

Infaunalization and resource partitioning during the Mesozoic marine revolution

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ABSTRACT

Infaunalization has been regarded as representing a response to increased predation pressures and is therefore central to the Mesozoic marine revolution, which gives pre-eminence to the role that enemy-directed evolution has played as a driving force of biotic change. Our ichnologic compilation from 39 Middle Triassic to Late Jurassic shallow-marine siliciclastic units allows us to evaluate the vertical partitioning of the infaunal ecospace through the application of the ichnoguild concept. This study shows that infaunal communities experienced a marked increase in ecospace utilization during the Early Jurassic, reaching a plateau during the rest of the Jurassic. This trend is expressed by an increase in the maximum number of ichnoguilds per community and per tier and in the number of ichnotaxa per ichnoguild. This pattern shows important partitioning of the infaunal ecospace into a series of tiers and that several organisms were able to exploit the same resources available at discrete sediment zones below the sea bottom. The increase in the maximum number of ichnoguilds per community and per tier suggests that niche partitioning was a key factor in a more efficient use of the infaunal ecospace and in driving alpha diversity. However, the increase in the number of ichnotaxa per ichnoguild indicates that ichnoguilds were packed with organisms exploiting similar resources, arguing against the role of competitive exclusion in structuring communities. Because several episodes of predation increase took place during the Mesozoic, an unequivocal link between predation pressures and infaunalization cannot be demonstrated empirically.

INTRODUCTION

The Mesozoic marine revolution (MMR) represents a large-scale restructuring of shallow-marine ecosystems expressed by an increase in drilling predation, intensification of grazing, diversification of durophagous predators, and increase in energy budgets (Vermeij, 1977, 1987; Kelley and Hansen, 2003; Finnegan et al., 2011; Whittle et al., 2018; Klompmaker and Landman, 2021; Petsios et al., 2021; Rojas et al., 2021). Central to the MMR is the concept of escalation, which implies that enemy-directed evolution has been a driving force of biotic change, including increases in prey sturdiness and frequency of shell repair (Vermeij, 1977,

1987, 2008). However, the timing of the MMR is unclear, with earlier studies indicating that most adaptive responses to predation took place during the Early Cretaceous (Vermeij, 1977, 1987) and subsequent studies underscoring increased response of prey to shell-crushing predators by the Late Triassic (Tackett and Bottjer, 2012) or a more protracted transition that was more pronounced during the mid-Cretaceous (Rojas et al., 2021) or the Late Cretaceous (Kowalewski et al., 1998; Walker and Brett, 2002).

The MMR is also characterized by an increase in the depth and extent of bioturbation resulting from higher burrowing ability (Thayer, 1979, 1983; Buatois et al., 2016). The

timing and details of infaunalization have not been explored from an ichnologic perspective, although a number of studies based on body fossils have been published (McRoberts, 2001; Harper, 2003). The aims of this study were to (1) document the infaunal tiering structure in Triassic–Jurassic shallow-marine environments, (2) assess the significance of infaunalization within the framework of the MMR, and (3) assess the importance of resource partitioning as a diversity driver.

MATERIALS AND METHODS

We compiled ichnologic information from 39 Middle Triassic to Late Jurassic stratigraphic units (see Table S1 in the Supplemental Material¹). Information was plotted in paleogeographic maps using PALEOMAPS (Scotese, 2016) to generate a series of figures in GPlates (<https://www.gplates.org>; Figs. S1–S5 in the Supplemental Material) and test potential latitudinal biases. In addition to units studied by the authors (61.5% of all units), various search engines (e.g., Google Scholar™) were used to collate data. Our analysis is mostly restricted to offshore deposits (i.e., below fair-weather wave base but above storm wave base), including from the lower offshore to the offshore transition, because it is assumed that this environment best captures the paleoecologic signal of the shallow-marine infaunal ambient communities (i.e., *Cruziana* ichnofacies). However, low-energy lower shoreface packages were included also because they tend to reflect similar environmental conditions to those from the offshore transition.

¹Supplemental Material. Supplemental text, Tables S1 and S2, and Figures S1–S6. Please visit <https://doi.org/10.1130/GEOL.S.19400924> to access the supplemental material, and contact editing@geosociety.org with any questions.

