	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Trigoniida	Laevitrigoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Lahillidae	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Venerida	Lasaeidae	2	2	4	6	5	6	6	6	6	6	8	8	8	9	9	11	10
Pholadomyida	Laternulidae	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Pectinida	Leiopectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Leptochondriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Limatulinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Limidae	8	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
Pectinida	Limipectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Limopsidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Modiomorphida	Lipanellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lucinida	Lucinidae	20	20	20	22	22	23	22	22	20	19	19	19	17	16	16	16	14
Myalinida	Lunulacardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pandorida	Lyonsiidae	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Venerida	Mactridae	4	5	5	7	9	9	10	9	9	11	11	11	11	11	10	12	10
Ostreida	Mallaeidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Malleidae	3	3	3	3	3	2	2	2	2	2	2	2	2	2	2	2	2
Nuculanida	Malletiidae	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	2	1
Solemyida	Manzanellidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
Pholadomyida	Megadesmidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Megalodontida	Megalodontidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Megatrigoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Mesodesmatidae	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	2	2
Mytilida	Modiolopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

order	family	Tremadocian	Floian	Dapingian	Darriwilian	Sandbian	Katian	Hirnantian	Rhuddanian	Aeronian	Telychian	Sheinwoodian	Homerian	Gorstian	Ludfordian	Pridoli	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Modiomorphida	Modiomorphidae	2	2	2	5	8	13	8	7	7	7	5	6	6	7	7	7	7	7	6	7	6	6
Hippuritida	Monopleuridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Monopteriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Monotidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Myidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraciida	Myochamidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Myophorellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Myophoricardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Myophoriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
Mytilida	Mysidiellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mytilida	Mytilidae	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	3	3	3	2	2
Pectinida	Neitheidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Neoleptonidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Neomiodontidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Noetiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculanida	Nuculanidae	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	2	2	2	2	2	2	2
Nuculida	Nuculidae	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	2	2	2	2	2
Solenidae	Orthonotidae	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ostreida	Ostreidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Oxytomidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Palaeocarditidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Pandoridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Parallelodontidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	2	2	2	2
Pectinida	Pectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Pergamidiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Periplomatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Permophoridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Petricolina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adapedonta	Pharidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Philobryidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Pholadidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Pholadomyidae	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
Ostreida	Pinnidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Placunidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Plagioptychidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Pleurodesmatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadida	Pleuromyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Plicatulidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Pollicidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Polyconitidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Poromyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Posidoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
Cyrtodontida	Praecardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2	2	1	1
Nuculida	Praenuculidae	0	0	0	2	2	2	3	2	2	3	3	3	2	2	2	1	1	1	0	0	0	0
Pectinida	Propeamussiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Prosogyrotrigoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Prospondylidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Psammobiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Pseudomonotidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Pteriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

order	family	Tournaisian	Visean	Serpukhovian	Bashkirian	Moscovian	Kasimovian	Gzhelian	Asselian	Sakmarian	Artinskian	Kungurian	Roadian	Wordian	Capitanian	Wuchiapingian	Changhsingian	Induan	Olenekian	Anisian	Ladinian	Carnian	Norian
Modiomorphida	Modiomorphidae	6	6	4	4	4	4	4	4	4	4	4	4	4	4	2	2	2	2	2	1	1	1
Hippuritida	Monopleuridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Monopteriidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Monotidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	2	3
Myida	Myidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thraciida	Myochamidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Myophorellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Myophoricardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2
Trigoniida	Myophoriidae	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	2	3	4	5
Mytilida	Mysidiellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Mytilida	Mytilidae	2	3	3	3	3	3	5	5	5	5	5	5	5	5	4	5	4	4	6	5	5	5
Pectinida	Neitheidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Neoleptonidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Cardiida	Neomiodontidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Noetiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculanida	Nuculanidae	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	1	1	2	2	2	2
Nuculida	Nuculidae	2	2	4	4	4	4	4	3	3	3	4	4	4	4	4	4	3	3	4	4	6	6
Solenidae	Orthonotidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Ostreidae	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2	2	2	2	2	2	2
Pectinida	Oxytomidae	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	2	2	2	2
Cardiida	Palaeocarditidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Pholadomyida	Pandoridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Parallelodontidae	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	4	3
Pectinida	Pectinidae	0	1	1	1	1	1	1	1	1	1	1	1	1	3	3	3	4	4	6	7	11	11
Ostreida	Pergamidiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Pholadomyida	Periplomatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Permophoridae	0	2	1	1	1	1	1	1	1	2	3	3	5	4	4	2	1	1	1	2	2	2
Cardiida	Petricolina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adapedonta	Pharidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Arcida	Philobryidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Pholadidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Pholadomyidae	0	1	1	2	2	2	3	4	4	4	4	4	3	3	3	3	1	1	2	2	3	3
Ostreida	Pinnidae	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	2	2	2	3
Pectinida	Placunidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Plagioptychidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Pleurodesmatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadida	Pleuromyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
Pectinida	Plicatulidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2
Cardiida	Pollicidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Polyconitidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Poromyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Posidoniidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Cyrtodontida	Praecardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculida	Praenuculidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Propeamussiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2
Trigoniida	Prosogyrotrigoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Pectinida	Prospondylidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	2	1	1
Cardiida	Psammobiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Pseudomonotidae	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pteriida	Pteriidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	2	2	2

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

order	family	Rhaetian	Hettangian	Sinemurian	Pliensbachian	Toarcian	Aalenian	Bajocian	Bathonian	Callovian	Oxfordian	Kimmeridgian	Tithonian	Berriasian	Valanginian	Hauterivian	Barremian	Aptian	Albian	Cenomanian	Turonian	Coniacian	Santonian	Campanian	Maastrichtian
Modiomorphida	Modiomorphidae	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Monopleuridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pteriida	Monopteriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Monotidae	2	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Myidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
Thraciida	Myochamidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Myophorellidae	0	1	1	2	2	2	2	2	2	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0
Carditida	Myophoricardiidae	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Myophoriidae	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mytilida	Mysidiellidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mytilida	Mytilidae	5	5	5	8	9	9	10	10	11	11	11	11	11	10	10	10	12	13	13	13	13	13	13	16
Pectinida	Neitheidae	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Neoleptonidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Neomiodontidae	0	1	2	2	2	2	2	3	3	3	3	3	3	2	2	1	1	2	2	0	0	0	0	0
Arcida	Noetiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculanida	Nuculanidae	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	5
Nuculida	Nuculidae	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6	5	5	5	5	5	5	5
Solenidae	Orthonotidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Ostreidae	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	6	6	8	7	8	9	10
Pectinida	Oxytomidae	2	2	2	3	3	3	3	3	3	3	3	3	3	3	2	2	2	2	2	2	2	2	2	2
Cardiida	Palaeocarditidae	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Pandoridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Parallelodontidae	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4
Pectinida	Pectinidae	11	9	9	9	8	8	10	10	10	10	10	9	9	9	10	10	10	10	8	8	8	8	8	8
Ostreida	Pergamidiidae	2	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Periplomatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
Venerida	Permophoridae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Petricolina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adapedonta	Pharidae	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	3	4	4	5	5	5	5	5
Arcida	Philobryidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Pholadidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	5	5	5	5	6	8
Pholadomyida	Pholadomyidae	4	4	6	6	6	6	6	6	7	5	5	4	4	4	4	4	4	4	4	4	4	4	4	4
Ostreida	Pinnidae	3	3	3	3	3	3	3	4	4	4	4	4	4	3	2	2	2	2	2	2	2	2	2	2
Pectinida	Placunidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Plagioptychidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	3
Myida	Pleurodesmatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadida	Pleuromyidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Pectinida	Plicatulidae	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Cardiida	Pollicidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Hippuritida	Polyconitidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0
Pholadomyida	Poromyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	2	3
Ostreida	Posidoniidae	1	1	2	2	2	1	1	1	1	1	2	1	0	0	0	0	1	1	1	1	1	0	0	0
Cyrtodontida	Praecardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculida	Praenuculidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Propeamussiidae	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Trigoniida	Prosogyrotrigoniidae	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Prospondylidae	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Psammobiidae	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
Pectinida	Pseudomonotidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Pteriida	Pteriidae	2	1	2	3	3	2	3	3	3	3	4	4	2	2	2	3	3	4	3	3	3	3	3	3

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

order	family	Danian	Selandian	Thanetian	Ypresian	Lutetian	Bartonian	Priabonian	Rupelian	Chattian	Aquitanian	Burdigalian	Langhian	Serravallian	Tortonian	Messinian	Zanclean	Piacenzian
Modiomorphida	Modiomorphidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Monopleuridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Monopteriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Monotidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Myidae	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3
Thraciida	Myochamidae	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
Trigoniida	Myophorellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carditida	Myophoricardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Myophoriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mytilida	Mysidiellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mytilida	Mytilidae	16	15	15	16	16	16	18	18	17	16	16	16	15	15	14	15	12
Pectinida	Neitheidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Neoleptonidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Cardiida	Neomiodontidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcida	Noetiidae	0	0	0	1	1	1	1	1	1	1	1	1	2	2	2	2	2
Nuculanida	Nuculanidae	5	5	5	7	6	7	6	6	6	6	6	6	6	5	5	5	5
Nuculida	Nuculidae	4	4	5	4	4	4	4	4	3	3	3	3	3	3	3	3	3
Solenidae	Orthonotidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Ostreidae	8	8	8	8	8	7	8	6	7	7	7	7	8	8	8	8	7
Pectinida	Oxytomidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Palaeocarditidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Pandoridae	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	2
Arcida	Parallelodontidae	3	2	2	2	1	1	1	1	0	0	0	0	0	0	0	0	0
Pectinida	Pectinidae	11	11	11	12	12	14	14	17	17	21	23	24	24	26	24	23	26
Ostreida	Pergamidiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Periplomatidae	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Venerida	Permophoridae	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Cardiida	Petricolina	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	1	1
Adapedonta	Pharidae	3	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3
Arcida	Philobryidae	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0
Myida	Pholadidae	3	3	3	5	5	6	6	6	7	6	7	7	7	7	7	8	6
Pholadomyida	Pholadomyidae	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1
Ostreida	Pinnidae	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Pectinida	Placunidae	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
Hippuritida	Plagioptychidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Pleurodesmatidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pholadida	Pleuromyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Plicatulidae	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Cardiida	Pollicidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Polyconitidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Poromyidae	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1
Ostreida	Posidoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Praecardiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculida	Praenuculidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Propeamussiidae	2	2	2	3	3	3	3	4	4	4	4	4	4	4	3	3	2
Trigoniida	Prosogyrotrigoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Prospondylidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Psammobiidae	1	1	1	1	2	3	3	4	4	4	4	4	4	4	4	4	3
Pectinida	Pseudomonotidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteriida	Pteriidae	4	3	3	3	3	3	3	2	2	2	2	2	2	2	2	2	2

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

order	family	Tremadocian	Floian	Dapingian	Darriwilian	Sandbian	Katian	Hirnantian	Rhuddanian	Aeronian	Telychian	Sheinwoodian	Homerian	Gorstian	Ludfordian	Pridoli	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Ostreida	Pterineidae	0	0	0	0	1	3	2	2	2	3	4	4	5	5	6	6	6	6	6	6	5	5
Pectinida	Pterinopectinidae	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	3	3	3	4	3
Cardiida	Quenstedtiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Radiolitidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Raetomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Requieniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Rhombopteriidae	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
Pholadomyida	Sanguinolitidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculanida	Sareptidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Trigoniida	Scaphellinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Schizodidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
Cardiida	Scrobiculariidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Semelidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Slavidae	0	0	0	0	0	0	0	0	0	1	2	2	2	1	0	0	0	0	0	0	0	0
Venerida	Solecurtidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Solemyida	Solemyidae	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	2	2	2	2	2	2
Adapedonta	Solenidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Sowerbyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Spanilidae	0	0	0	0	0	0	0	0	0	0	0	2	2	2	1	1	0	0	0	0	0	0
Myida	Spheniopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Spondylidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Sportellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Stolidotidae	0	0	0	0	0	0	0	0	0	2	2	2	2	1	1	0	0	0	0	0	0	0
Pectinida	Streblochondriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cardiida	Tancrediidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Tellinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Teredinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Terquemiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Thraciidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lucinida	Thyasiridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculanida	Tindariidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Trapezidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Trigoniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Trigonioididae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Trigonodidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Ungulinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadida	Vacunellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Veneridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Verticordiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Vesicomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Vlastidae	0	0	0	0	1	2	1	1	1	1	1	2	2	2	2	2	0	0	0	0	0	0
Ostreida	Vulsellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

order	family	Tournaisian	Visean	Serpukhovian	Bashkirian	Moscovian	Kasimovian	Gzhelian	Asselian	Sakmarian	Artinskian	Kungurian	Roadian	Wordian	Capitanian	Wuchiapingian	Changhsingian	Induan	Olenekian	Anisian	Ladinian	Carnian	Norian
Ostreida	Pterineidae	4	5	4	3	3	2	2	2	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Pectinida	Pterinopectinidae	3	3	1	1	1	2	2	2	2	2	2	2	3	2	2	2	1	1	1	0	0	0
Cardiida	Quenstedtiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Radiolitidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Raetomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Requieniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Rhombopteriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Sanguinolitidae	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Nuculanida	Sareptidae	1	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	2	2	2	2
Trigoniida	Scaphellinidae	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0
Trigoniida	Schizodidae	1	1	1	1	1	1	2	2	2	2	3	3	3	3	3	2	1	1	1	1	1	1
Cardiida	Scrobiculariidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Semelidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Slavidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Solecurtidae	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Solemyida	Solemyidae	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1
Adapedonta	Solenidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Sowerbyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Spanilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Spheniopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Spondylidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Venerida	Sportellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
Cyrtodontida	Stolidotidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Streblochondriidae	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	1	0	0	0	0	0
Cardiida	Tancrediidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1
Cardiida	Tellinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
Myida	Teredinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Terquemiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Pholadomyida	Thraciidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Lucinida	Thyasiridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculanida	Tindariidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Trapezidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Trigoniidae	0	0	0	0	0	0	1	2	2	2	2	2	2	2	2	2	1	1	1	1	2	5
Trigoniida	Trigonioididae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Trigonodidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	2	2	3	2
Venerida	Ungulinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadida	Vacunellidae	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0
Venerida	Veneridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Verticordiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Vesicomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Vlastidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Vulsellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

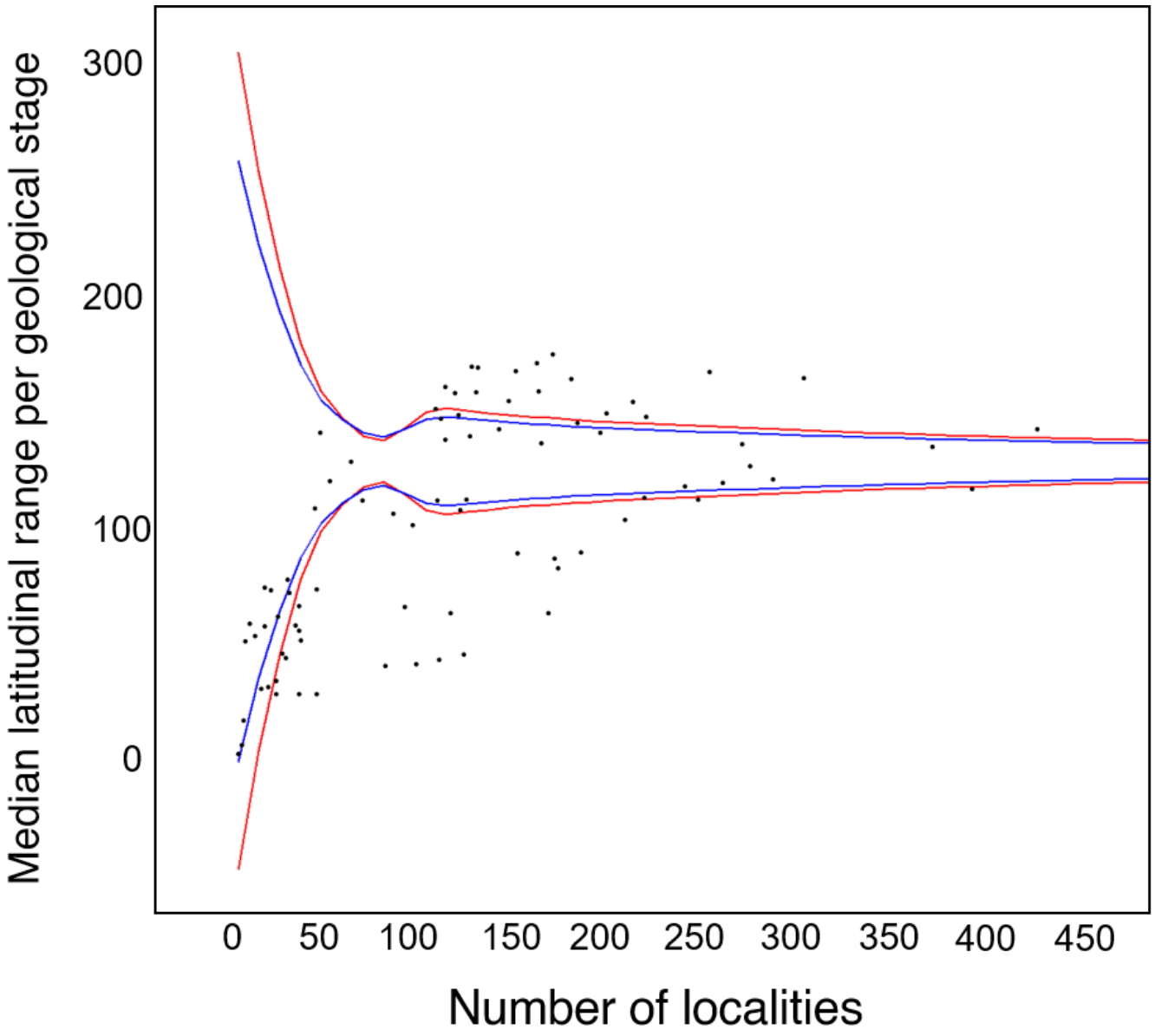
order	family	Rhaetian	Hettangian	Sinemurian	Pliensbachian	Toarcian	Aalenian	Bajocian	Bathonian	Callovian	Oxfordian	Kimmeridgian	Tithonian	Berriasian	Valanginian	Hauterivian	Barremian	Aptian	Albian	Cenomanian	Turonian	Coniacian	Santonian	Campanian	Maastrichtian
Ostreida	Pterineidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Pterinopectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Quenstedtiidae	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Radiolitidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	4	5	7	8	8	11
Myida	Raetomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Requieniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	3	2	1	1	1	1	1
Ostreida	Rhombopteriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Sanguinolitidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculanida	Sareptidae	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	4
Trigoniida	Scaphellinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Schizodidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Scrobiculariidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Semelidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Slavidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Solecurtidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Solemyida	Solemyidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2
Adapedonta	Solenidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Cardiida	Sowerbyidae	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Spanilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Spheniopsidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Spondylidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Venerida	Sportellidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
Cyrtodontida	Stolidotidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Streblochondriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Tancrediidae	1	1	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	2	2	2	2	2	2
Cardiida	Tellinidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	3	5	5	4	4	5	7
Myida	Teredinidae	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	3	3	2	2	2	2	2
Pectinida	Terquemiidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Thraciidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lucinida	Thyasiridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	2
Nuculanida	Tindariidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Venerida	Trapezidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Trigoniidae	4	2	2	2	1	1	3	3	5	3	4	6	7	7	6	6	7	8	5	4	4	4	6	6
Trigoniida	Trigonioididae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1	0	0	0	0	0
Trigoniida	Trigonodidae	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Ungulinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	2	1
Pholadida	Vacunellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Veneridae	0	0	0	0	0	0	0	0	0	0	0	0	1	2	3	3	6	11	18	18	17	17	17	21
Pholadomyida	Verticordiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Cardiida	Vesicomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Vlastidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Vulsellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplementary table B : Occurence matrix of each bivalves family in each stage, used for the evolutionary fauna analysis (continued)

