Review of Edgar et al., „Reviews and Syntheses: Trait-based approach to constrain controls on planktic foraminiferal ecology: key trade-offs and current knowledge gaps“

Summary

In this review and syntheses article, Edgar et al. promote the use of trait-based approaches to improve our understanding of planktonic foraminiferal ecology. The authors review the state of knowledge on key traits of planktonic foraminifera and conclude that trait-based modeling, metabarcoding, eDNA, and higher standards of data collection can fill critical knowledge gaps and make foraminifera key model organisms for ecological questions.

General comments

The article presents a well-structured summary of our current knowledge of planktonic foraminiferal ecology and clearly points out current knowledge gaps. Perspectives for future research are highlighted in the abstract and the conclusions, but they remain rather vague in the article itself, so that both the abstract and the conclusions seem to be disconnected from the main body of the article. For example, eDNA and eRNA approaches are mentioned in the abstract and/or the conclusions, but not in the main article. Similarly, it is repeatedly stated that observational and experimental data as well as modeling approaches are needed to improve our understanding of foraminiferal ecology, but the suggestions for future studies remain rather vague. What exactly should be done in future experimental/observational studies? How exactly can trait-based models help to understand foraminiferal ecology and fill current knowledge gaps? In my opinion, this aspect needs more focus and concrete examples if it is to be emphasized in the abstract and in the conclusions.

In addition, the article lacks a robust discussion of what challenges future studies may face when following the author's suggestions. Since this is a review and syntheses article, I do not expect an extensive discussion. However, I think that the reader should at least be made aware of the major challenges associated with the suggested approaches. This is already partly done for observational and experimental studies, but modeling approaches are, in my opinion, presented much too idealized. For example, it is stated in the conclusions that models "can create theoretical frameworks akin to laboratory experiments". I think it is essential to mention that models are based on assumptions and simplifications, i.e., they will never be an exact replica of nature. The only model limitation discussed in the article is the lack of input data for foraminifera. But what does this imply for the reliability of model simulations? Under what conditions and to what extent can models be compared to real-life experiments and/or observations? Such thoughts should be included in the argumentation.

Finally, the language lacks clarity. Long sentences with punctuation problems and sometimes minor grammatical problems make it difficult to follow the argumentation of the article. However, this problem should be straightforward and easy to fix.

Specific comments

- It may be helpful to specify some technical terms as not all readers may be experts in the field:
  - L. 43: pseudopodial network, l. 45: pseudopodia
  - L. 95: cryptic species
  - Table 2: rhizopodial (rhizopodia is explained in l. 248; I would add the same short explanation to the table caption)
  - L. 146: shell flux
  - L. 432: blue water
- L. 34: Do you mean "fossil records among all phytoplankton groups"?
- L. 54-55: There is no clear link between these two paragraphs, which disrupts the flow of the text. Maybe you could add a connecting sentence to the paragraph beginning in l. 55.
- L. 70-72: I think it is important to state here how successful these trait-based models actually were in reproducing the sedimentary record, so that the reader can get an understanding of the current state of research. In the Gibbs et al. (2020) model, for example, the simulated evolutionary response progressed orders of magnitude too fast.
- L. 77: Since models are based on assumptions and simplifications, their results have to be interpreted with care. Therefore, I would not use the term "vastly" here.
- L. 78: The current formulation is quite misleading; do you mean the first modeling study on foraminifera?
- L. 97-99: This sentence seems to contradict itself. Do you mean "their presence in shallow marine seas…"? If not, please elaborate on this further.
- Table 2: Why is an increased area to volume ratio beneficial? Is it due to the increased capture area? If yes, you should make clear that this is meant here. If not, you should explain this somewhere in the text.
- L. 138-139: This sentence seems to contradict itself. What do you mean by individuals reaching larger sizes in the tropics but smaller sizes in equatorial regions?
- L. 145: Do you mean "greater reproductive success"?
- L. 172-176: Why is an increased sinking rate beneficial? This seems to contradict Table 2, where negative buoyancy is listed as a cost, while positive buoyancy is listed as a benefit.
- L. 205: "also" instead of "though"?
- L. 212: What exactly do you mean by "resolving the aforementioned biological factors"? Could you elaborate on this further?
- L. 217-220: This sentence is very long and difficult to read, maybe split it into two sentences?
- L. 219: Do you mean reduced calcification?
- L. 261: Do you mean that foraminifera can capture prey items 2-3 times bigger than themselves while most zooplankton cannot? If yes, I would write "contrary to most zooplankton".
- L. 275-276: This sentence is difficult to understand. Maybe replace with something like "Under laboratory conditions, non-spinose species exhibit cannibalism, but whether they cannibalise in the natural habitat is unknown and considered unlikely due to very low foraminiferal abundance."
- L. 278-279: This sentence is difficult to understand. Do you mean "The temporal and spatial distribution of prey is a major cause of the regional distribution of foraminiferal species, which affects growth and fecundity via temperature."?
- L. 316-325: This paragraph seems to contradict the previous one in which it is stated that planktonic foraminifera do not undergo diapause. Could you elaborate more on the dormancy