Wherever possible, occurrences in these units were subdivided into trace-fossil suites ($n = 55$) reflecting different subenvironments along the shoreface to offshore depositional profile. Previous paleoenvironmental interpretations have been revised based on our own sedimentologic observations or critical reevaluation of available data. Although the bulk of cases are from siliciclastic successions, units dominated by siliciclastics but with a minor carbonate component (Table S1) were considered also. Restricting our analysis to a specific depositional belt allows a valid comparison of the various trace-fossil suites that formed under roughly the same paleoenvironmental conditions, therefore reflecting similar sedimentologic factors and preservational constraints. In cases where some degree of deltaic influence has been recorded along strike of the study areas, we assess the role that stressors may have played in causing a departure from a fully marine trace-fossil signature. Ichnotaxonomic assignments were checked on a case-by-case basis to ensure a coherent systematic approach. Analysis of infaunal communities was conducted through the application of the ichnoguild concept, which is based on the fact that organisms tend to group together within the same tier to exploit the same resources in similar ways (Bromley, 1996). An ichnoguild is characterized by three parameters: (1) bauplan (i.e., permanent burrows resulting from the activity of stationary organisms or transitory structures produced by vagile to semi-vagile animals); (2) food source (i.e., feeding modes), and (3) use of space (i.e., tier or vertical position within substrate). Ichnoguild characterization follows the classic approach stated in previous work (e.g., Bromley, 1996; Buatois and Mángano, 2011a). The number of ichnoguilds per community, ichnoguilds per tier, and ichnotaxa per ichnoguild are quantified (Figs. 1A and 1B). We also plotted global and alpha ichnodiversity as number of ichnotaxa per time span and per trace-fossil suite, respectively, as well as by using the Shannon coefficient (Fig. 1C). In addition, a randomization (random sample generation) technique was employed to assess the probability that the observed changes could be produced by chance (see the text and Table S2 of the Supplemental Material).

RESULTS

Our compilation shows that the complexity of infaunal tiering structure was low during the Middle to Late Triassic (Figs. 1A and 1B; Table S1). Middle Triassic ichnofaunas show limited utilization of the deep tier. As many as five ichnoguilds per community, three ichnoguilds per tier, and three ichnospecies per ichnoguild are documented (Figs. 1A and 1B). A slight increase in complexity is apparent for the Late Triassic, as revealed by an increase in the number of maximum number of ichnotaxa per ichnoguild