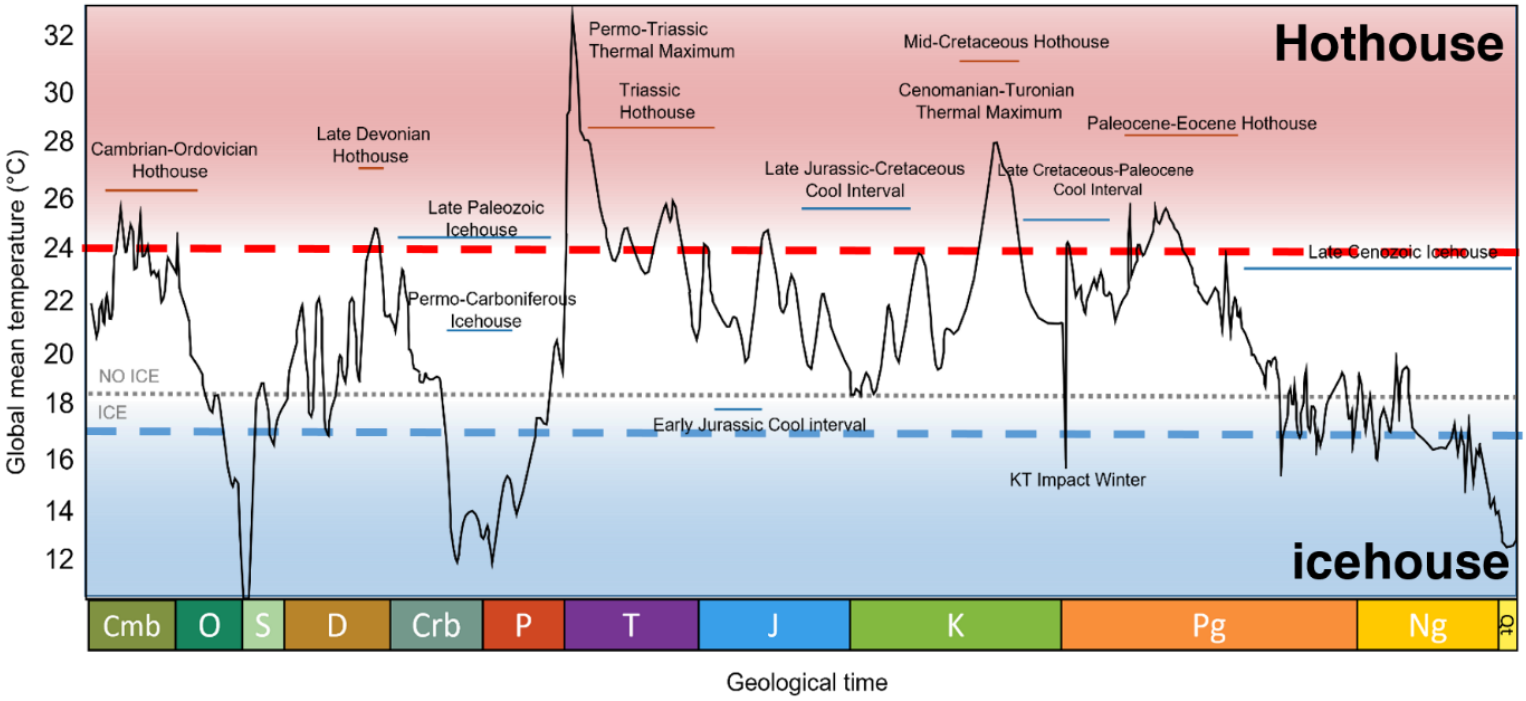
order	family	Danian	Selandian	Thanetian	Ypresian	Lutetian	Bartonian	Priabonian	Rupelian	Chattian	Aquitanian	Burdigalian	Langhian	Serravallian	Tortonian	Messinian	Zanclean	Piacenzian
Ostreida	Pterineidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Pterinopectinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Quenstedtiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hippuritida	Radiolitidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Raetomyidae	0	0	0	2	2	2	2	0	0	0	0	0	0	0	0	0	0
Hippuritida	Requieniidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Rhombopteriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Sanguinolitidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculanida	Sareptidae	4	4	4	4	4	4	4	5	4	4	4	4	4	4	4	4	3
Trigoniida	Scaphellinidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Schizodidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Scrobiculariidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Cardiida	Semelidae	0	0	2	3	3	4	4	4	4	4	4	4	4	4	4	4	5
Cyrtodontida	Slavidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Solecurtidae	1	1	1	1	1	1	2	2	2	3	3	3	3	3	3	3	3
Solemyida	Solemyidae	2	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1
Adapedonta	Solenidae	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Cardiida	Sowerbyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cyrtodontida	Spanilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myida	Spheniopsidae	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0
Pectinida	Spondylidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Venerida	Sportellidae	3	3	3	4	4	4	4	4	4	4	4	3	3	3	3	3	4
Cyrtodontida	Stolidotidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pectinida	Streblochondriidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Tancrediidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiida	Tellinidae	5	4	4	6	5	5	6	6	6	6	9	9	9	10	9	10	9
Myida	Teredinidae	3	3	3	4	3	3	3	3	3	3	3	3	3	3	3	3	2
Pectinida	Terquemiidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomyida	Thraciidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lucinida	Thyasiridae	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	2
Nuculanida	Tindariidae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Venerida	Trapezidae	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1
Trigoniida	Trigoniidae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Trigoniida	Trigonioididae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigoniida	Trigonodidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Ungulinidae	1	1	1	2	2	3	2	3	3	3	3	3	3	3	3	3	3
Pholadida	Vacunellidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Venerida	Veneridae	17	18	18	24	28	30	37	40	40	42	45	46	44	44	44	47	43
Pholadomyida	Verticordiidae	2	1	1	3	3	3	4	3	3	3	3	3	3	3	3	3	3
Cardiida	Vesicomyidae	0	0	0	0	0	0	2	3	2	1	1	1	1	1	1	1	1
Ostreida	Vlastidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ostreida	Vulsellidae	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0

Supplementary table C : Taxonomical correction made in the original database

Taxonomical rank	Initial spelling	Corrections
order	Pholadomyoida	Pholadomyida
order	Myoida	Myida
order	Veneroidea	Venerida
family	Corbiculidae	Cyrenidae
family	Erycinidae	Lasaeidae
family	Kellidae	Lasaeidae
family	Kelliidae	Lasaeidae
family	Leptonidae	Lasaeidae
family	Gaimardiidae	Cymiidae
family	Hippopodiidae	Hippopodiumidae
family	Mactromyidae	Edmondidae
family	Pulvinitinae	Mallaeidae
family	Ptychomyinae	Astaridae
order	Pteroida	Pteriida
order	Pterioida	Pteriida
family	Archanodontidae	Amnigeniidae
family	Costatoriidae	Myophoriidae
family	Crenellidae	Mytilidae
family	Prospondylidea	Prospondylidae
family	Saxicavellidae	Basterotiidae
family	Solenida	Solenidae
family	Thraciida	Thraciidae
family	Turtoniina	Veneridae
family	Zadimerodiidae	Nyassidae
family	Sinodorinae	Schizodidae
family	Montacutidae	Lasaeidae
family	Cultellidae	Pharidae
genus	*Posidoniella*	*Aulacomyella*
genus	*Astartopis*	*Myophoriopis*
genus	*Balabania*	*Colveraia*
genus	*Cardilona*	*Pecchiolia*
genus	*Eodiceras*	*Epidiceras*
genus	*Eriphylopsis*	*Astarte*
genus	*Gemmelarodus*	*Neomegalodon*
genus	*Glycydonta*	*Timoclea*
genus	*Hemicyclonosta*	*Cardilia*
genus	*Hippagus*	*Crenella*
genus	*Inoceramya*	*Inoceramus*
genus	*Isocrassina*	*Astarte*
genus	*Lauberiereia*	*Laubriereia*
genus	*Leinzia*	*Acantholeaia*
genus	*Libitina*	*Trapezium*
genus	*Lithodomina*	*Lithophaginae*
genus	*Lucinopsis*	*Mysia*
genus	*Macrodiceras*	*Diceras*
genus	*Mancosinodia*	*Cordiopsis*
genus	*Megadiceras*	*Epidiceras*
genus	*Monniera*	*Matheronia*
genus	*Neithella*	*Neithea*
genus	*Notirus*	*Irus*
genus	*Paradiceras*	*Epidiceras*
genus	*Parvivenus*	*Timoclea*
genus	*Pholadopsis*	*Jouannetia*
genus	*Potamomya*	*Panamicorbula*
genus	*Praeamonotis*	*Praemonotis*
genus	*Productae*	*Productea*
genus	*Pseudocardita*	*Didacna*
genus	*Recticardo*	*Miltha*
genus	*Rhedensia*	*Vaccinites*
genus	*Semierycina*	*Hemilepton*
genus	*Serrula*	*Donax*
genus	*Solidicorbula*	*Corbula*
genus	*Tivellina*	*Tevelina*
genus	*Trigonella*	*Pachydesma*
genus	*Trigonellites*	*Myophoria*



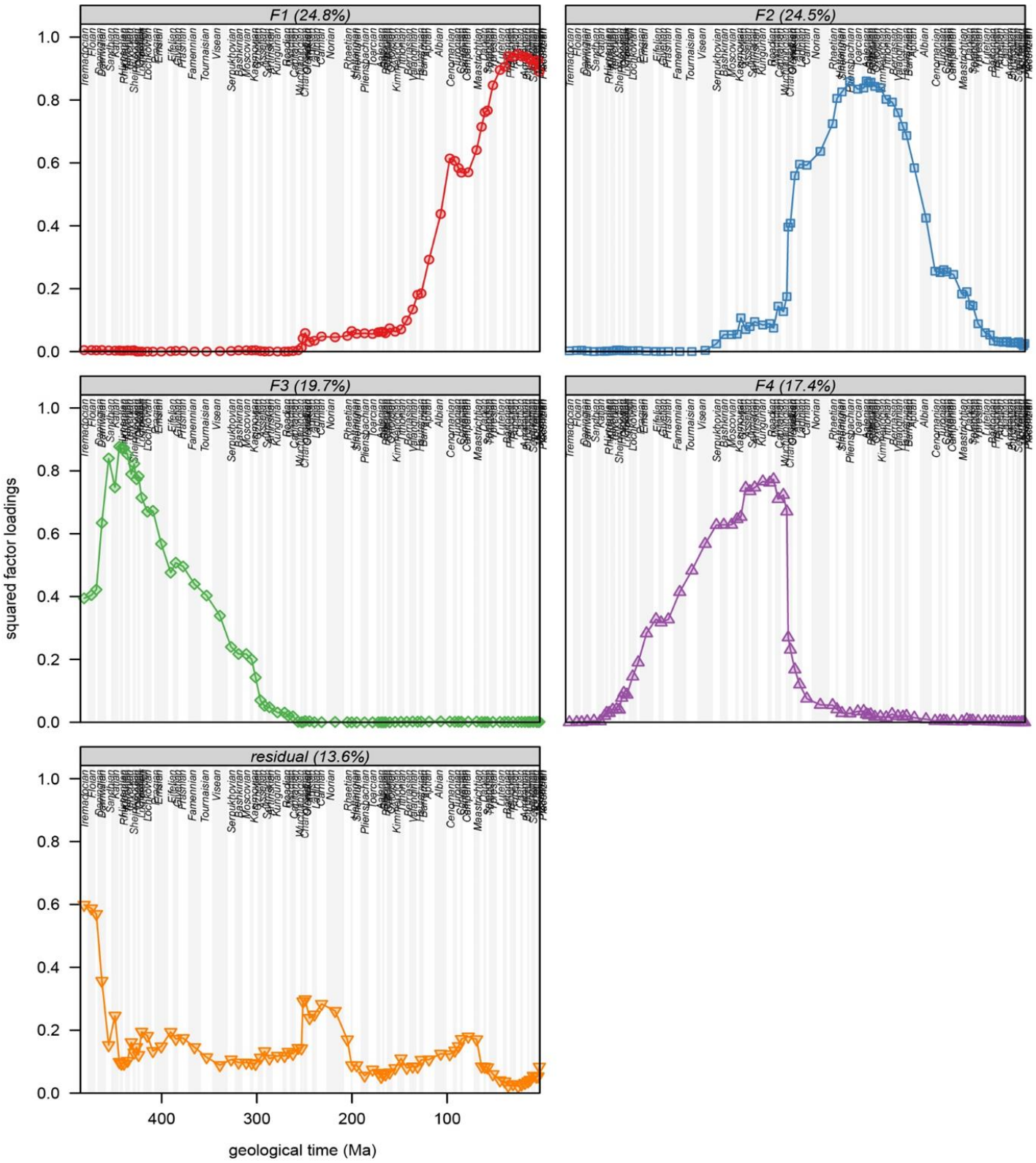
Supplementary figure A : Funnel plot of the median latitudinal range per geological stages and the number of localities. Each dot represent a stage. The constriction around 50 localities indicates the number of localities needed to avoid spatial biasis



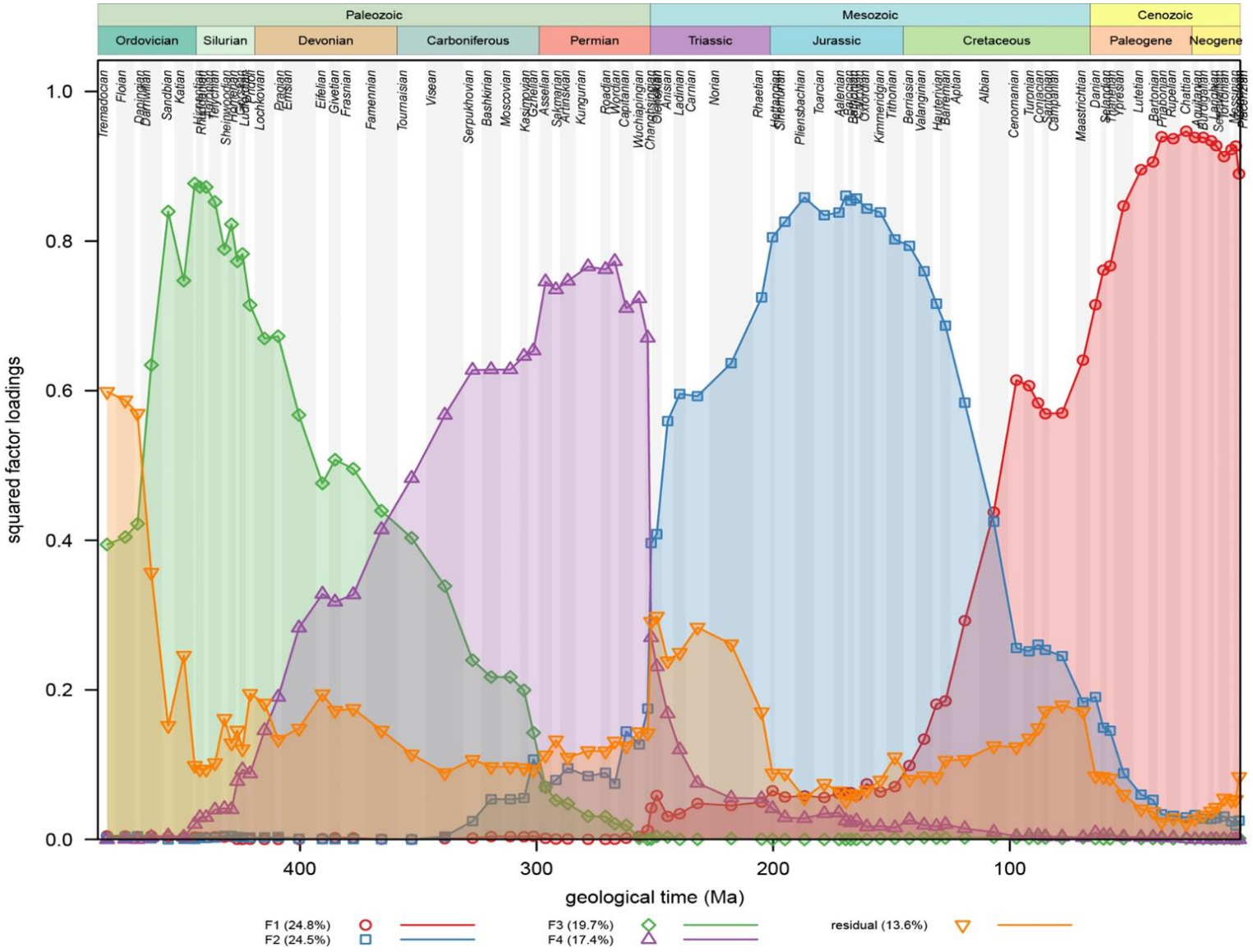
Supplementary figure B : Phanerozoic temperature curve and the definition of hothouse and icehouse (modified from Scotese, 2016)

Supplementary table D : List of major contributing families to each bivalve evolutionary faunas as indicated by their score in the factor analysis.