of *Neogloboquadrina pachyderma* and how it differs from those of benthic foraminifera and dinoflagellates mentioned in the previous paragraph?

- L. 348-358: The different variants of symbiosis described here are unknown to the reader when they read Table 1. Maybe it would be helpful to include a short definition of these terms in the table caption.
- L. 381-382: What impact may it have on modeled foraminiferal ecology that we cannot simulate facutatively symbiont-bearing species?
- L. 432-434: How does this sentence connect to the previous one?
- L. 451-453: I don't understand the part starting with "and ability". Maybe it would help to rewrite this part and put it into a new sentence.
- L. 457-459: You mention repeatedly that most traits are poorly constrained. What I am missing is a discussion of the actual potential and limitation of trait-based modeling in this regard. Which traits can be modeled, under which assumptions/simplifications can they be modeled, and which impact may that have on the informative value of the model results? I suggest discussion this briefly for each trait and giving a short summary in the conclusions.
- L. 478-483: I think that models are presented too idealized in this manuscript. It should at least be mentioned that models are based on assumptions and simplifications, which means that they are not equivalent to observations of real organisms.

Technical corrections

- L. 30: calcite budget, with their carbonate shells covering
- L. 32: … and, over longer timescales, modulating…
- L. 50: challenges in culturing them
- L. 67: years, where new traits
- L. 68: adaptation to the novel climates and environments, as it permits
- L. 70: Either the Knoll and Follows (2016) model or the model of Knoll and Follows (2016)
- L. 82: understanding~~,~~ to facilitate
- L. 92: studies, until ~~relatively~~ recently, ~~were from~~ have been seminal papers
- L. 93-94: adult morphology, with
- L. 95: 2017), many but not all of which
- L. 102: Species are listed ~~here~~ alphabetically here
- L. 103-104: Summary of ~~ecology~~ ecological information
- L. 109: replace "each" with "all"
- L. 135: 2004), although
- L. 138: tropics, while
- L. 141: factors, including higher temperatures and thus~~,~~ metabolic
- L. 146 and l. 419: semilunar or semi-lunar? Use one of both versions consistently throughout the manuscript
- L. 156: and, to a lesser extent, the spines
- L. 161: total mass, making
- L. 163: biomineralisation, and foraminifera (as ~~with~~ many organisms) can
- L. 164: A/the lack
- L. 166 currently exist~~s~~
- L. 167: budget ~~is apportioned~~ to