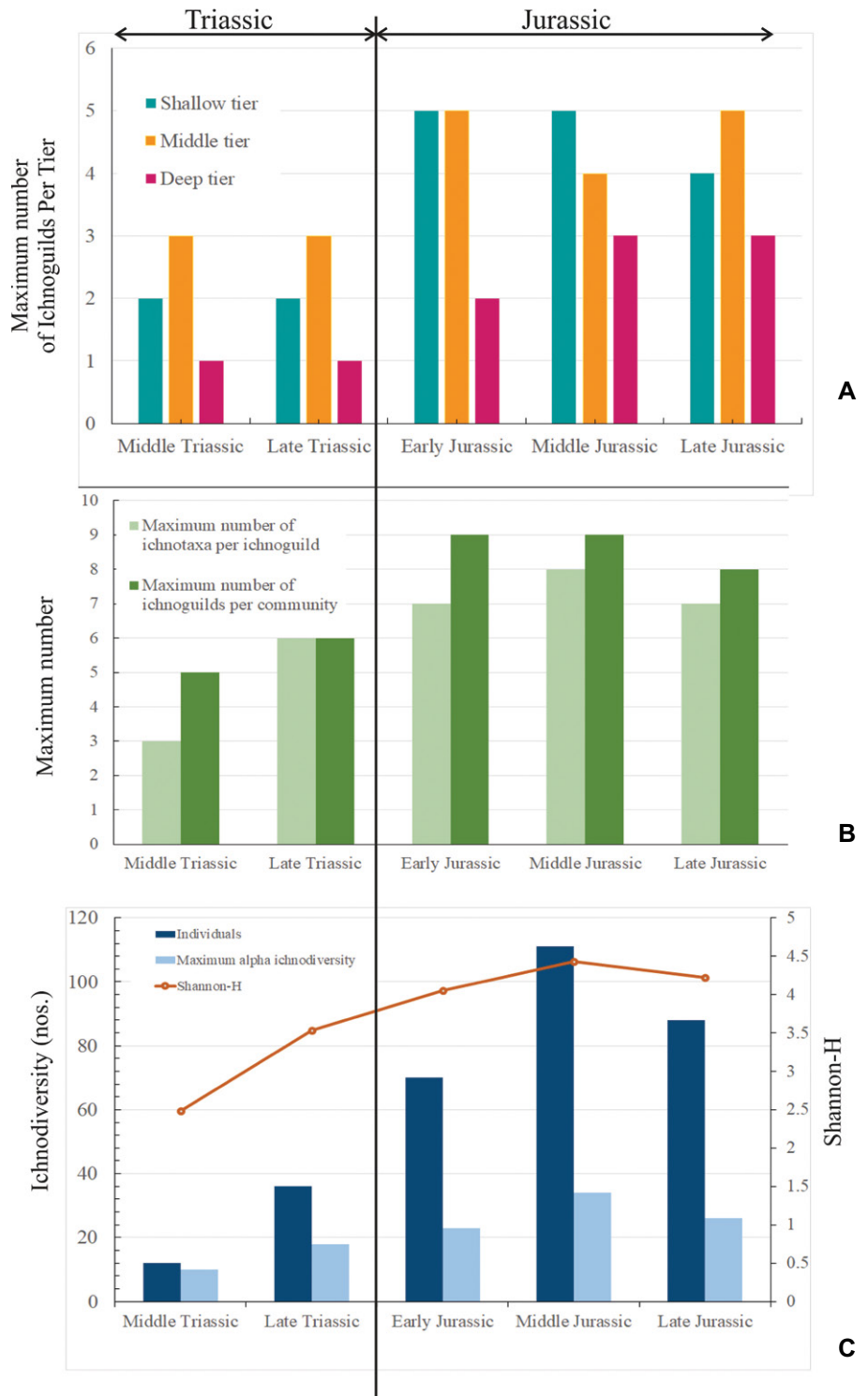


Figure 1. Changes in ichnologic metrics of ecospace utilization in offshore settings during the Middle Triassic to Late Jurassic. (A) Maximum number of ichnoguilds per tier. (B) Maximum number of ichnotaxa per ichnoguild and of ichnoguilds per community. (C) Global and alpha ichnodiversity. Shannon-H was calculated as follows: (1) An alphabetical list of all trace fossils from Table S1 (see footnote 1) was compiled. (2) Age data were compiled. If any ichnotaxa was present, it was marked "1". (3) If ichnotaxa was absent for any age, it was marked "0". (4) If any ichnotaxa occurred more than one time, its count was noted in the data sheet. (5) Diversity was calculated using PAST software (https://palaeo-electronica.org/2001_1/past/issue1_01.htm), and Shannon-H was then plotted on a Microsoft Excel spreadsheet.

and the maximum number of ichnoguilds per community (Figs. 1A and 1B). In addition, a maximum of six ichnoguilds per community and

as many as three ichnoguilds per tier are present. However, these higher values are driven by a single occurrence (Nayband Formation, Iran; see