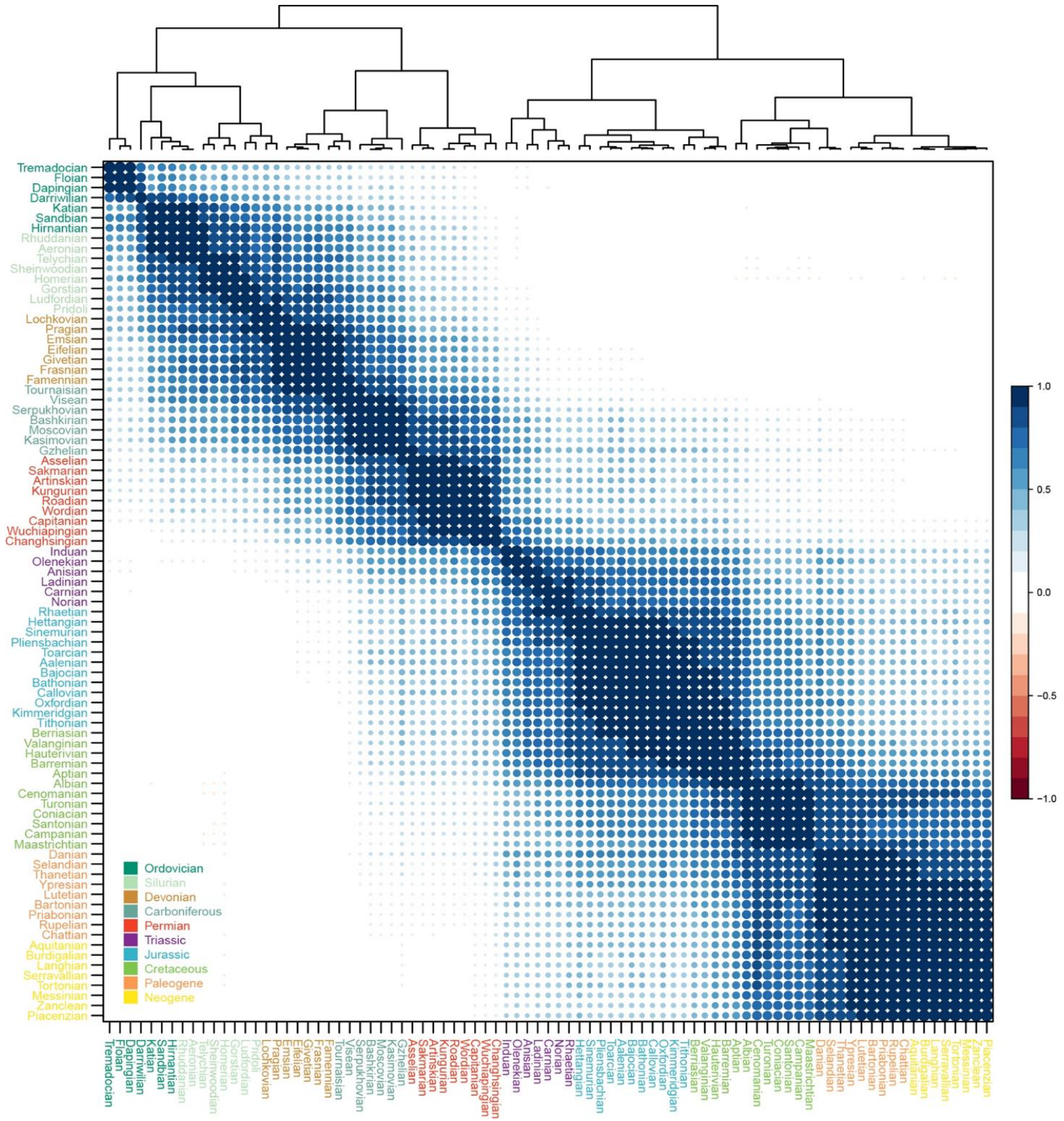
Score	OrDe-BEF	CarPe-BEF	TriJu-BEF	CreNeo-BEF
> 2.0	Modiomorphidae Malletiidae Grammysiidae Ctenodontidae Pterineidae Ambonychiidae Cyrtodontidae Praenuculidae	Grammysidae Deltopectinidae Heteropectinidae Nuculidae Mytilidae Aviculopectinidae Pterinopectinidae Permophorisae Schizodidae Nuculanidae Solemyidae	Limidae Pectinidae Mytilidae Astartidae Pholadomyidae Nuculidae Arctidae Trigoniidae Gryphaeidae Bakevelliidae	Veneridae Lucinidae Cardiidae Mytilidae Pectinidae Carditidae Arcidae
> 1.0	Cardiolariidae Cardiniidae Edmondiidae Vlastidae	Entoliidae Megadesmidae Pterineidae Crassatellidae Sareptidae Pholadomyidae Edmondidae Parallelodontidae Limidae Streblochondriidae Pinnidae Chaenocardiidae	Parallelodontidae Lucinidae Laternulidae Oxytomidae Pinnidae Malletiidae Ceratomyidae Pteriidae Ostreidae	Mactridae Ostreidae Pholadidae Tellinidae Crassatellidae Lasaeidae Corbulidae Gryphaeidae
> 0.5	Orthonotidae Antipleuridae Lipanellidae	Euchondriidae Limipectinidae Modiomorphidae Atomodesmatidae Posidoniidae Cucullaeidae Megalodontidae Solecurtidae Lucinidae Kalenteridae	Malleidae Laevitrigoniidae Plicatulidae Anomiidae Cardiidae Neomiodontidae Nuculanidae Tancrediidae Kalenteridae Edmondiidae Cardiolariidae Propeamussidae	Nuculanidae Psammobiidae Pharidae
> 0.1	Stolidotidae Cardiolidae Lunulacardiidae Spanilidae Slavidae Arcticidae Solemyidae Carydiidae Gryphaeidae Nuculanidae Pholadomyidae	Annuliconchidae Vacunellidae Pteriidae Pseudomonotidae Trigoniidae Myophoriidae Sanguinolitidae Trigonodidae	Myophorellidae Megalodontidae Sareptidae Inoceramidae Pleuromyidae Gastrochaenidae Pharidae Hiatellidae Isoarcidae Mallaeidae Monotidae Spondylidae Thraciidae Manzanellidae Modiomorphidae Pergamidiidae Buchiidae Trigonodidae Teredinidae Pseudomonotidae Cucullaeidae Posidoniidae Semelidae Sareptidae Verticordiidae Propeamussidae Glycymeridae Anomiidae Sportellidae Ungulinidae Flemingostreidae Chamidae Cuspidariidae	Thyasiridae Condylocardiidae Arcticidae Grammysiidae Radiolitidae Periplomatidae Pterineidae Solenidae Kelliellidae Myidae Galeommatidae Pteriidae



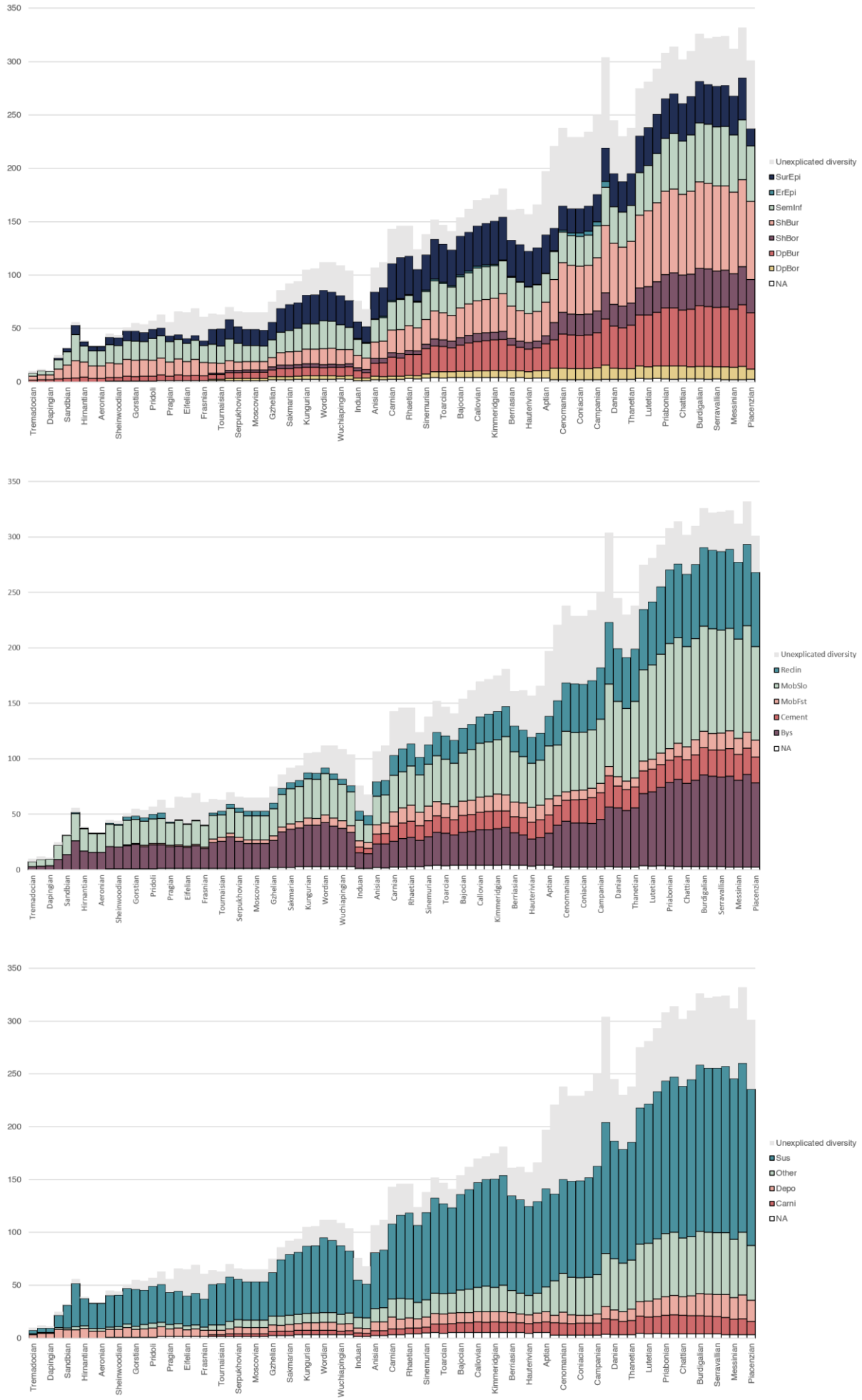
Supplementary figure C : : Loadings of stratigraphic intervals from a four-factor analysis of genus richness within bivalve families



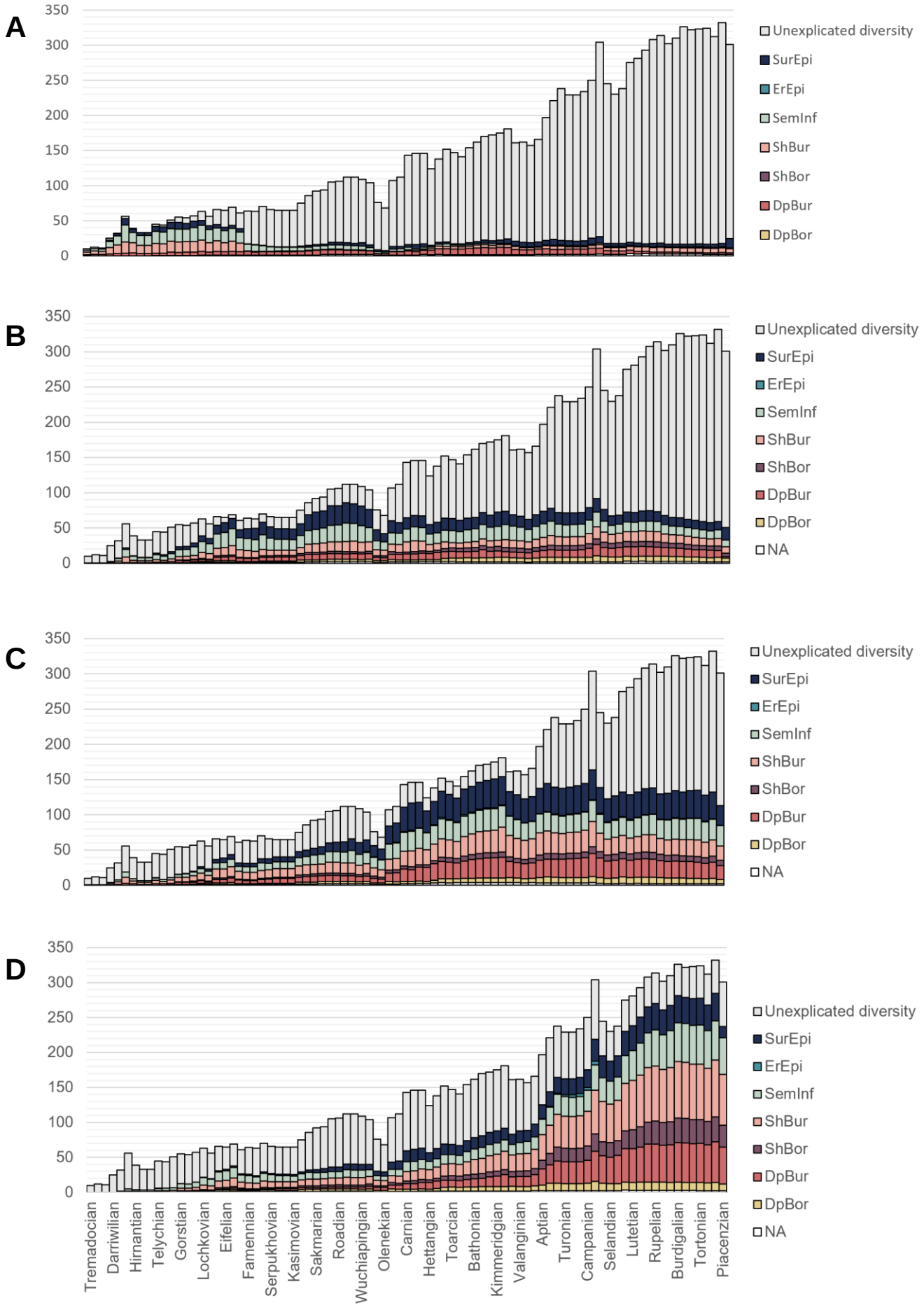
Supplementary figure D : Overlaid loadings of stratigraphic intervals from a four-factor analysis of genus richness within bivalve families.



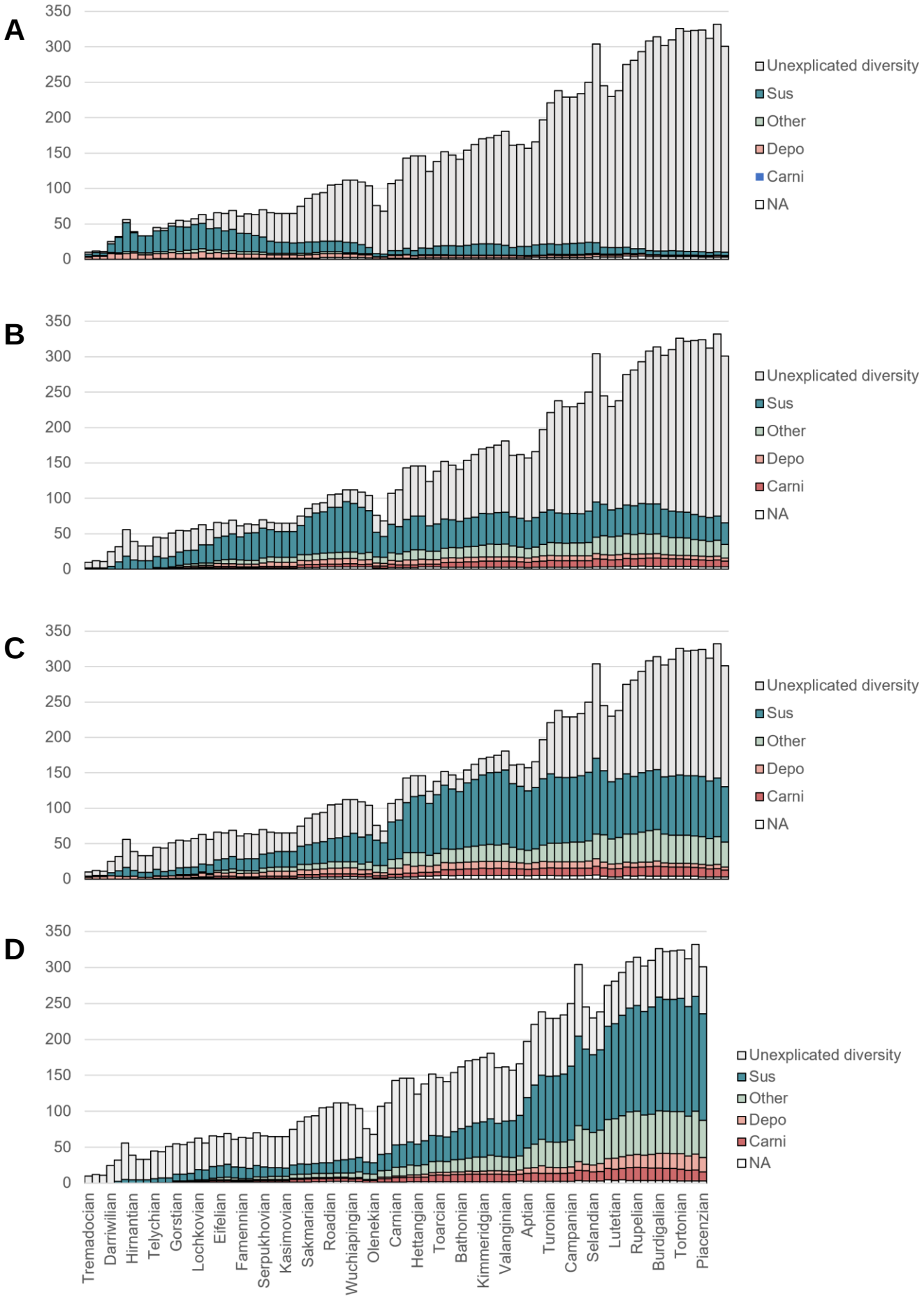
Supplementary figure E : Correlation matrix and hierarchical cluster analysis (Pearson's correlation and complete agglomeration method) on genus richness within bivalve families through geological stages.