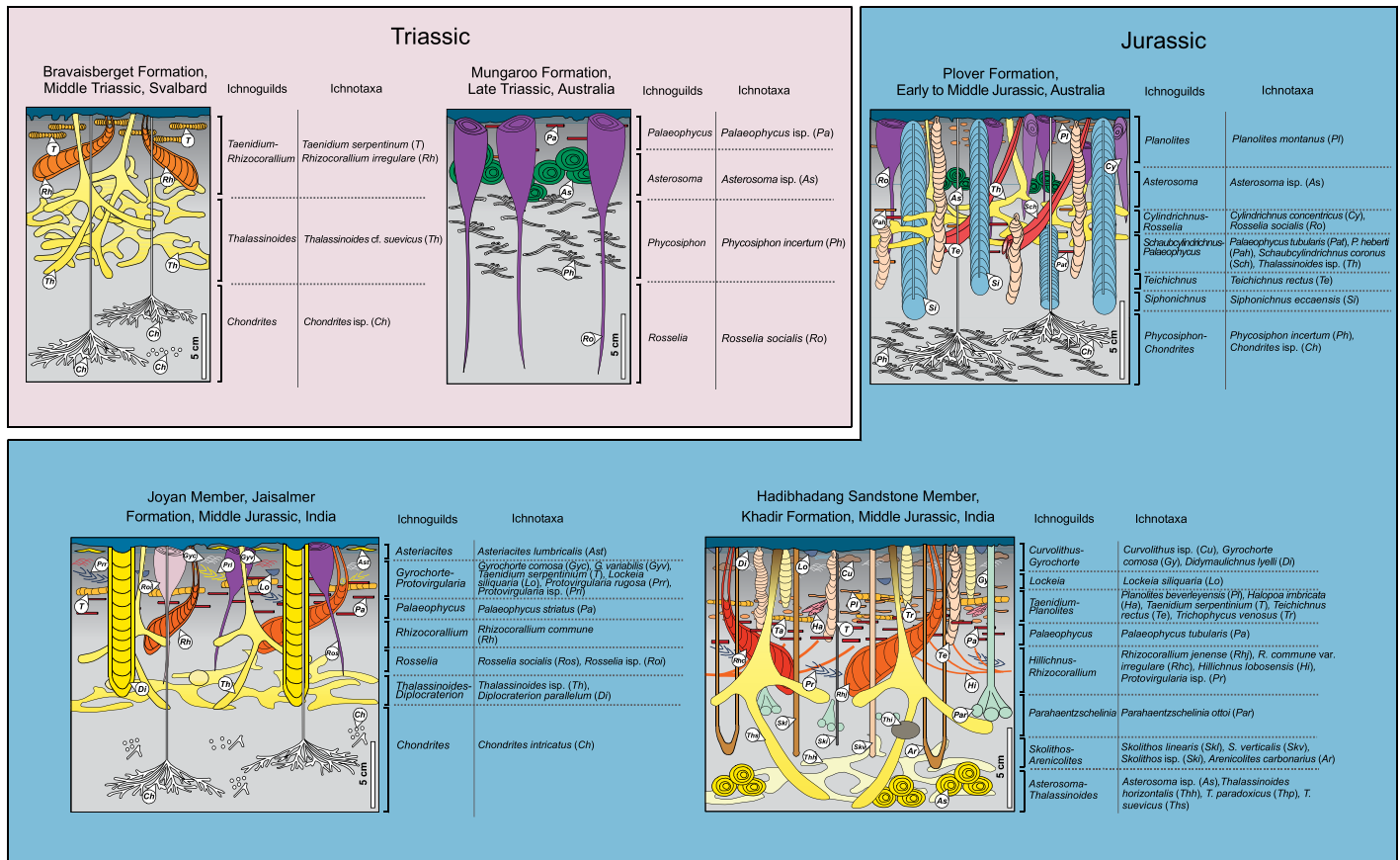


Figure 2. Representative offshore ichnofabrics showing limited complexity of infaunal tiering structure during the Middle to Late Triassic and marked increase during the Early Jurassic. See Table S1 (see footnote 1) for details.

Table S1). In some cases, environmental disturbance due to deltaic influence may have affected stability of the infaunal community, resulting in much simpler tiering structures (e.g., Bravaisberget Formation, Svalbard; Fig. 2; Table S1).

In contrast, Early Jurassic ichnofaunas show a more complex vertical partitioning of the infaunal ecospace, including extensive colonization of deep tiers. This episode of infaunalization is best illustrated by the Plover Formation of Australia (Fig. S6). This unit shows that the increase in the complexity of vertical partitioning of the substrate is not restricted to the offshore but extends all across the depositional profile (Buatois et al., 2016). As many as nine ichnoguilds per community, five ichnoguilds per tier, and seven ichnospecies per ichnoguild are documented in the Early Jurassic. Paleogeographic distribution of the studied Jurassic units (Fig. S1) suggests that infaunalization took place across a broad latitudinal spectrum, from low to high latitudes. Roughly similar values are seen for the rest of the Jurassic (Figs. 1A and 1B).

DISCUSSION

Ichnologic information suggests that the tiering structure of Triassic infaunal communities in shallow-marine siliciclastic settings was relatively simple. Early Triassic ichnofaunas are

characterized by the predominance of shallow to very shallow-tier structures (Twitchett and Barras, 2004; Buatois and Mángano, 2011b; Hofmann et al., 2015; Cribb and Bottjer, 2020; Luo et al., 2021). Preservation of these near-surface structures is linked to firmground conditions in the absence of a well-developed mixed layer (i.e., uppermost centimeters of sediment characterized by high water content and poorly defined burrow mottling), given that bioturbation of this upper zone of the sediment was severely affected by the end-Permian mass extinction (Buatois and Mángano, 2011b; Hofmann et al., 2015; Luo et al., 2021). Although Middle to Late Triassic ichnofaunas show an increase in depth and extent of bioturbation with respect to their Early Triassic counterparts, the number of ichnoguilds during the Middle to Late Triassic remained relatively low (Figs. 1A, 1B, and 2) and only local more-complex tiering structures have been detected by the end of this period (Table S1). The only unit with relatively complex tiering structure occurs in low latitudes (Fig. S1), but elaboration on potential climatic controls on early infaunalization is not possible based on available data. In addition, the scarcity of shallow-marine siliciclastic units of Late Triassic age ($n = 3$) in comparison with Early Jurassic ones ($n = 7$) may be invoked to argue that

complexity during the former may have been underappreciated by lack of studies. Although this possibility cannot be completely ruled out, the marine infauna was severely affected in terms of ichnodiversity, depth of bioturbation, and tiering structure during the end-Triassic mass extinction (Twitchett and Barras, 2004; Barras and Twitchett, 2016). This pattern is supported by available data on Hettangian ichnofaunas that show low levels of infaunalization in the aftermath of the extinction (Table S1).