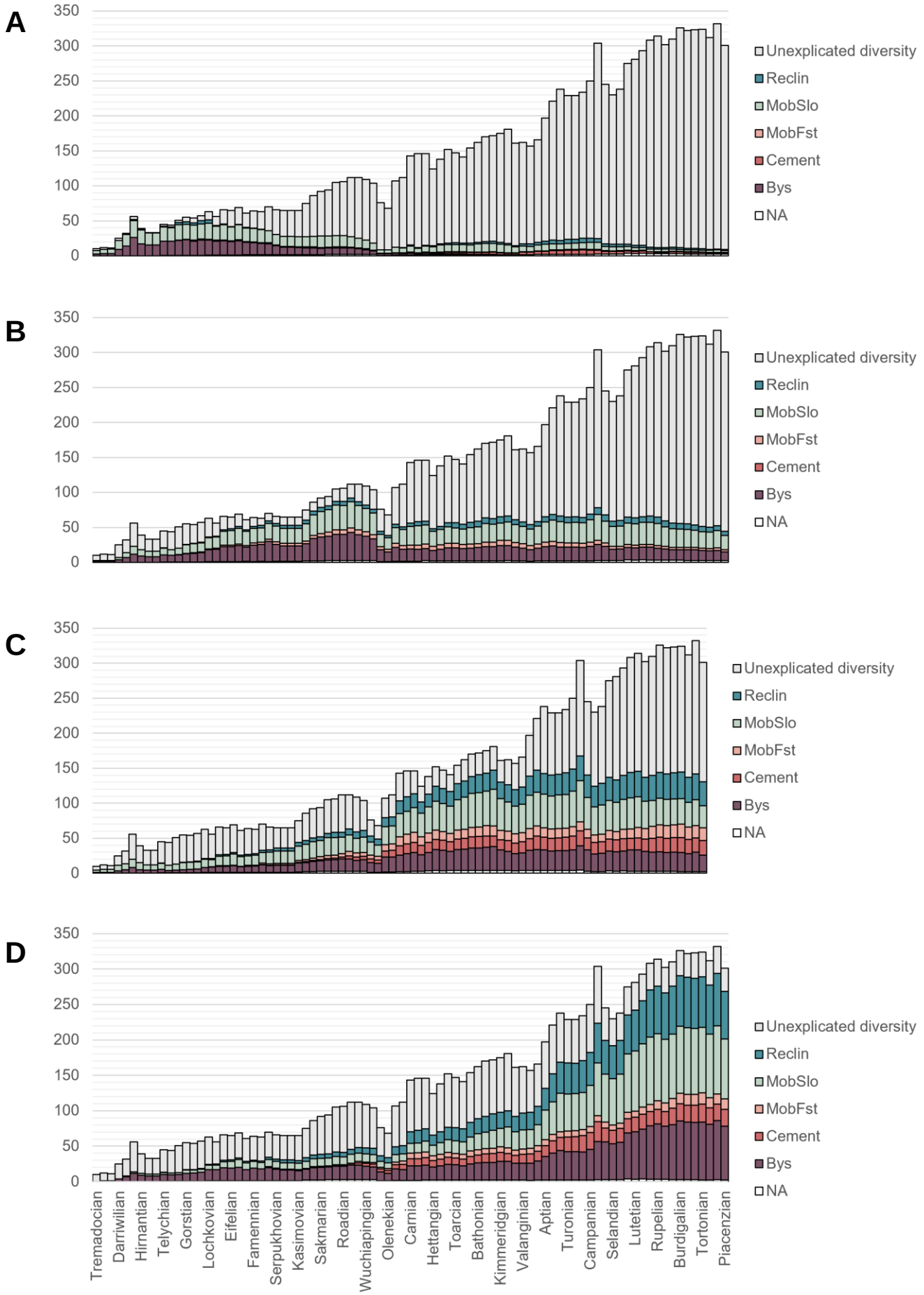
Supplementary figure F : Time series of the proportions of life habits (tiering, feeding, motility) of bivalve genera



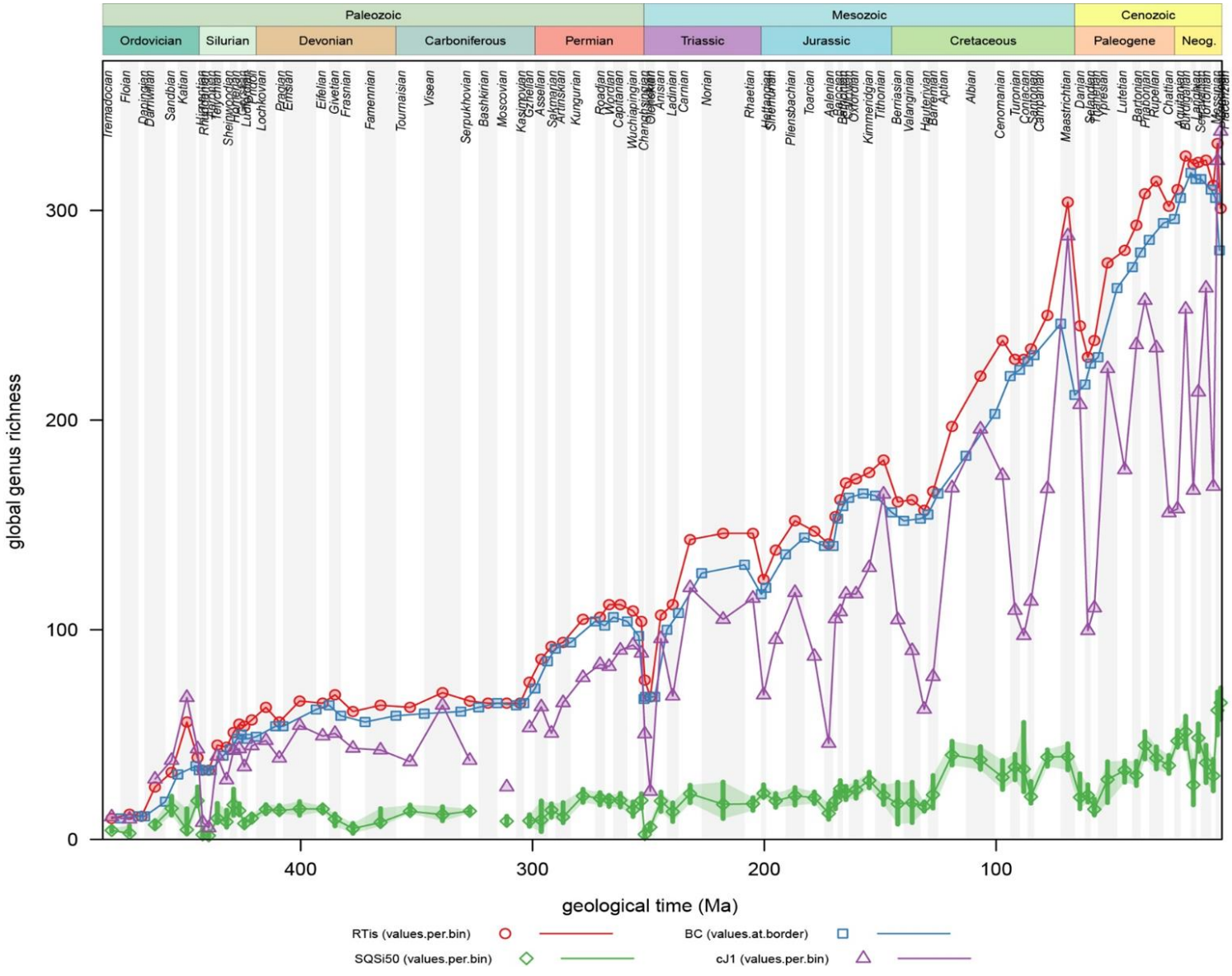
Supplementary figure G : Time series of the proportions of tiering for each BEF; A) OrDe BEF, B) CarPe BEF, C) TriJu BEF, D) CreNeo BEF



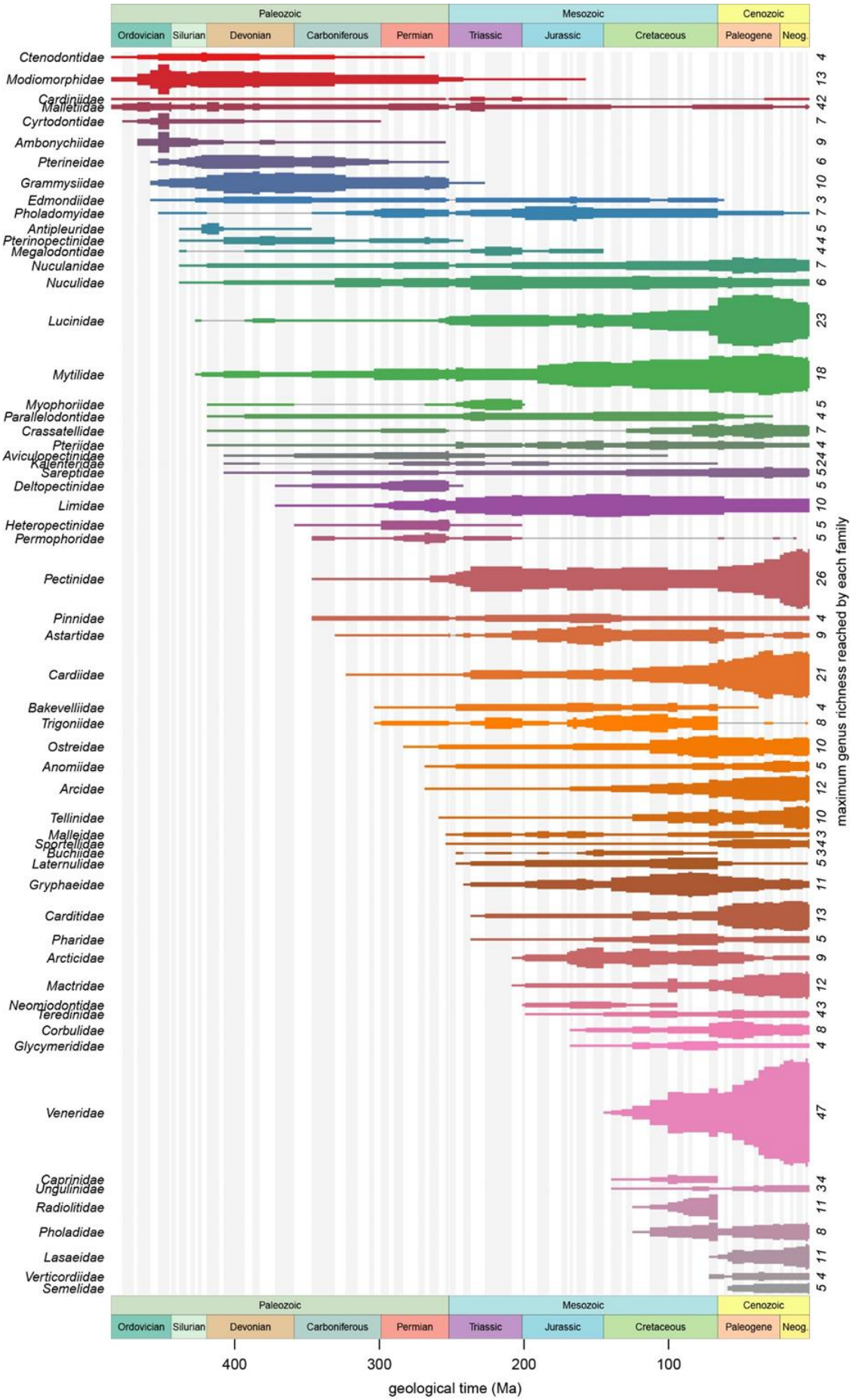
Supplementary figure H : Time series of the proportions of feeding for each BEF ; A) OrDe BEF, B) CarPe BEF, C) TriJu BEF, D) CreNeo BEF



Supplementary figure I : Time series of the proportions of motility for each BEF ; A) OrDe BEF, B) CarPe BEF, C) TriJu BEF, D) CreNeo BEF



Supplementary figure J : Genus richness of all bivalves through the Phanerozoic. Total diversity (RTis) and boundary-crosser diversity (BC) are classical face-value richness metrics; coverage rarefaction (SQS) and corrected first-order jackknife (cJ1) are sample-standardized



Supplementary figure K : Genus diversity through the Phanerozoic of all bivalve families containing at least ten genera (thickness is proportional to genus richness).

Code A : R functions used to make the matrice distance excluding occurences which are less than 10km appart and the function primary created for the latitudinal range of a genus.

Informations needed in the database :

- A column with paleolatitudinal coordinates
- A column with paleolongitudinal coordinates
- A column with the genus
- A column with the stage of each occurences

```
#------------------------------------------------------------------

# function for cleaning db : delete all occurences with distance <
10km

sample_bias_dist <- function(dx, seuil = 10000) {

  dx <- dx[(dx$paleolat >= -90 & dx$paleolat <= 90),]

  keeps <- rep(0, nrow(dx))

  maxdists <- numeric()

  for(s in levels(dx$genus)) {

    for(t in levels(dx$early_interval)) {

      k <- (as.character(dx$genus) == s) &
(as.character(dx$early_interval) == t)

      if(sum(k) > 2) {


        x <- geosphere::distm(dx[k, c("paleolng", "paleolat")])

        p <- max(x, na.rm = TRUE)

        maxdists <- c(maxdists, p)

        if(p > seuil) keeps[k] <- keeps[k] + 1


      }

    }

  }

  dy <- dx[(keeps > 0),]

  return(dy)

}
```

```
#-----------------------------------------------------------------------
# function for the latitudinal range of a genus
ie_minmax <- function(x) {
  if(all(x>=0)) y <- abs(diff((range(x))))
  else if(all(x<0)) y <- abs(diff((range(x))))
  else {
    y <- c(0, max(abs(x)))
  }

  return(y)
}
```

Code B : R program used to perform range size and body size analysis by genus by stage, using spearman correlations.

```
# Loading library
library(geosphere)
library(dplyr)
library(tidyr)
library(ggplot2)
library(palaeoverse)

# Function for applying sampling bias with distance threshold
sample_bias_dist <- function(dx, seuil = 1) {
  dx <- dx[(dx$paleolat >= -90 & dx$paleolat <= 90),]
  keeps <- rep(0, nrow(dx))

  for(s in levels(dx$genus)) {
    for(t in levels(dx$early_interval)) {
      k <- (as.character(dx$genus) == s) &
(as.character(dx$early_interval) == t)
      if(sum(k) > 2) {
        x <- geosphere::distm(dx[k, c("paleolng", "paleolat")])
        if(max(x, na.rm = TRUE) > seuil) keeps[k] <- keeps[k] + 1
      }
    }
  }
  return(dx[(keeps > 0), ])
}

# Function for filtering according to a threshold of occurrences by
gender and by stage
filter_by_occurrences <- function(data, min_occurrences = 1) {
  data %>%
    group_by(early_interval, genus) %>%
    filter(n() >= min_occurrences)
}
```

```
# Define occurrence and distance thresholds
occurences_thresholds <- c(3, 5, 10, 15, 20, 25)  # Exemple de
seuils
distance_thresholds <- c(100, 500, 1000, 3000, 5000, 10000, 15000)
# Exemple de seuils


Bivalves_tot <- read.csv("new_biv.csv", fill = FALSE,
stringsAsFactors = TRUE)


# Recovering unique geological stages
etages_uniques <- unique(Bivalves_tot$early_interval)


# Initialise a list to store results
resultats <- list()


# Loop on each combination of thresholds
for (occurence_seuil in occurences_thresholds) {
  for (distance_seuil in distance_thresholds) {
    cat("Analyse pour seuil d'occurrences :", occurence_seuil,
        "et seuil de distance :", distance_seuil, "\n")


    # Filtering data according to thresholds
    Bivalves_filtre <- Bivalves_tot %>%
      group_by(genus) %>%
      filter(n() >= occurence_seuil) %>%  # Seuil d'occurrences
      ungroup()


    # Apply filtering according to distance threshold using
sample_bias_dist
    Bivalves_filtre <- sample_bias_dist(Bivalves_filtre, seuil =
distance_seuil)


    # Loop on each geological stage
    for (etage in etages_uniques) {
      # Sub-assembly for the current stage
```

```
      subset_stage <- subset(Bivalves_filtre, early_interval ==
etage)


      # Check whether the subset contains sufficient data
      if (nrow(subset_stage) == 0) {
        cat("Pas de données pour l'étage", etage, "avec ce
seuil.\n")
        next
      }


      # Calculate the latitudinal range
      range_lat <- tax_range_space(
        occdf = subset_stage,
        name = "genus",
        lat = "paleolat",
        lng = "paleolng",
        method = "lat"
      )
      names(range_lat)[2] <- "early_interval"
      range_lat$early_interval <- etage
      names(range_lat)[3:5] <- c("max_lat", "min_lat", "range_lat")
      range_lat$early_interval <-
as.character(range_lat$early_interval)


      # Calculate the covexhull
      convex <- tax_range_space(
        occdf = subset_stage,
        name = "genus",
        lat = "paleolat",
        lng = "paleolng",
        method = "con",
        coords = TRUE
      )
      names(convex)[2] <- "early_interval"
      convex$early_interval <- etage
```

```
      names(convex)[3:5] <- c("paleolng", "paleolat", "area")
      convex$early_interval <- as.character(convex$early_interval)

      # Calculate the gcd
      gcd <- tax_range_space(
        occdf = subset_stage,
        name = "genus",
        method = "gcd"
      )
      names(gcd)[2] <- "early_interval"
      gcd$early_interval <- etage
      names(gcd)[3] <- "gcd"
      gcd$early_interval <- as.character(gcd$early_interval)

      # join results
      data_tot <- full_join(range_lat, convex, by = c("taxon",
"early_interval"))
      data_tot <- full_join(data_tot, gcd, by = c("taxon",
"early_interval"))

      # Add threshold information
      data_tot$occurence_seuil <- occurence_seuil
      data_tot$distance_seuil <- distance_seuil

      # Store results
      resultats[[paste(etage, occurence_seuil, distance_seuil, sep =
"_")]] <- data_tot
    }
  }
}

# Combine all the results into a single final dataframe
resultats_final <- bind_rows(resultats)
print(head(resultats_final))
```

```
cat("Nombre total de lignes dans les résultats finaux :",
nrow(resultats_final), "\n")


# Save the results in a CSV file if necessary

write.csv(resultats_final, "resultats_analyse_bivalves.csv",
row.names = FALSE)


range_size <- read.csv("range_log.csv", fill = FALSE,
stringsAsFactors = TRUE)

test_range <- full_join(resultats_final, range_size)


# Load necessary libraries for analysis and plotting

library(ggplot2)

library(dplyr)

library(tidyr)


# Combine the results into one data frame

combined_results <- bind_rows(test_range, .id = "sensitivity_level")


# Create a new column to split the sensitivity_level into
'occurrence_threshold' and 'distance_threshold'

combined_results <- combined_results %>%

  mutate(

    occurences_threshold = as.numeric(sub("occ_(\\d+)_dist_\\d+",
"\\1", sensitivity_level)),

    distance_threshold = as.numeric(sub("occ_\\d+_dist_(\\d+)",
"\\1", sensitivity_level))

  )


# summary statistics

summary_stats <- combined_results %>%

  group_by(occurence_seuil, distance_seuil) %>%

  summarise(

    mean_latitudinal_range = mean(paleolat, na.rm = TRUE),

    median_latitudinal_range = median(paleolat, na.rm = TRUE),

    mean_body_size = mean(logvol, na.rm = TRUE),
```

```
    median_body_size = median(logvol, na.rm = TRUE),
    mean_convex_hull = mean(area, na.rm = TRUE),
    median_convex_hull = median(area, na.rm = TRUE),
    mean_gcd = mean(gcd, na.rm = TRUE),
    median_gcd = median(gcd, na.rm = TRUE)
  )
print(summary_stats)


# 3. Visualize the impact of sensitivity levels on key variables


# 3.1. Plot for Latitudinal Range
mean_latitudinal_range <- ggplot(summary_stats, aes(x =
factor(occurence_seuil), y = mean_latitudinal_range, color =
factor(distance_seuil))) +
  geom_point() +
  geom_line(aes(group = distance_seuil)) +
  labs(
    title = "Impact of Occurrence and Distance Thresholds on
Latitudinal Range",
    x = "Occurrence Threshold",
    y = "Mean Latitudinal Range (degrees)",
    color = "Distance Threshold (m)"
  ) +
  theme_minimal()
ggsave(plot = mean_latitudinal_range, , width = 297, height = 210,
units = "mm", filename = paste0('E:\\Thèse\\Analyses thèse\\Analyse
latitudinal extension_size\\Last but not
least\\mean_latitudinal_range', '.png'))


# 3.2. Plot for Body Size (log volume)
mean_bodysize <- ggplot(summary_stats, aes(x =
factor(occurence_seuil), y = mean_body_size, color =
factor(distance_seuil))) +
  geom_point() +
  geom_line(aes(group = distance_seuil)) +
  labs(
    title = "Impact of Occurrence and Distance Thresholds on Body
Size (log volume)",
```

```
    x = "Occurrence Threshold",
    y = "Mean Body Size (log volume)",
    color = "Distance Threshold (m)"
  ) +
  theme_minimal()
ggsave(plot = mean_bodysize, , width = 297, height = 210, units =
"mm", filename = paste0('E:\\Thèse\\Analyses thèse\\Analyse
latitudinal extension_size\\Last but not least\\mean_bodysize',
'.png'))



# 3.3. Plot for Convex Hull Area
mean_convex_hull <- ggplot(summary_stats, aes(x =
factor(occurence_seuil), y = mean_convex_hull, color =
factor(distance_seuil))) +
  geom_point() +
  geom_line(aes(group = distance_seuil)) +
  labs(
    title = "Impact of Occurrence and Distance Thresholds on Convex
Hull Area",
    x = "Occurrence Threshold",
    y = "Mean Convex Hull Area (km²)",
    color = "Distance Threshold (m)"
  ) +
  theme_minimal()
ggsave(plot = mean_convex_hull, , width = 297, height = 210, units =
"mm", filename = paste0('E:\\Thèse\\Analyses thèse\\Analyse
latitudinal extension_size\\Last but not least\\mean_convex_hull',
'.png'))


# 3.4. Plot for Maximum great circle distance
mean_gcd <- ggplot(summary_stats, aes(x = factor(occurence_seuil), y
= mean_gcd, color = factor(distance_seuil))) +
  geom_point() +
  geom_line(aes(group = distance_seuil)) +
  labs(
    title = "Impact of Occurrence and Distance Thresholds on Maximum
Great Circle",
```

```
    x = "Occurrence Threshold",
    y = "Mean Maximum Great circle distance (km²)",
    color = "Distance Threshold (m)"
  ) +
  theme_minimal()
ggsave(plot = mean_gcd, , width = 297, height = 210, units = "mm",
filename = paste0('E:\\Thèse\\Analyses thèse\\Analyse latitudinal
extension_size\\Last but not least\\mean_gcd', '.png'))



# 3.5. Plot for multiple variables in a faceted plot
ggplot(summary_stats, aes(x = factor(occurence_seuil), y =
mean_latitudinal_range, color = factor(distance_seuil))) +
  geom_point() +
  geom_line(aes(group = distance_seuil)) +
  facet_wrap(~ distance_seuil) +
  labs(
    title = "Impact of Occurrence Threshold on Latitudinal Range by
Distance Threshold",
    x = "Occurrence Threshold",
    y = "Mean Latitudinal Range (degrees)",
    color = "Distance Threshold (m)"
  ) +
  theme_minimal()



ggplot(summary_stats, aes(x = factor(occurence_seuil), y =
mean_body_size, color = factor(distance_seuil))) +
  geom_point() +
  geom_line(aes(group = distance_seuil)) +
  facet_wrap(~ distance_seuil) +
  labs(
    title = "Impact of Occurrence Threshold on Latitudinal Range by
Distance Threshold",
    x = "Occurrence Threshold",
    y = "Mean Latitudinal Range (degrees)",
```

```
    color = "Distance Threshold (m)"
  ) +
  theme_minimal()

#4. Sensitivity testing and formatting of results
# Loading libraries
library(ggplot2)
library(dplyr)
library(car)
library(multcomp)
library(knitr)  # To format tables
library(kableExtra)  # For a better layout

data <- summary_stats

# Convertir le seuil en facteur
data$occurence_seuil <- as.factor(data$occurence_seuil)
data$distance_seuil <- as.factor(data$distance_seuil)

# ANOVA occurence
anova_results <- list(
  "mean_body_size" = aov(mean_body_size ~ occurence_seuil, data =
data),
  "mean_latitudinal_range" = aov(mean_latitudinal_range ~
occurence_seuil, data = data),
  "mean_convex_hull" = aov(mean_convex_hull ~ occurence_seuil, data
= data),
  "mean_gcd" = aov(mean_gcd ~ occurence_seuil, data = data)
)

# Extract results in table form
anova_table <- do.call(rbind, lapply(names(anova_results),
function(var) {
  res <- summary(anova_results[[var]])[[1]]
  data.frame(
    Variable = var,
```

```
    DF_Between = res[1, "Df"],
    DF_Within = res[2, "Df"],
    F_Value = round(res[1, "F value"], 3),
    P_Value = signif(res[1, "Pr(>F)"], 3)
  )
}))

# Verification of homoscedasticity (Levene's test)
levene_results <- do.call(rbind, lapply(names(anova_results),
function(var) {
  res <- leveneTest(as.formula(paste(var, "~ occurence_seuil")),
data = data)
  data.frame(
    Variable = var,
    Levene_F = round(res$`F value`[1], 3),
    Levene_P = signif(res$`Pr(>F)`[1], 3)
  )
}))

# Kruskal-Wallis test if Levene is significant
kruskal_results <- do.call(rbind, lapply(names(anova_results),
function(var) {
  res <- kruskal.test(as.formula(paste(var, "~ occurence_seuil")),
data = data)
  data.frame(
    Variable = var,
    Kruskal_Chi2 = round(res$statistic, 3),
    Kruskal_P = signif(res$p.value, 3)
  )
}))

# Tukey post-hoc test
tukey_results <- do.call(rbind, lapply(names(anova_results),
function(var) {
  tukey_res <- TukeyHSD(anova_results[[var]])$occurence_seuil
```

```
  tukey_df <- data.frame(Comparison = rownames(tukey_res),
tukey_res)

  tukey_df$Variable <- var

  tukey_df

}))


# Display of results in table format

kable(anova_table, caption = "Tableau des résultats de l'ANOVA pour
les seuils d'occurence") %>% kable_styling()

kable(levene_results, caption = "Test de Levene pour l'homogénéité
des variances pour les seuils d'occurence") %>% kable_styling()

kable(kruskal_results, caption = "Test de Kruskal-Wallis (si
nécessaire) pour les seuils d'occurence") %>% kable_styling()

kable(tukey_results, caption = "Test post-hoc de Tukey pour les
seuils d'occurence") %>% kable_styling()


# Export the results

#write.csv(anova_table, "ANOVA_results_occurence.csv", row.names =
FALSE)

#write.csv(levene_results, "Levene_results_occurence.csv", row.names
= FALSE)

#write.csv(kruskal_results, "Kruskal_results_occurence.csv",
row.names = FALSE)

#write.csv(tukey_results, "Tukey_results_occurence.csv", row.names =
FALSE)




# ANOVA distance

anova_results <- list(

  "mean_body_size" = aov(mean_body_size ~ distance_seuil, data =
data),

  "mean_latitudinal_range" = aov(mean_latitudinal_range ~
distance_seuil, data = data),

  "mean_convex_hull" = aov(mean_convex_hull ~ distance_seuil, data =
data),

  "mean_gcd" = aov(mean_gcd ~ distance_seuil, data = data)

)


# Extract results in table form
```

```
anova_table <- do.call(rbind, lapply(names(anova_results),
function(var) {
  res <- summary(anova_results[[var]])[[1]]
  data.frame(
    Variable = var,
    DF_Between = res[1, "Df"],
    DF_Within = res[2, "Df"],
    F_Value = round(res[1, "F value"], 3),
    P_Value = signif(res[1, "Pr(>F)"], 3)
  )
}))


# Verification of homoscedasticity (Levene's test)
levene_results <- do.call(rbind, lapply(names(anova_results),
function(var) {
  res <- leveneTest(as.formula(paste(var, "~ distance_seuil")), data
= data)
  data.frame(
    Variable = var,
    Levene_F = round(res$`F value`[1], 3),
    Levene_P = signif(res$`Pr(>F)`[1], 3)
  )
}))


# Kruskal-Wallis test if Levene is significant
kruskal_results <- do.call(rbind, lapply(names(anova_results),
function(var) {
  res <- kruskal.test(as.formula(paste(var, "~ distance_seuil")),
data = data)
  data.frame(
    Variable = var,
    Kruskal_Chi2 = round(res$statistic, 3),
    Kruskal_P = signif(res$p.value, 3)
  )
}))
```

```
# Tukey post-hoc test

tukey_results <- do.call(rbind, lapply(names(anova_results),
function(var) {

  tukey_res <- TukeyHSD(anova_results[[var]])$distance_seuil

  tukey_df <- data.frame(Comparison = rownames(tukey_res),
tukey_res)

  tukey_df$Variable <- var

  tukey_df

}))


# Display of results in table format

kable(anova_table, caption = "Tableau des résultats de l'ANOVA pour
les seuils de distance") %>% kable_styling()

kable(levene_results, caption = "Test de Levene pour l'homogénéité
des variances pour les seuils de distance") %>% kable_styling()

kable(kruskal_results, caption = "Test de Kruskal-Wallis (si
nécessaire) pour les seuils de distance") %>% kable_styling()

kable(tukey_results, caption = "Test post-hoc de Tukey pour les
seuils de distance") %>% kable_styling()


# Export results

#write.csv(anova_table, "ANOVA_results_distance.csv", row.names =
FALSE)

#write.csv(levene_results, "Levene_results_distance.csv", row.names
= FALSE)

#write.csv(kruskal_results, "Kruskal_results_distance.csv",
row.names = FALSE)

#write.csv(tukey_results, "Tukey_results_distance.csv", row.names =
FALSE)
```

Code C : R program used to perform range size and body size analysis by genus by stage, using spearman correlations.

Arguments:

- bivalves_correct: file in .csv format containing informations extracted from PBDB, with paleocoordinates corrected.
- Temp: file in .csv format containing informations of geological stages ; name, start date, end date, length…
- all_proxies: file in .csv format containing environnemental proxies values for each stage
- biogeographic_connectedness : file in .csv containing previously calculated biogeographic index (see 3.2.3).

Programme outputs:

- A dataframe containing correlations results (rhô, p-value, estimate, confidence intervals) for each pairwise correlation
- A dataframe with the results for each occurences
- A dataframe with the results for each stage

```
#------------------------------------------------------------------------
# Clear memory and graphic devices.
remove(list = ls(all = TRUE, pos = .GlobalEnv), pos = .GlobalEnv)
graphics.off()
while(rgl::rgl.cur()) rgl::rgl.close()

#------------------------------------------------------------------------
library(dplyr)
library(palaeoverse)
library(RVAideMemoire)
library(ggplot2)
library(ggpubr)

#------------------------------------------------------------------------

# Load datasets.

paleotemp <- read.csv("Temp.csv", fill = FALSE, stringsAsFactors =
TRUE)

#stages preparation
stages_fads <- rev(c(
  Actual = 0, Holocene = 0.0117, Uppleisto = 0.126, Chibanian =
0.781, Calabrian = 1.80, Gelasian = 2.58, Piacenzian = 3.600,
Zanclean = 5.333, Messinian = 7.246, Tortonian = 11.63, Serravallian
= 13.82, Langhian = 15.97, Burdigalian = 20.44, Aquitanian = 23.03,
Chattian = 27.82, Rupelian = 33.9, Priabonian = 37.8, Bartonian =
41.2, Lutetian = 47.8, Ypresian = 56.0, Thanetian = 59.2, Selandian
= 61.6, Danian = 66.0, Maastrichtian = 72.1, Campanian = 83.6,
Santonian = 86.3, Coniacian = 89.8, Turonian = 93.9, Cenomanian =
100.5, Albian = 113.0, Aptian = 125.0, Barremian = 129.4,
Hauterivian = 132.9, Valanginian = 139.8, Berriasian = 145.0,
Tithonian = 152.1, Kimmeridgian = 157.3, Oxfordian = 163.5,
Callovian = 166.1, Bathonian = 168.3, Bajocian = 170.3, Aalenian =
174.1, Toarcian = 182.7, Pliensbachian = 190.8, Sinemurian = 199.3,
Hettangian = 201.3, Rhaetian = 208.5, Norian = 227.0, Carnian =
```

```
237.0, Ladinian = 242.0, Anisian = 247.2, Olenekian = 251.2, Induan
= 251.902, Changhsingian = 254.14, Wuchiapingian = 259.1, Capitanian
= 265.1, Wordian = 268.8, Roadian = 272.95, Kungurian = 283.5,
Artinskian = 290.1, Sakmarian = 293.52, Asselian = 298.9, Gzhelian =
303.7, Kasimovian = 307.0, Moscovian = 315.2, Bashkirian = 323.2,
Serpukhovian = 330.9, Visean = 346.7, Tournaisian = 358.9, Famennian
= 372.2, Frasnian = 382.7, Givetian = 387.7, Eifelian = 393.3,
Emsian = 407.6, Pragian = 410.8, Lochkovian = 419.2, Pridoli =
423.0, Ludfordian = 425.6, Gorstian = 427.4, Homerian = 430.5,
Sheinwoodian = 433.4, Telychian = 438.5, Aeronian = 440.8,
Rhuddanian = 443.8, Hirnantian = 445.2, Katian = 453.0, Sandbian =
458.4, Darriwilian = 467.3, Dapingian = 470.0, Floian = 477.7,
Tremadocian = 485.4))
str(stages_fads)
print(head(stages_fads))



# Database loading
Bivalves_tot <- read.csv("bivalves_correct.csv", fill = FALSE,
stringsAsFactors = TRUE)

#-----------------------------------------------------------------------
# Make the midpoint of genus per stage

midpoints <- Bivalves_tot %>%
  group_by(genus, early_interval) %>%
  dplyr:: summarise(
    mean_latitude = abs(mean(paleolat, na.rm = TRUE)),
    mean_longitude = abs(mean(paleolng, na.rm = TRUE)),
    mean_size = mean(logvol, na.rm = TRUE),
    num_occurrences = length(genus)
  )

#join datasets
Bivalves_tot <- full_join(Bivalves_tot, paleotemp)
Bivalves_tot <- full_join(Bivalves_tot, midpoints)

#subset for climatic partitionings (run the code for one
partitioning at a time
#Bivalves_tot <- Bivalves_tot %>% filter(mean_latitude <= 30)
#Bivalves_tot <- Bivalves_tot %>% filter(mean_latitude > 30)
#Bivalves_tot <- Bivalves_tot %>% filter(diff_temp >0)
#Bivalves_tot <- Bivalves_tot %>% filter(diff_temp <0)
#Bivalves_tot <- Bivalves_tot %>% filter(mean_temp >24)
#Bivalves_tot <- Bivalves_tot %>% filter(mean_temp <17)

# Bring all the stages present in the dataset
etages_uniques <- names(which(table(Bivalves_tot$early_interval) >
0))

# Initialization
resultats <- list()

# Stage loop
for (etage in etages_uniques) {
```

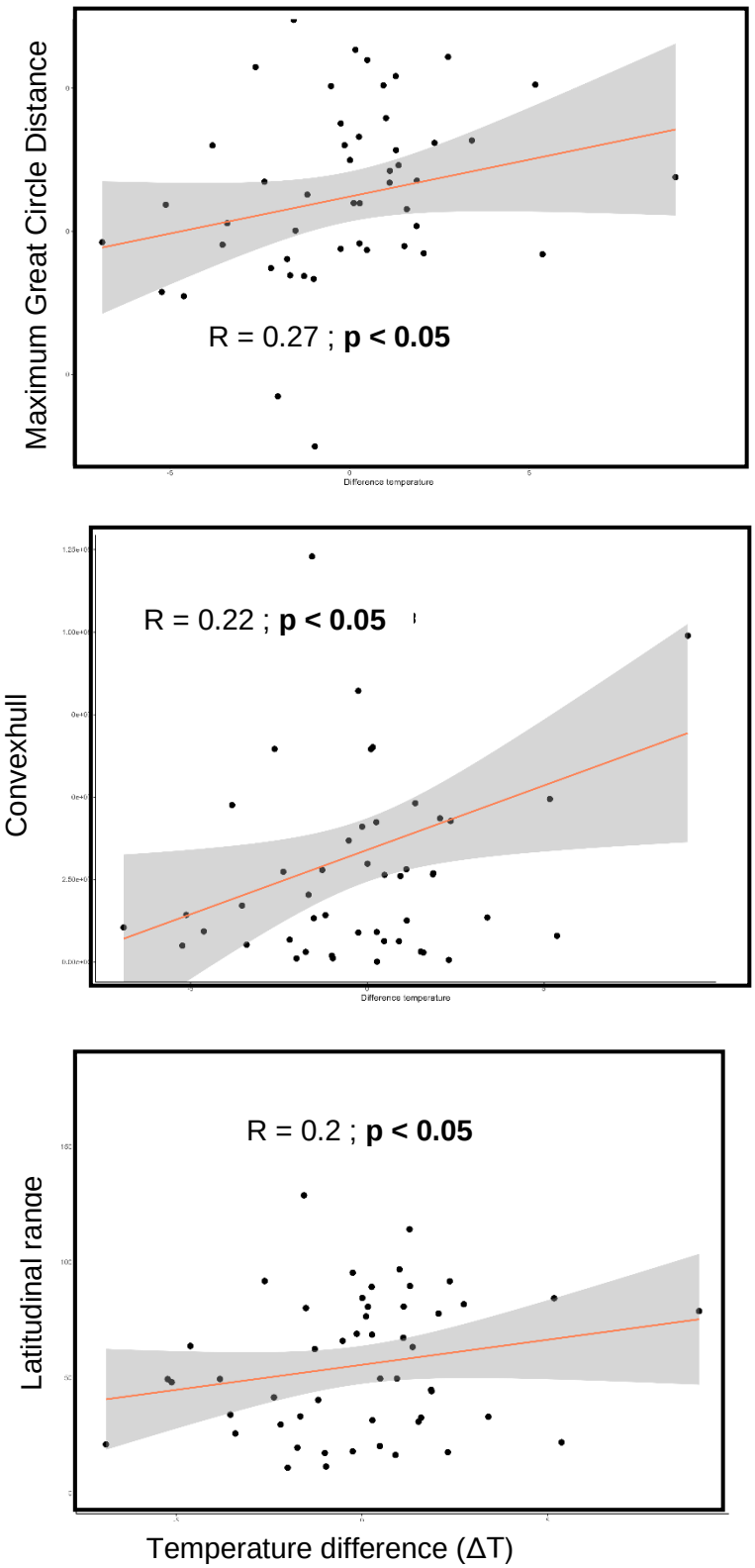
```
  # Actual stage subset
  subset_stage <- subset(Bivalves_tot, early_interval == etage)

  # Check columns
  cat("Columns in the subset_stage", etage, ":",
colnames(subset_stage), "\n")

  # Check column presence if necessary
  required_columns <- c("genus", "paleolat", "paleolng")
  if (!all(required_columns %in% colnames(subset_stage))) {
    warning(paste("Missing column :", etage))
    next  # Passer à l'étage suivant
  }

  # Check if subset is empty
  if (nrow(subset_stage) > 0) {
    # Check vectors length
    if (nrow(subset_stage) <= length(subset_stage$genus)) {
      subset_stage$genus <- subset_stage$genus[1:nrow(subset_stage)]
# Replace with column values
    } else {
      warning("Not enough values.")
    }
  } else {
    warning("Empty subset")
  }

  subset_stage <- subset_stage %>% filter(!is.na(paleolat))

  # Unique values in genus
  unique_taxa <- unique(subset_stage$genus)

  # Create a sequence if unique_taxa is not empty
  if (!is.null(unique_taxa) && length(unique_taxa) > 0) {
    seq_values <- seq(1, length(unique_taxa), by = 1)
    print(seq_values)
  } else {
    warning("unique_taxa est vide ou NULL.")
    next  # Passer à l'étage suivant
  }

  # Calculation (with palaeoverse)
  range_lat <- tax_range_space(occdf = subset_stage, name = "genus",
lat = "paleolat", lng = "paleolng", method = "lat")
  names(range_lat)[2] <- "early_interval"
  range_lat$early_interval <- etage
  names(range_lat)[3] <- "max_lat"
  names(range_lat)[4] <- "min_lat"
  names(range_lat)[5] <- "range_lat"

  convex <- tax_range_space(occdf = subset_stage, name = "genus",
lat = "paleolat", lng = "paleolng", method = "con", coords = TRUE)
  names(convex)[3] <- "paleolng"
  names(convex)[4] <- "paleolat"
  names(convex)[5] <- "area"
```

```
  gcd <- tax_range_space(occdf = subset_stage, name = "genus",
method = "gcd")
  names(gcd)[2] <- "early_interval"
  gcd$early_interval <- etage
  names(gcd)[3] <- "gcd"

  # data_stage <- tax_range_space(occdf = subset_stage, name =
"genus", lat = "paleolat", lng = "paleolng", method = "occ", spacing
= 100)
  # names(data_stage)[2] <- "early_interval"
  # data_stage$early_interval <- etage
  # names(data_stage)[3] <- "n_cells"
  # names(data_stage)[4] <- "proportional_occ"
  # names(data_stage)[5] <- "spacing"

  # Join results dataframes
  # data_tot <- full_join(range_lat, data_stage)
  data_tot <- full_join(range_lat, convex)
  data_tot <- full_join(data_tot, gcd)

  # Stock
  resultats[[etage]] <- data_tot
}

# Combine in one data frame
resultats_combines <- bind_rows(resultats, .id = "early_interval")

# Print results
print(resultats_combines)
databiv <- as.data.frame(resultats_combines)

#-----------------------------------------------------------------------
#Load proxies datasets (environmental + biogeographic connectedness)

allproxies    <-    read.csv("allproxies.csv",    fill    =    FALSE,
stringsAsFactors = TRUE)
range_size    <-    read.csv("range_log.csv",    fill    =    FALSE,
stringsAsFactors = TRUE)
biogeographic_connectedness                                        <-
read.csv("biogeographic_connectedness.csv", sep = ";", fill = FALSE,
stringsAsFactors = TRUE)

test_range <- full_join(databiv, allproxies)
test_range <- full_join(test_range, paleotemp)
test_range <- full_join(test_range, range_size)
test_range <- full_join(test_range, biogeographic_connectedness)

test_range <- test_range[!is.na(test_range[["range_lat"]]),]

# Calculate values per stage

mediane_range_lat <- test_range%>%
  group_by(early_interval)%>%
  summarise_at(vars(range_lat), list(name=median))
names(mediane_range_lat)[2]<-"Latitudinal_range"
```