Our compilation shows that infaunal communities in offshore areas experienced a marked increase in ecospace utilization during the Early Jurassic, particularly since the Sinemurian, reaching a plateau during the rest of the Jurassic (Figs. 1A, 1B, and 2). This is expressed by an increase in the maximum number of ichnoguilds per community and per tier and in the number of ichnotaxa per ichnoguild (Figs. 1A and 1B; Table S1). This pattern shows important vertical partitioning of the infaunal ecospace into a series of tiers and that several infaunal organisms were able to use essentially the same resources available for them at well-defined sediment zones with respect to the sediment-water interface (Fig. 2).

The role that interspecific competition and resource partitioning has played in macroevolution

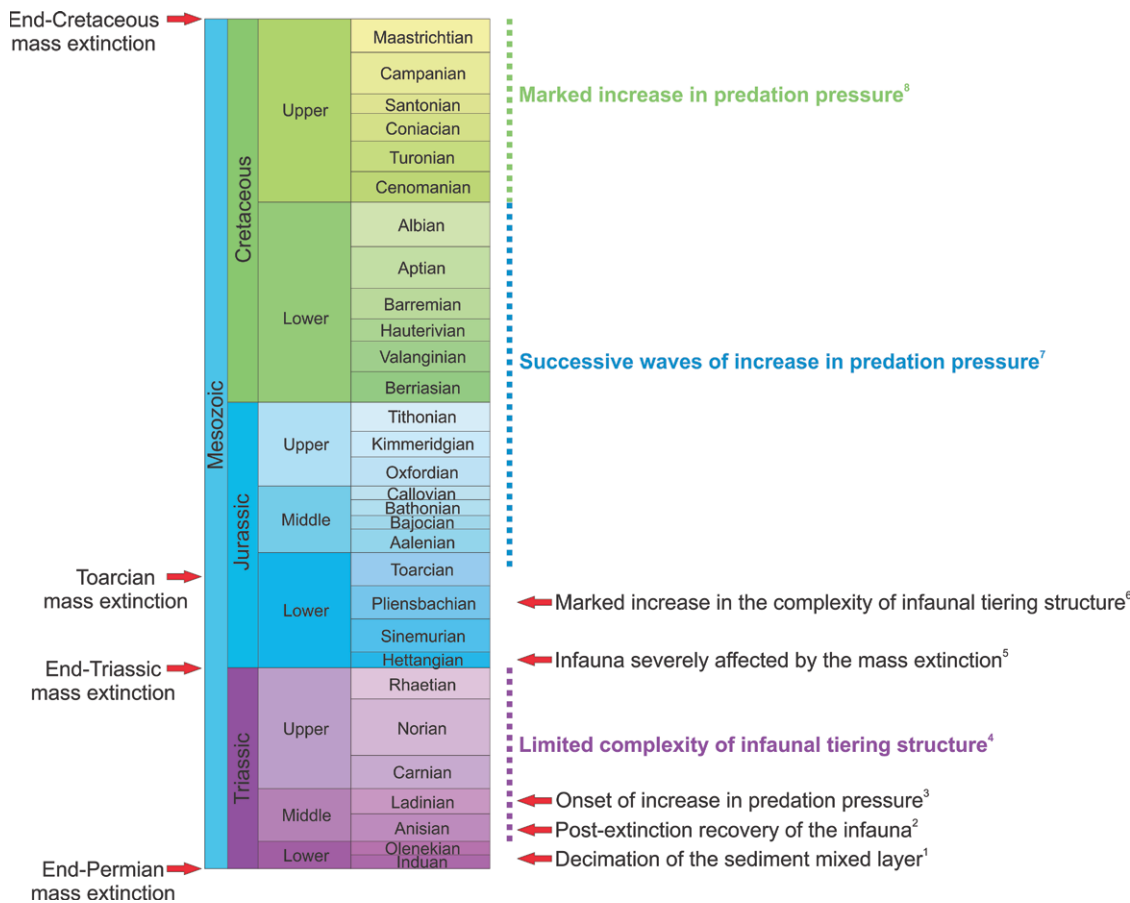


Figure 3. Milestones in predation pressure and animal-substrate interactions in Mesozoic shallow-marine environments. Sources: 1—Buatois and Mángano (2011b), Hofmann et al. (2015); 2—Twitchett and Barras (2004), Luo et al. (2021); 3—Walker and Brett (2002), Tackett and Bottjer (2012), Tackett (2016); 4—Twitchett and Barras (2004), Hofmann et al. (2015), this study; 5—Twitchett and Barras (2004), Barras and Twitchett (2016); 6—this study; 7—Walker and Brett (2002), Zatoń and Salamon (2008), Vermeij (2008); 8—Kowalewski et al. (1998), Walker and Brett (2002), Rojas et al. (2021).

is a topic of debate (Stanley, 2008; Ezard and Purvis, 2016; Weber et al., 2017). The traditional view is that two species exploiting the same resource would result in one of them driving the other one to extinction through competition. However, this view has been challenged through highlighting the role of predation and environmental change in reducing the density of certain species and, therefore, allowing the persistence of others that share the same resources (Stanley, 2008; Ezard and Purvis, 2016). In this scenario, the very same notion of carrying capacity is called into question and individual guilds may become populated by multiple species (Stanley, 2008). The implications of our analysis are twofold. First, the Early Jurassic increase in the number of ichnoguilds per community and per tier suggests that niche partitioning was instrumental in a more efficient utilization of the infaunal ecospace and in driving alpha diversity. Second, the increase in the number of ichnotaxa per ichnoguild demonstrates that ichnoguilds were packed with organisms exploiting similar resources, casting doubt on the notion of competitive exclusion.

Ecosystem engineering, which implies modulation of resources among species (e.g., changing nutrient fluxes, increasing microbial activity), may be a potential mechanism to explain the tight packing of infaunal bioturbators. This is supported by modern studies that show

that some bioturbators are key in maintaining ecosystem function, being drivers of diversity (Lohrer et al., 2004; Solan et al., 2004). The role of bioturbation as an example of ecosystem engineering in the fossil record has been highlighted, particularly for the Cambrian explosion (e.g., Mángano and Buatois, 2014). However, there is still a paucity of studies assessing the role of bioturbators as diversity drivers at the scale of interspecific interactions among burrowers.

Escalation is at the core of the MMR: while predators increase their efficiency, prey develops ways to avoid or repel their enemies, resulting in a process of “arms race” (Vermeij, 1977). Infaunalization can be seen in this light as a strategy for escaping predation (Vermeij, 1987). Assessing the relative timing of infaunalization with respect to an increase in predation pressure may, in principle, help to illuminate the role of escalation (Fig. 3) (Buatois et al., 2016). Predation pressures seem to have experienced an unprecedented increase during the mid- to Late Cretaceous interval (Kowalewski et al., 1998; Walker and Brett, 2002; Rojas et al., 2021). In this view, predation pressures during the early Mesozoic were considered generally low (Vermeij et al., 1981; Kowalewski et al., 1998). If this was the case, infaunalization pre-dated the main phase of increase in predation pressures, casting doubts on the interpretation of the former as a haven from the latter. However, there are significant

caveats with this scenario because successive episodes of predation increase have been identified since the Middle Triassic (Walker and Brett, 2002; Zatoń and Salamon, 2008; Vermeij, 2008; Tackett and Bottjer, 2012; Tackett, 2016). Accordingly, the increase in infaunalization during the Early Jurassic may be seen as representing a response to the earlier Triassic episode. These uncertainties in the chronology preclude establishing an unequivocal link between predation pressures and infaunalization.

CONCLUSIONS

Infaunalization experienced a marked increase within shallow-marine siliciclastic environments during the Early Jurassic, reaching a plateau during the rest of the Jurassic. Ichnoguild analysis demonstrates the vertical partitioning of the infaunal ecospace into a series of tiers and that several organisms were able to exploit similar resources available to them. This pattern suggests that niche partitioning was instrumental in a more efficient utilization of the infaunal ecospace and in driving alpha diversity but does not support a strong role of competitive exclusion as a driving force in structuring marine communities. Although episodes of predation increase occurred throughout the Mesozoic, a relationship between the increase in infaunalization and increased predation during the Early Jurassic has not been established.

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