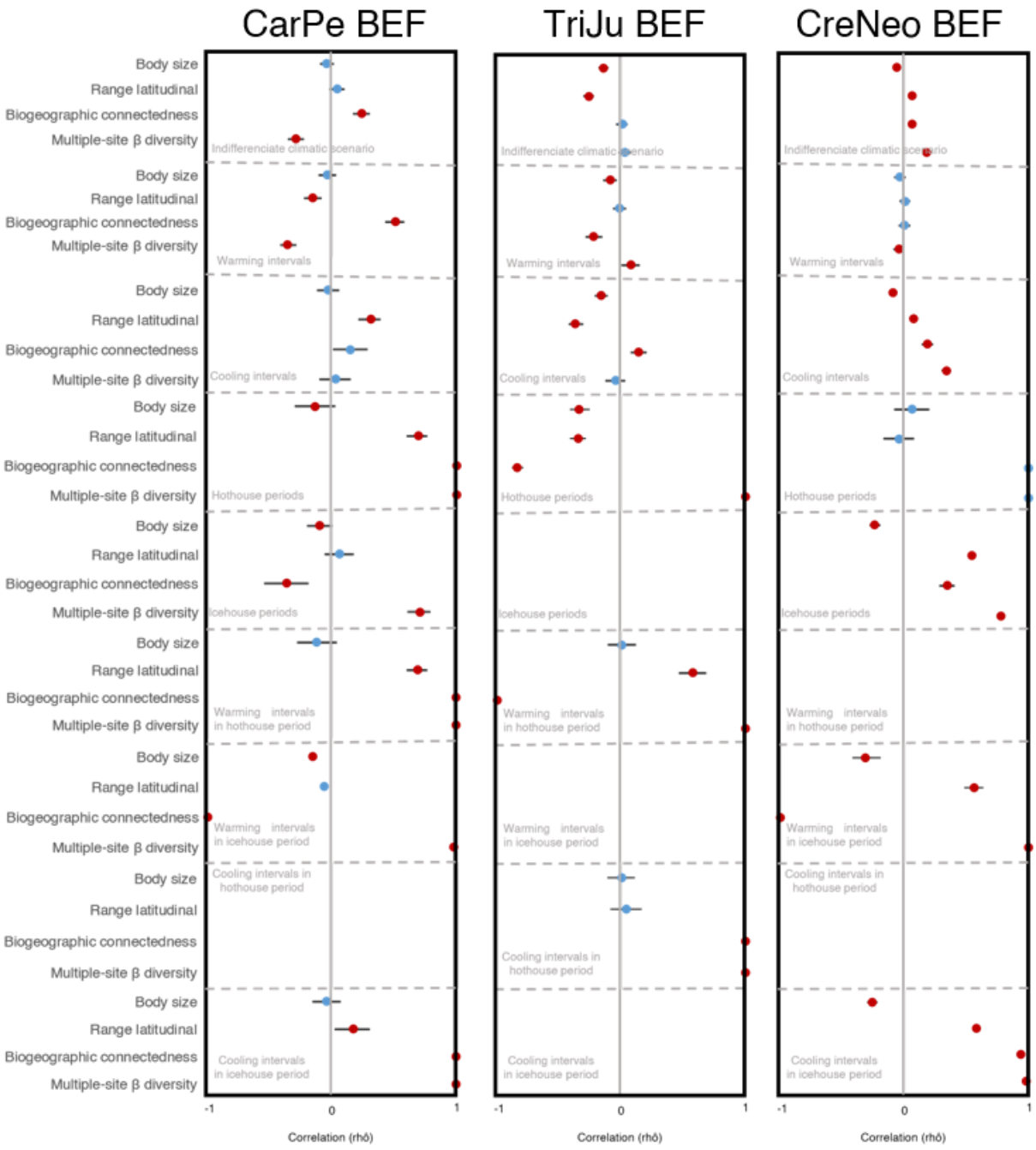
```
mediane_body_size <- test_range%>%
  group_by(early_interval)%>%
  summarise_at(vars(logvol), list(name=median))
names(mediane_body_size)[2]<-"logvol"

mediane_max_greatcircle <- test_range%>%
  group_by(early_interval)%>%
  summarise_at(vars(gcd), list(name=median))
names(mediane_max_greatcircle)[2]<-"maximum_great_circle"

mediane_convex_hull <- test_range%>%
  group_by(early_interval)%>%
  summarise_at(vars(convex_hull), list(name=median))
names(mediane_convex_hull)[2]<-"convex_hull_max"

mediane_tot <- full_join(mediane_range_lat, mediane_body_size)
mediane_tot <- full_join(mediane_tot, mediane_max_greatcircle)
mediane_tot <- full_join(mediane_tot, mediane_convex_hull)
mediane_tot <- full_join(mediane_tot, allproxies)
mediane_tot <- full_join(mediane_tot, paleotemp)
mediane_tot                                                    <-
mediane_tot[!is.na(mediane_tot[["Latitudinal_range"]]),]

mediane_tot <- full_join(mediane_tot, biogeographic_connectedness)

#-----------------------------------------------------------------
#Correlation test (spearman)

# Initialization
resultats_corr <- list()

# Make correlation function
effectuer_correlation <- function(x, y, nom_x, nom_y) {
  test_result <- cor.test(x, y, method = "spearman", exact = FALSE)
  ci_result <- spearman.ci(x, y)

  # ci with 2 values
  ci_lower <- ifelse(length(ci_result) >= 1, ci_result[5], NA)
  ci_upper <- ifelse(length(ci_result) >= 2, ci_result[6], NA)

  return(data.frame(
    Variable1 = nom_x,
    Variable2 = nom_y,
    Correlation = test_result$estimate,
    P_value = test_result$p.value,
    CI_Lower = ci_result[5],
    CI_Upper = ci_result[6]
  ))
}

# Pairwise variables list
paires <- list(
  c("logvol", "temp_scotese"),
  c("range_lat", "temp_scotese"),
  c("convex_hull", "temp_scotese"),
  c("gcd", "temp_scotese"),
```

```
  c("range_lat", "meanBC_tropical"),
  c("convex_hull", "meanBC_tropical"),
  c("gcd", "meanBC_tropical"),
  c("temp_scotese", "meanBC_tropical"),
  c("range_lat", "meanjbeta"),
  c("convex_hull", "meanjbeta"),
  c("gcd", "meanjbeta"),
  c("temp_scotese", "meanjbeta")
)

# Loop for pairwise correlation
for (p in paires) {
  nom_x <- p[1]
  nom_y <- p[2]
  resultat       <-       effectuer_correlation(test_range[[nom_x]],
test_range[[nom_y]], nom_x, nom_y)
  resultats_corr[[length(resultats_corr) + 1]] <- resultat
}

# Dataframe
resultats_final <- do.call(rbind, resultats_corr)
# Print results
print(resultats_final)

#------------------------------------------------------------------------
#calculate difference of range size between stages
calculate_diff_range <- function(test_range) {
  test_range %>%
    group_by(taxon) %>%
    mutate(diff_range = c(NA, diff(range_lat))) %>%
    ungroup()
}

df_result_range <- calculate_diff_range(test_range)

#calculate difference of body size between stages
calculate_diff_size <- function(test_range) {
  test_range %>%
    group_by(taxon) %>%
    mutate(diff_size = c(NA, diff(logvol))) %>%
    ungroup()
}

df_result_size <- calculate_diff_size(test_range)

#join in a dataframe
test_range <- full_join(test_range, df_result_range)
test_range <- full_join(test_range, df_result_size)

test_range <- test_range[!is.na(test_range[["diff_range"]]),]

#calculate % of values in each config
percentage_positive_negative <- test_range %>%
  filter(diff_range > 0 & diff_size < 0) %>%
  nrow() / nrow(test_range) * 100
```

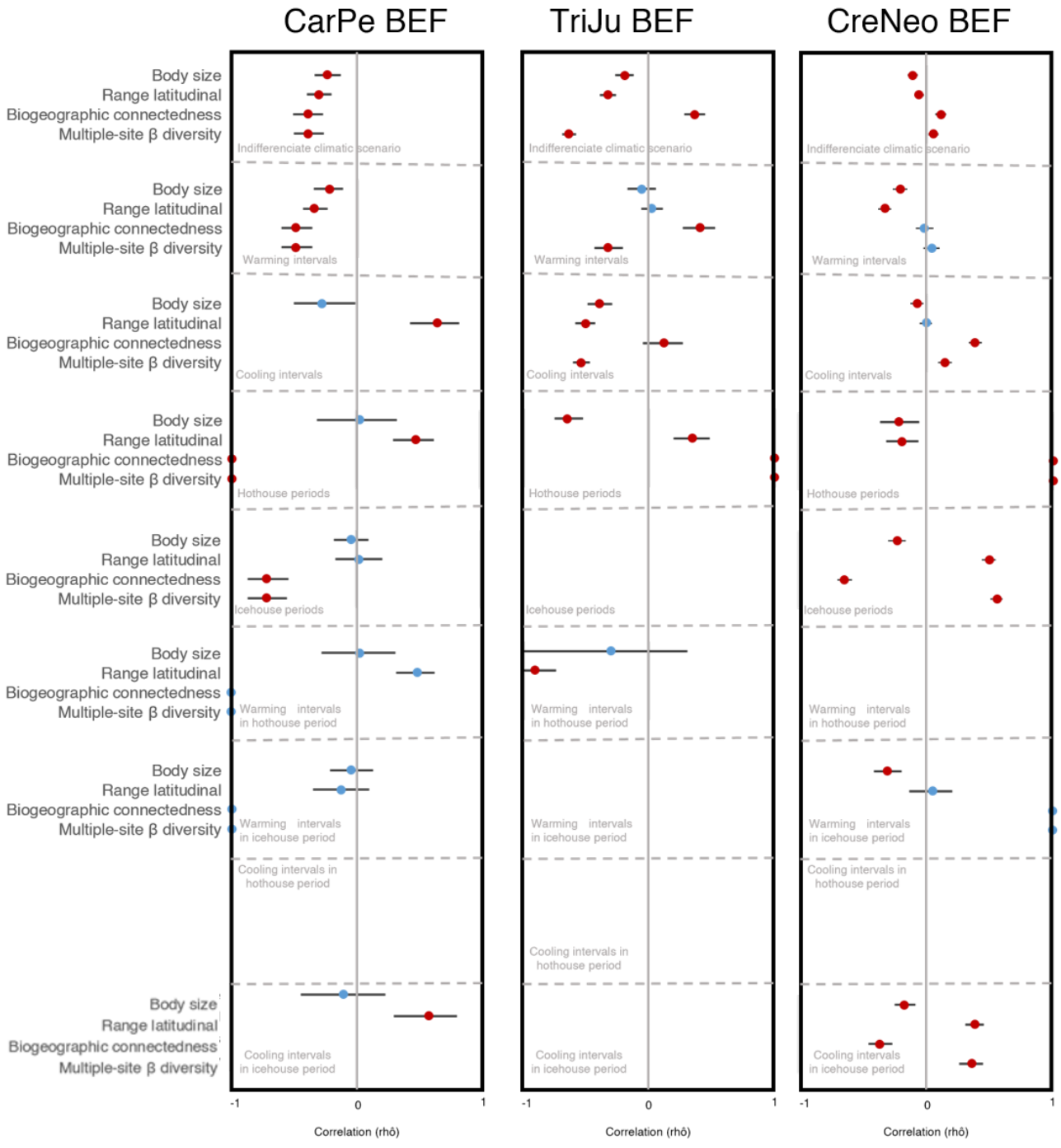
```
percentage_positive_positive <- test_range %>%
  filter(diff_range > 0 & diff_size > 0) %>%
  nrow() / nrow(test_range) * 100

percentage_negative_negative <- test_range %>%
  filter(diff_range < 0 & diff_size < 0) %>%
  nrow() / nrow(test_range) * 100

percentage_negative_positive <- test_range %>%
  filter(diff_range < 0 & diff_size > 0) %>%
  nrow() / nrow(test_range) * 100
```



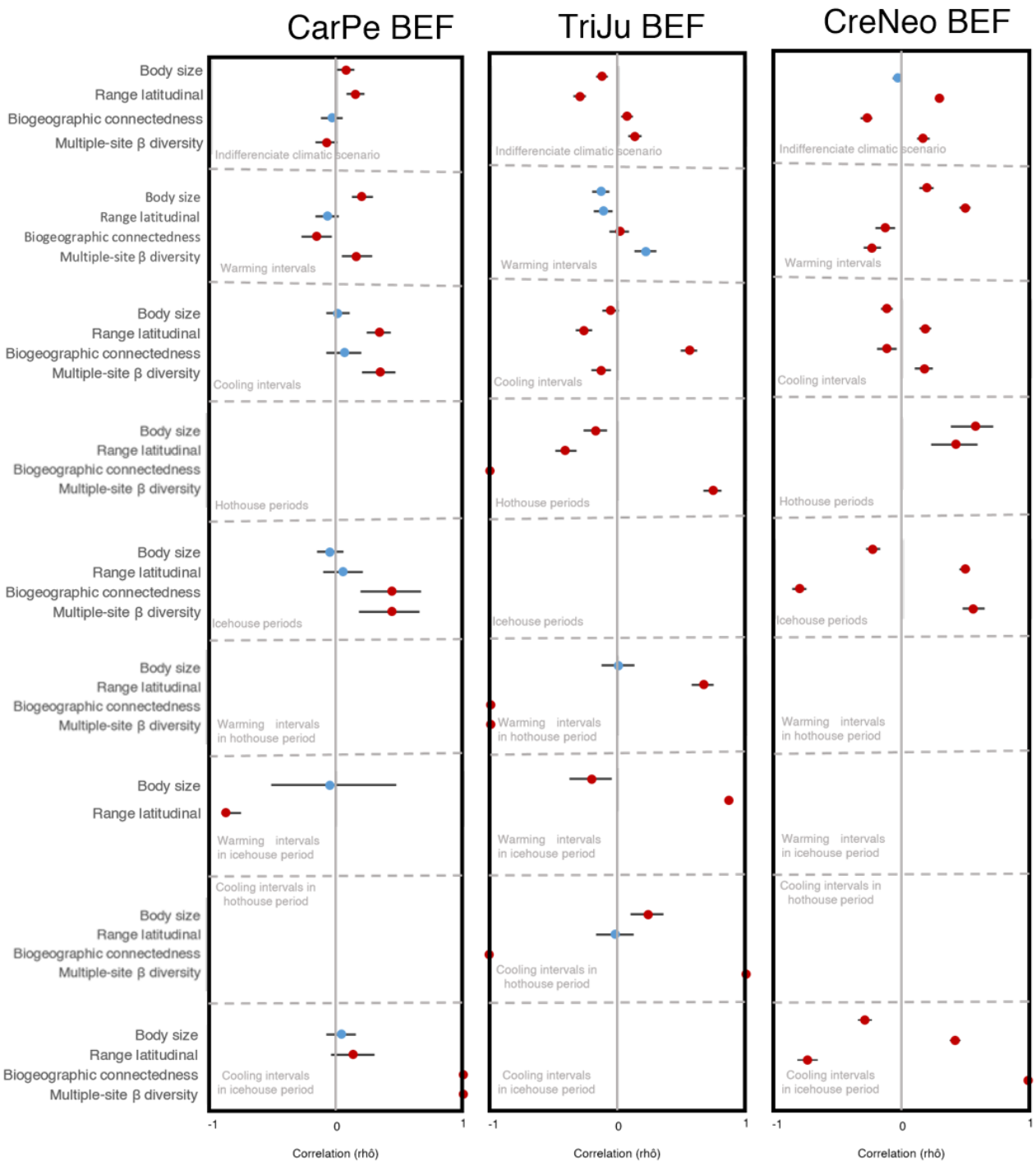
Supplementary figure L: Example of the correlation of the three different geographic range methods with the temperature difference



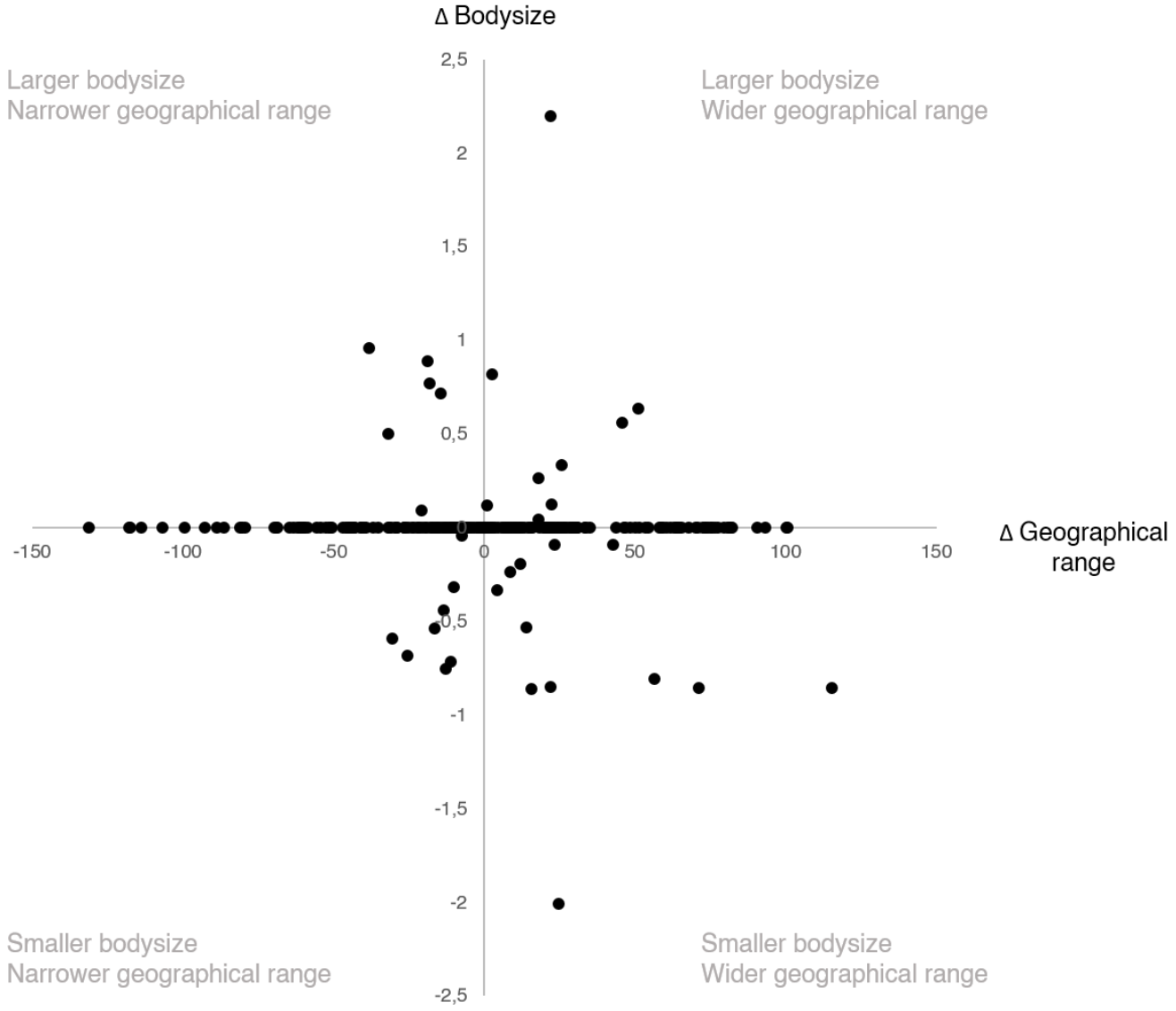
Supplementary figure M : Correlations between morphological and ecological variables of bivalves genus with temperature, for each evolutionary fauna. for all latitudes



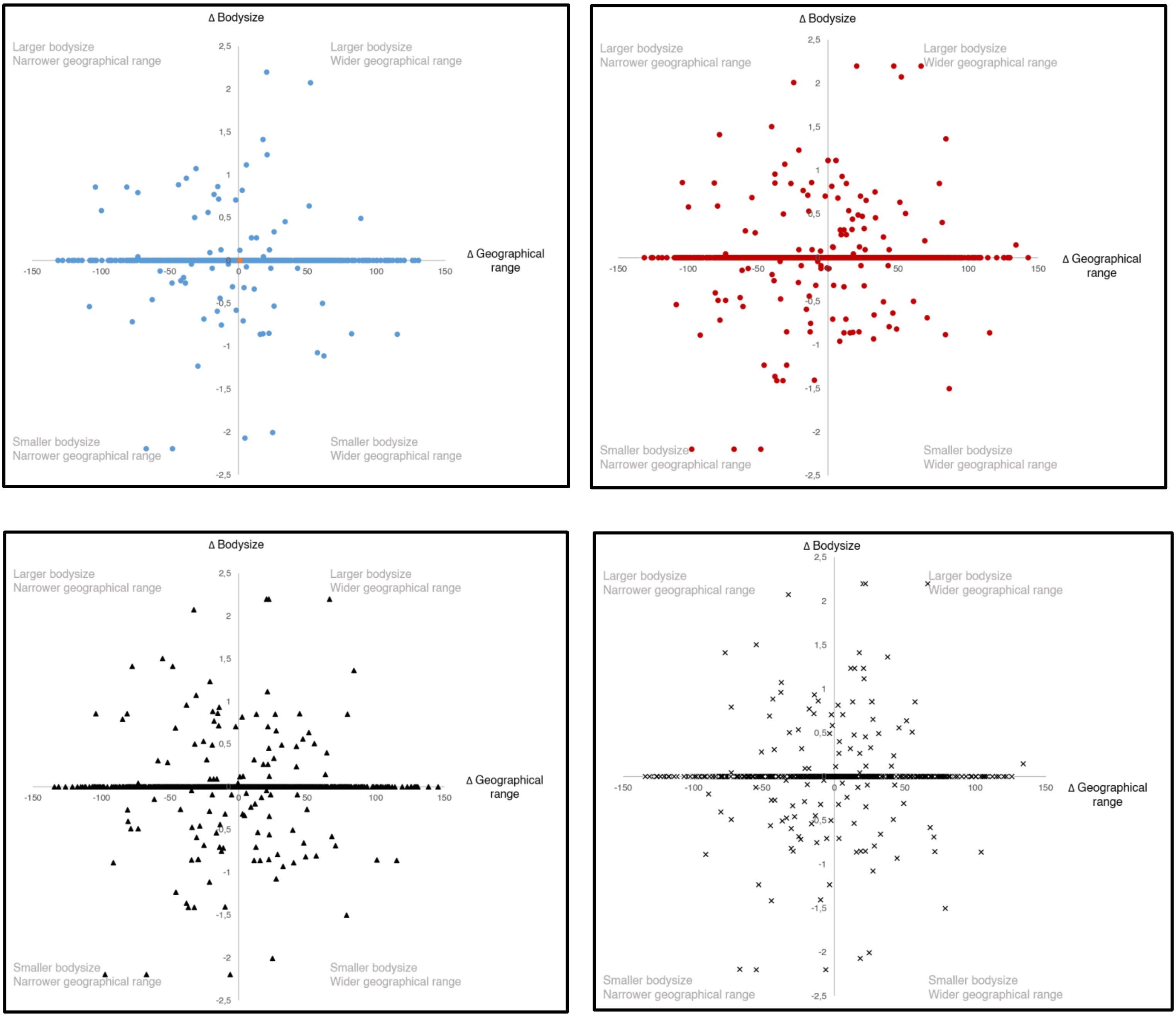
Supplementary figure N: Correlations between morphological and ecological variables of bivalves genus with temperature, for each evolutionary fauna. for non-tropical genera



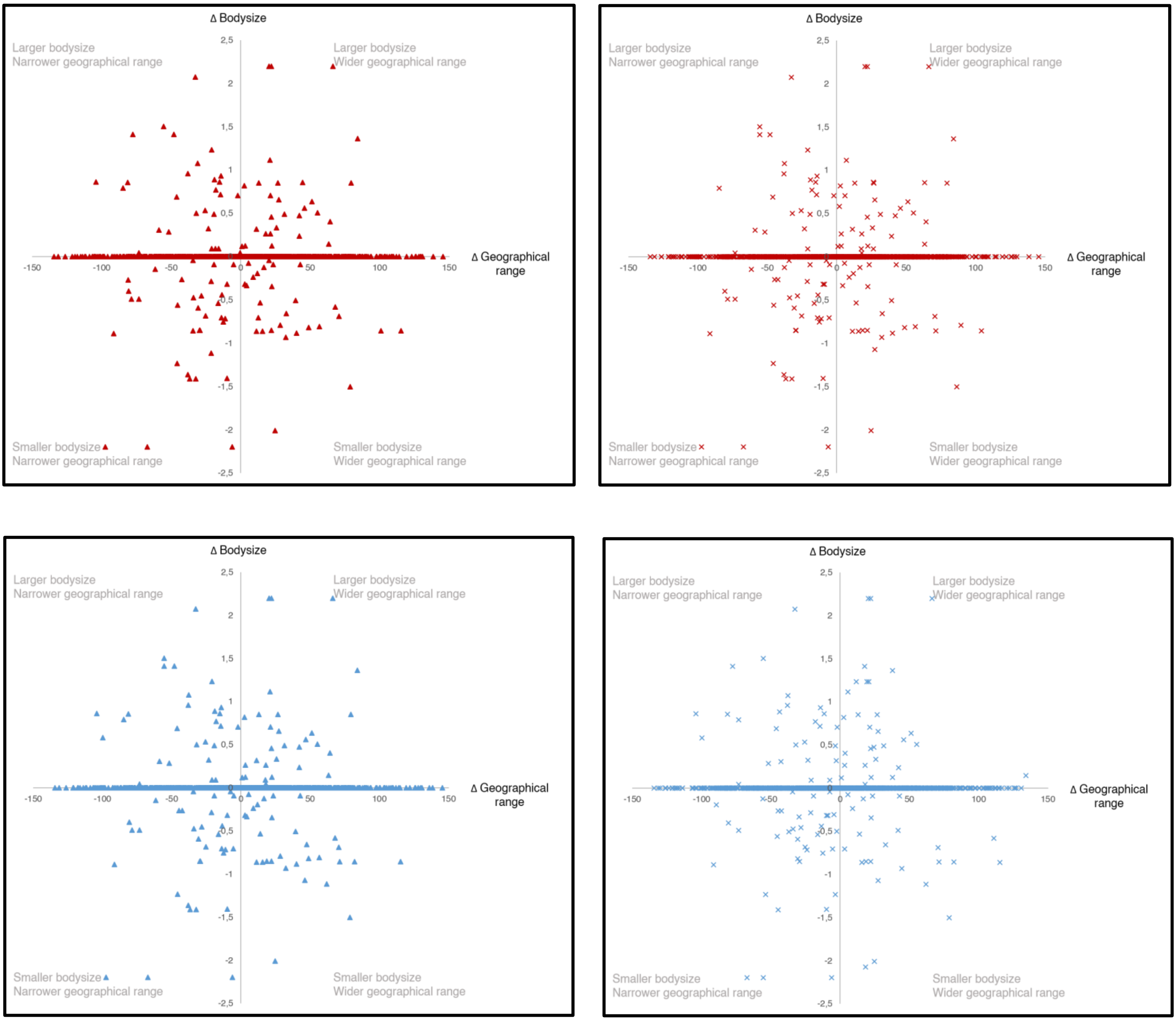
Supplementary figure O: Correlations between morphological and ecological variables of bivalves genus with temperature, for each evolutionary fauna. for tropical genera



Supplementary figure P: Styles of size and geographic cha*nge (''Jablonski's target'') for the und*ifferenciate climate. The vertical axis shows *Δbody size (difference of the body size between two successive time intervals) and the horizontal axis shows Δgeographic range (difference of the geographic range between two successive* time intervals). The right diagonal corresponds to the initial hypothesis.



Supplementary figure Q : Styles of size and geographic cha*nge ("Jablonski's target") for A) cooling intervals B)* warming intervals C) Icehouse periods and D) Hothouse periods. The vertical axis shows *Δ*body size (difference *of the body size between two successive time intervals) and the horizontal axis shows Δgeographic range* (difference of the geographic range between two successive time intervals). The right diagonal corresponds to the initial hypothesis.



Supplementary figure R: Styles of size and geographic change *("Jablonski's target") for A)* warming intervals in icehouse period B) warming intervals in hothouse period C) cooling intervals in Icehouse periods and D) cooling intervals in Hothouse periods. The vertical axis shows *Δ*body size (difference of the body size between two successive time interva

Code D : R code for genus-level analysis of geographic range size and body size testing Bergmann's & Rapoport's rules, incorporating Spearman correlations, sensitivity analysis and spatial autoregressive modelling

Arguments:

- bivalves_correct: file in .csv format containing informations extracted from PBDB, with paleocoordinates corrected.
- paleotemp: file in .csv format containing informations of geological stages ; name, start date, end date, length…
- range : file in .csv format containing range previously calculated for each genus and each stage

Programme outputs:

- A graphical representation of K sensitivity testing for geographic range
- A graphical representation of K sensitivity testing for body size
- Several dataframes containing SAR & GLS results
- A graphical representation of body size and midpoints after data correction by the SAR model
- A graphical representation of geographical range and midpoints after data correction by the SAR model

```
#-----------------------------------------------------------------
# Istall packages if necessary

# install.packages(c("dplyr", "ggplot2", "spatialEco", "spatialreg",
"spdep", "webshot", "webshot2"))


# Load packages

library(dplyr)

library(ggplot2)

library(spatialEco)

library(nlme)

library(spdep)

library(spatialreg)

library(kableExtra)

library(webshot)

library(webshot2)


# Import data

paleotemp <- read.csv("Temp.csv", fill = FALSE, stringsAsFactors =
TRUE)

data <- read.csv("bivalves_correct.csv")

range <- read.csv("range_tot.csv")
```

```
data <- full_join(paleotemp, data)

# Filtering of data according to specified climatic conditions
#data <- data %>% filter(diff_temp >0) #Warming
#data <- data %>% filter(diff_temp <0) #Cooling
#data <- data %>% filter(mean_temp >24) #Hothouse
#data <- data %>% filter(mean_temp <17) #Icehouse

# Calculation of actual geographical midpoints (average latitude and
longitude)
midpoints <- data %>%
  group_by(genus, stage) %>%
  summarise(
    mean_latitude = abs(mean(paleolat, na.rm = TRUE)),
    mean_longitude = abs(mean(paleolng, na.rm = TRUE)),
    mean_size = mean(logvol, na.rm = TRUE),
    num_occurrences = n()
  ) %>%
  #filter(num_occurrences >= 1) #all latitudes
  #filter(mean_latitude > 30) #temperate zone
  #filter(mean_latitude <= 30) #tropical zone

  # Calculating the geographical range
dist_range <- data %>%
  group_by(genus, stage) %>%
  summarise(
    lat_range = max(paleolat, na.rm = TRUE) - min(paleolat, na.rm =
TRUE),
    lon_range = max(paleolng, na.rm = TRUE) - min(paleolng, na.rm =
TRUE),
    total_range = sqrt(lat_range^2 + lon_range^2)
  )

# Merging datasets
```

```
midpoints <- merge(midpoints, dist_range, by = c("genus", "stage"))
midpoints <- na.omit(midpoints)
midpoints <- full_join(midpoints, range)
midpoints <- full_join(midpoints, paleotemp)
midpoints <- na.omit(midpoints)


## K SENSITIVITY ANALYSIS


# Coordinates for spatial analysis
coords <- na.omit(cbind(midpoints$mean_longitude,
midpoints$mean_latitude))


# List of K values to be tested
k_values <- seq(2, 30, by = 1)
results <- data.frame(K = integer(), AICc_Size = numeric(),
AICc_Range = numeric())


# AICc calculation function
calc_aicc <- function(model, n) {
  k <- length(coef(model))  # number of estimated parameters
  aic <- AIC(model)
  aicc <- aic + (2 * k * (k + 1)) / (n - k - 1)
  return(aicc)
}
# Loop on each K
for (k in k_values) {
  cat("Test pour K =", k, "\n")


  # Creation of spatial neighbours
  neighbors <- knn2nb(knearneigh(coords, k = k))
  listw <- nb2listw(neighbors, style = "W")


  # SAR model for body size
  sar_model_size <- lagsarlm(mean_size ~ mean_latitude, data =
midpoints, listw = listw)
```

```
  aicc_size <- calc_aicc(sar_model_size, nrow(midpoints))


  # SAR model for the geographical range
  sar_model_range <- lagsarlm(lat_range ~ mean_latitude, data =
midpoints, listw = listw)
  aicc_range <- calc_aicc(sar_model_range, nrow(midpoints))


  # Storage
  results <- rbind(results, data.frame(K = k, AICc_Size = aicc_size,
AICc_Range = aicc_range))
}


# Best K by cross optimisation
# Addition of an AICc sum column for each K
results <- results %>%
  mutate(AICc_inf30al = AICc_Size + AICc_Range)


# Find the K that minimises the total sum of AICc
best_k_consensus <- results$K[which.min(results$AICc_inf30al)]


cat("K optimal par optimisation croisée (min somme AICc) :",
best_k_consensus, "\n")


# Plot the evolution of AICc as a function of K
k_size <- ggplot(results, aes(x = K)) +
  geom_line(aes(y = AICc_Size, color = "Body Size")) +
  geom_point(aes(y = AICc_Size, color = "Body Size")) +
  scale_color_manual(values = c("Body Size" = "blue", "Geographical
Range" = "red")) +
  theme_minimal() +
  labs(title = "Analyse de sensibilité du paramètre K",
       x = "Nombre de voisins K",
       y = "AICc",
       color = "Modèle")
k_size
```

```
ggsave(plot = k_size, filename = paste0("k_size_inf30", ".png"),
width = 10, height = 6)


k_range <- ggplot(results, aes(x = K)) +
  geom_line(aes(y = AICc_Range, color = "Geographical Range")) +
  geom_point(aes(y = AICc_Range, color = "Geographical Range")) +
  scale_color_manual(values = c("Body Size" = "blue", "Geographical
Range" = "red")) +
  theme_minimal() +
  labs(title = "Analyse de sensibilité du paramètre K",
       x = "Nombre de voisins K",
       y = "AICc",
       color = "Modèle")
k_range
ggsave(plot = k_range, filename = paste0("k_range_inf30", ".png"),
width = 10, height = 6)


## MODEL SAR K-NEAREST NEIGHBOR


# Creation of a matrix of spatial neighbours
coords <- cbind(midpoints$mean_longitude, midpoints$mean_latitude)
coords <- na.omit(cbind(midpoints$mean_longitude,
midpoints$mean_latitude))
optimal_k <- best_k_consensus
neighbors <- knn2nb(knearneigh(coords, k = optimal_k))
listw <- nb2listw(neighbors, style = "W")


# SAR model for bivalve body size
sar_model_size <- lagsarlm(mean_size ~ mean_latitude, data =
midpoints, listw = listw)
summary(sar_model_size)
rho_value_SAR_size <- sar_model_size$rho
p_value_SAR_size <- summary(sar_model_size)$LR1$p.value  # Test du
rapport de vraisemblance pour rho


# SAR model for the geographical range
```

```
sar_model_range <- lagsarlm(range_lat ~ mean_latitude, data =
midpoints, listw = listw)

summary(sar_model_range)

rho_value_SAR_range <- sar_model_range$rho

p_value_SAR_range <- summary(sar_model_range)$LR1$p.value  # Test du
rapport de vraisemblance pour rho


# Add fitted values to the data

midpoints$SAR_fitted_size <- fitted(sar_model_size)

midpoints$SAR_fitted_range <- fitted(sar_model_range)


# Classic linear model for body size

lm_size <- lm(mean_size ~ mean_temp, data = midpoints)


# Classic linear model for the size of the geographical range

lm_range <- lm(range_lat ~ mean_temp, data = midpoints)


results_table <- data.frame(

  Variable = c("Body-size", "Latitudinal range"),

  Coefficient = round(c(coef(sar_model_size)[2],
coef(sar_model_range)[2]), 4),

  Rho = round(c(sar_model_size$rho, sar_model_range$rho), 4),

  P_Value = c(summary(sar_model_size)$LR1$p.value,
summary(sar_model_range)$LR1$p.value),

  AIC_SAR = round(c(AIC(sar_model_size), AIC(sar_model_range)), 2),

  AIC_Linear = round(c(AIC(lm_size), AIC(lm_range)), 2)

)


# Convert p-values to '< 0.05' if significant

results_table$P_Value <- ifelse(results_table$P_Value < 0.05, "p <
0.05", round(results_table$P_Value, 4))


# Display in table form

kable(results_table, caption = "Comparison between SAR & linear
model") %>%

  kable_styling(full_width = FALSE) %>%
```

```
  save_kable("comparaison_modeles_SAR_lm.png", zoom = 2)


# Export to CSV
write.csv(results_table, "SAR_results_inf30.csv", row.names = FALSE)


# Display formatted table
kable(results_table, format = "html", caption = "SAR Model results")
%>%
  kable_styling(full_width = FALSE, bootstrap_options = c("striped",
"hover", "condensed"))%>%
  save_kable("resultats_modeles_sar.png", zoom = 2)


# Extract SAR model results for body size
results_size <- data.frame(
  Paramètre = c("Intercept", "Latitude moyenne", "Rho", "AIC"),
  Coefficient = round(c(coef(sar_model_size)[1],
coef(sar_model_size)[2], sar_model_size$rho, AIC(sar_model_size)),
4),
  Erreur_Standard = c(round(summary(sar_model_size)$Coef[1, 2], 4),
                      round(summary(sar_model_size)$Coef[2, 2], 4),
                      round(summary(sar_model_size)$rho.se, 4), ""),
  Z_Value = c(round(summary(sar_model_size)$Coef[1, 3], 4),
              round(summary(sar_model_size)$Coef[2, 3], 4),
              round(summary(sar_model_size)$Wald1$statistic, 4),
""),
  P_Value = c(summary(sar_model_size)$Coef[1, 4],
              summary(sar_model_size)$Coef[2, 4],
              summary(sar_model_size)$Wald1$p.value, "")
)


# Convert p-values to '< 0.05' if significant
results_size$P_Value <- as.numeric(results_size$P_Value)
results_size$P_Value <- ifelse(results_size$P_Value < 0.05, "p <
0.05", round(results_size$P_Value, 4))


# Export to CSV
```

```
write.csv(results_size, "SAR_results_size.csv", row.names = FALSE)


# Display formatted table
kable(results_size, format = "html", caption = "SAR Model results - Body size") %>%
  kable_styling(full_width = FALSE, bootstrap_options = c("striped", "hover", "condensed"))%>%
  save_kable("resultats_modeles_sar_taille.png", zoom = 2)


# Extraire les résultats du modèle SAR pour l'extension latitudinale
results_range <- data.frame(
  Paramètre = c("Intercept", "Latitude moyenne", "Rho", "AIC"),
  Coefficient = round(c(coef(sar_model_range)[1], coef(sar_model_range)[2], sar_model_range$rho, AIC(sar_model_range)), 4),
  Erreur_Standard = c(round(summary(sar_model_range)$Coef[1, 2], 4),
                      round(summary(sar_model_range)$Coef[2, 2], 4),
                      round(summary(sar_model_range)$rho.se, 4), ""),
  Z_Value = c(round(summary(sar_model_range)$Coef[1, 3], 4),
              round(summary(sar_model_range)$Coef[2, 3], 4),
              round(summary(sar_model_range)$Wald1$statistic, 4), ""),
  P_Value = c(summary(sar_model_range)$Coef[1, 4],
              summary(sar_model_range)$Coef[2, 4],
              summary(sar_model_range)$Wald1$p.value, "")
)


# Convert p-values to '< 0.05' if significant
results_range$P_Value <- as.numeric(results_range$P_Value)
results_range$P_Value <- ifelse(results_range$P_Value < 0.05, "p < 0.05", round(results_range$P_Value, 4))


# Export to CSV
write.csv(results_range, "SAR_results_range_inf30.csv", row.names = FALSE)
```

```
# Display formatted table

kable(results_range, format = "html", caption = "SAR Model results - Latitudinal range") %>%

  kable_styling(full_width = FALSE, bootstrap_options = c("striped", "hover", "condensed"))%>%

  save_kable("resultats_modeles_sar_range.png", zoom = 2)


##VISUALISATION


# Scatterplot for body size vs latitude

spearman_corr_size <- cor.test(midpoints$mean_latitude, midpoints$SAR_fitted_size, method = "spearman")


# Extract rho & p-value

rho_size <- spearman_corr_size$estimate  # coefficient de corrélation Spearman

p_val_spearman_size <- spearman_corr_size$p.value  # p-value


# Create annotation text with condition on p-value

p_val_label_size <- ifelse(p_val_spearman_size < 0.05, "p < 0.05", paste0("p = ", signif(p_val_spearman_size, 3)))


# Plotting

Fitted_size <- ggplot(midpoints, aes(x = mean_latitude, y = SAR_fitted_size)) +

  geom_point(alpha = 0.6, size = 3, color = "lightblue") +  # Points

  geom_smooth(method = "lm", se = FALSE, color = "red", linetype = "dashed") +  # Ligne de régression

  annotate("text", x = Inf, y = Inf,

           label = paste0("rho = ", signif(rho_size, 3), "\n", p_val_label_size),

           hjust = 1.1, vjust = 1.5, size = 3, fontface = "italic") +  # Affichage du rho et p-value

  theme_classic() +

  labs(x = "Mean Latitude (°)",

       y = "Body size (cm)") +

  theme(axis.title = element_text(size = 12))
```

```
Fitted_size

ggsave(plot = Fitted_size, filename =
paste0("Bergmann_fitted_inf30", ".png"), width = 10, height = 6)


# Scatterplot for geographic range size vs latitude

# Calculation of Spearman correlation

spearman_corr_range <- cor.test(midpoints$mean_latitude,
midpoints$SAR_fitted_range, method = "spearman")


# Extract rho & p-value

rho_range <- spearman_corr_range$estimate  # coefficient de
corrélation Spearman

p_val_spearman_range <- spearman_corr_range$p.value  # p-value


# Create annotation text with condition on p-value

p_val_label_range <- ifelse(p_val_spearman_range < 0.05, "p < 0.05",
paste0("p = ", signif(p_val_spearman_range, 3)))


# Plotting

Fitted_range <- ggplot(midpoints, aes(x = mean_latitude, y =
SAR_fitted_range)) +

  geom_point(alpha = 0.6, size = 3, color = "lightgreen") +  #
Points

  geom_smooth(method = "lm", se = FALSE, color = "red", linetype =
"dashed") +  # Ligne de régression

  annotate("text", x = Inf, y = Inf,

           label = paste0("rho = ", signif(rho_range, 3), "\n",
p_val_label_range),

           hjust = 1.1, vjust = 1.5, size = 3, fontface = "italic")
+  # Affichage du rho et p-value

  theme_classic() +

  labs(x = "Mean Latitude (°)",

       y = "Geographic range size (km)") +

  theme(axis.title = element_text(size = 12))


Fitted_range

ggsave(plot = Fitted_range, filename =
paste0("Rapoport_fitted_inf30", ".png"), width = 10, height = 6)
```

All latitudes

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	2.6254	0.4099	p < 0.05	3548.93	3578.12
Latitudinal range	28.7972	0.6573	p < 0.05	11550.18	11724.81

Tropical zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	2.8464	0.3172	p < 0.05	2169.70	2195.91
Latitudinal range	29.2756	0.6293	p < 0.05	6882.64	6945.67

Temperate zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	3.4746	0.2849	p < 0.05	1379.85	1380.68
Latitudinal range	22.1786	0.4886	p < 0.05	4661.42	4689.90

Supplementary figure S : Comparison of Spatial Autoregressive (SAR) and Linear Models for body size and latitudinal range in bivalve genera for the undifferenciate partitioning

All latitudes

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	4.4744	0.0050	0.9522	1659.43	1662.31
Latitudinal range	37.7024	0.5479	p < 0.05	5320.74	5438.94

Tropical zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	4.5257	-0.0914	0.4051	1053.53	1070.08
Latitudinal range	31.7933	0.5381	p < 0.05	3322.72	3366.24

Temperate zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	6.5897	-0.2123	0.1836	591.98	593.13
Latitudinal range	44.1749	0.4818	p < 0.05	1998.53	2002.61

Supplementary figure T : Comparison of Spatial Autoregressive (SAR) and Linear Models for body size and latitudinal range in bivalve genera for the warming partitioning

All latitudes

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	2.7020	0.3867	p < 0.05	1901.21	1915.94
Latitudinal range	39.2854	0.5078	p < 0.05	6218.86	6284.83

Tropical zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	2.7679	0.3476	p < 0.05	1123.34	1126.54
Latitudinal range	38.8836	0.4871	p < 0.05	3549.72	3538.93

Temperate zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	2.6089	0.410	p < 0.05	783.73	792.65
Latitudinal range	6.9705	0.438	p < 0.05	2660.37	2662.40

Supplementary figure U : Comparison of Spatial Autoregressive (SAR) and Linear Models for body size and latitudinal range in bivalve genera for the cooling partitioning

All latitudes

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	5.5996	-0.1874	0.0921	287.80	287.03
Latitudinal range	64.6099	0.2254	p < 0.05	940.31	955.10

Tropical zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	8.1615	-0.7451	0.2872	198.19	196.02
Latitudinal range	209.5631	-1.8108	p < 0.05	587.86	598.83

Temperate zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	35.6391	-6.2266	p < 0.05	80.46	91.51
Latitudinal range	275.4312	-4.8081	p < 0.05	348.97	351.53

Supplementary figure V : Comparison of Spatial Autoregressive (SAR) and Linear Models for body size and latitudinal range in bivalve genera for the hothouse partitioning

All latitudes

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	3.9581	0.1450	0.2635	836.36	834.93
Latitudinal range	48.1323	0.5594	p < 0.05	2724.61	2807.95

Tropical zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	2.3107	0.4441	p < 0.05	476.68	479.23
Latitudinal range	33.3027	0.6866	p < 0.05	1525.71	1552.73

Temperate zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	4.0660	0.1012	0.3986	357.63	356.37
Latitudinal range	40.0848	0.4044	p < 0.05	1198.31	1212.56

Supplementary figure W : Comparison of Spatial Autoregressive (SAR) and Linear Models for body size and latitudinal range in bivalve genera for the icehouse partitioning

All latitudes

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	2.6254	0.4099	p < 0.05	3548.93	3578.12
Latitudinal range	28.7972	0.6573	p < 0.05	11550.18	11724.81

Tropical zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	2.8464	0.3172	p < 0.05	2169.70	2195.91
Latitudinal range	29.2756	0.6293	p < 0.05	6882.64	6945.67

Temperate zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	3.4746	0.2849	p < 0.05	1379.85	1380.68
Latitudinal range	22.1786	0.4886	p < 0.05	4661.42	4689.90

Supplementary figure X : Summary of Spatial Autoregressive (SAR) model results for body size and latitudinal range in bivalves for the undifferenciate partitioning

All latitudes

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	4.4744	0.0050	0.9522	1659.43	1662.31
Latitudinal range	37.7024	0.5479	p < 0.05	5320.74	5438.94

Tropical zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	4.5257	-0.0914	0.4051	1053.53	1070.08
Latitudinal range	31.7933	0.5381	p < 0.05	3322.72	3366.24

Temperate zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	6.5897	-0.2123	0.1836	591.98	593.13
Latitudinal range	44.1749	0.4818	p < 0.05	1998.53	2002.61

Supplementary figure Y: Summary of Spatial Autoregressive (SAR) model results for body size and latitudinal range in bivalves for the warming partitioning

All latitudes

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	2.7020	0.3867	p < 0.05	1901.21	1915.94
Latitudinal range	39.2854	0.5078	p < 0.05	6218.86	6284.83

Tropical zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	2.7679	0.3476	p < 0.05	1123.34	1126.54
Latitudinal range	38.8836	0.4871	p < 0.05	3549.72	3538.93

Temperate zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	2.6089	0.410	p < 0.05	783.73	792.65
Latitudinal range	6.9705	0.438	p < 0.05	2660.37	2662.40

Supplementary figure 1 : Summary of Spatial Autoregressive (SAR) model results for body size and latitudinal range in bivalves for the cooling partitioning

All latitudes

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	5.5996	-0.1874	0.0921	287.80	287.03
Latitudinal range	64.6099	0.2254	p < 0.05	940.31	955.10

Tropical zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	8.1615	-0.7451	0.2872	198.19	196.02
Latitudinal range	209.5631	-1.8108	p < 0.05	587.86	598.83

Temperate zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	35.6391	-6.2266	p < 0.05	80.46	91.51
Latitudinal range	275.4312	-4.8081	p < 0.05	348.97	351.53

Supplementary figure AA : Summary of Spatial Autoregressive (SAR) model results for body size and latitudinal range in bivalves for the hothouse partitioning

All latitudes

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	3.9581	0.1450	0.2635	836.36	834.93
Latitudinal range	48.1323	0.5594	p < 0.05	2724.61	2807.95

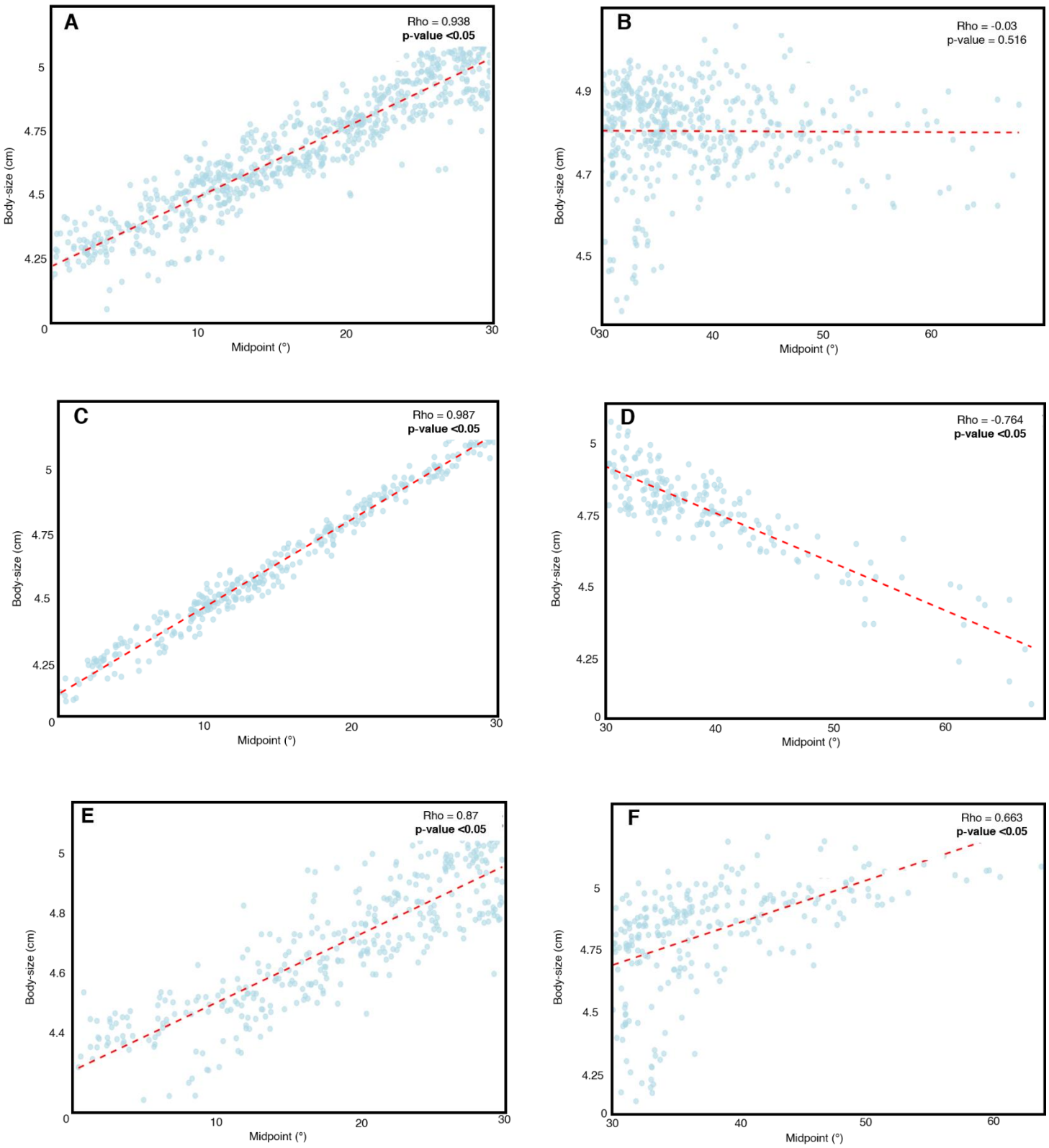
Tropical zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	2.3107	0.4441	p < 0.05	476.68	479.23
Latitudinal range	33.3027	0.6866	p < 0.05	1525.71	1552.73

Temperate zone

Variable	Coefficient	Rho	P_Value	AIC_SAR	AIC_Linear
Body-size	4.0660	0.1012	0.3986	357.63	356.37
Latitudinal range	40.0848	0.4044	p < 0.05	1198.31	1212.56

Supplementary figure AB : Summary of Spatial Autoregressive (SAR) model results for body size and latitudinal range in bivalves for the icehouse partitioning



Supplementary figure 2 : Correlation between body size and midpoint of bivalves at different latitudes; (A-B) : all stages are included ; (C-D) : only warming stages are considered ; (E-F) : only cooling stages are considered. The tropical zone extend from 0° to 30° and the non-tropical zone from 30° to 90°