- L. 171: 2014)~~,~~ ~~though~~ although this is
- L. 172: write “centimeters” instead of “cm” when not followed by a number
- L. 173: thus~~,~~ sinking rate
- L. 174: include an increased capture area
- L. 176: Logically, the development
- L. 177: trait-based modelling suggests
- L. 180: carnivorous, which provides
- L. 190: dramatically), including
- L. 196: underestimated, as many juveniles
- L. 197: lack of numerous spines
- L. 205 identify ~~a~~ species-specific responses
- L. 208: a/the lack of understanding ~~of~~ the controls of thickness of gametogenic calcite~~,~~ or the biomineralization pathway
- L. 210: data, as well as
- L. 213: practices, e.g.
- L. 214: changes ~~to~~ in the pelagic
- L. 220: 2020), supporting
- L. 240: investment, as organisms do not need to move to acquire their prey, and reduced
- L. 242-243: populations, with passive ambush feeders having lower~~ed~~ metabolic and mortality rates
- L. 250: Caron et al., 1987)), foraminifera
- L. 252: shell diameter), they
- L. 253: 2019), allowing them
- L. 261: 1984), indicating
- L. 261: I don’t think that the use of “notably” is correct here. You could write “It is noteworthy that”
- L. 266-267: 2017), preying
- L. 267: ~~eukaryote~~ eukaryotic algae
- L. 269: *obliquiloculata*), but it was found that these taxa are unable to capture and hold live zooplankton~~,~~ and are only able to consume
- L. 271: rhizopodia, as evidenced
- L. 280: gyres (Fig. 3), where copepods are most abundant (Grice and Hart, 1962), whereas
- L. 287: this information is scarce~~,~~ and limited to a few taxa
- L. 288: *universa*), which
- L. 293, l. 423, and l. 447: multigenerational or multi-generational?
- L. 297: gaps in knowledge ~~of around~~ about the costs and benefits
- L. 298: close relatives
- L. 299: ~~between~~ with zooplankton
- L. 311: lower standing stocks~~, and or~~ and/or smaller body sizes, threatening
- L. 316: of the non-spinose
- L. 318: assemblages)
- L. 321-322: At >50 psu, though, individuals were unable to undergo gametogenesis, at >73 psu, pseudopodal activity and movement ceased, but they were able to… (I would use present tense here or write “At 50 psu, individuals were found to be unable...”)

- L. 337: photoendosymbionts, either
- L. 338: c), which
- L. 339: photosymbionts, there
- L. 342: foraminifera, or just utilise waste products, is
- L. 345: 2007), suggesting
- L. 346: activities, they are not essential (and therefore, this is not
- L. 349: species, making them functionally mixotrophic) or facultative (not essential to the host success and thus, only
- L. 351: a spectrum, as proposed by Stoecker et al (2009), from non-symbiosis
- L. 355: ontogeny, is
- L. 362: ocean, presumably
- L. 363: No symbiont bearing-taxa
- L. 365: fixed carbon, aiding
- L. 366: 1982), but photosymbionts
- L. 373: acquired as juveniles, or, as new evidence suggests, provided to gametes
- L. 375-376: 2016), with the symbionts eventually being consumed
- L. 381-382: facultatively symbiont bearing-taxa, making it impossible to model these them as
- L. 385: eutrophic regions, including
- L. 386: its trait-offs trade-offs and
- L. 387: experiments, including
- L. 389: photosymbionts, [1] they
- L. 390: 2017), and [2] the host is dependent to on changes
- L. 391: symbionts, which
- L. 391: Studies suggesting that
- L. 392: light limitations
- L. 395-396: individuals may have persisted for thousands of years with smaller sizes and lower population abundances (Edgar et al., 2013; Wade et al., 2008), which may have impacted
- L. 399: symbioses, beyond
- L. 402: cannot be explored fully, nor can the importance
- L. 409: reproduce sexually only, but recent
- L. 416: 1983), resulting in
- L. 419: (~2-4 weeks), whereas
- L. 421: chlorophyll maximum, where there are
- L. 426: short-lived
- L. 429: reproduction provides a definite (if though difficult to quantify) advantage
- L. 432-434: The structure of that sentence doesn't make sense. Do you mean: "Delayed reproduction potentially reduceds the chance of fertilization by putting because individuals are out-of-sync with the rest of the population and/or because the organism is smaller and thus, produces fewer gametes."?
- L. 436: As such, p Planktic foraminifera
- L. 437: water column, including
- L. 439: from each adult, thereby increasing encounter and survival rates, and

- L. 442: The structure of that sentence seems wrong to me. Do you mean: “Modelling the development of foraminifera in a way that resembles their accretionary growth has not yet been achieved.”?
- L. 443: information ~~of~~ on the different ~~trades~~ traits and ~~trait offs~~ trade-offs in their development, such as changes
- L. 444-445: breakthrough, which enables ~~enabling~~ us to explore the full life cycle of planktic foraminifera, opens ~~to~~ the door
- L 447: *N. pachyderma*, which, as discussed above, can
- L. 448: sea ice, *N. pachyderma*
- L. 449: and/or, as the ice melts, are released
- L. 450: lifespan, potentially surviving
- L. 454: small, resulting
- L. 457: thus~~,~~ an ideal target group
- L. 458: constrained, requiring new
- L. 463: datasets, there are clear groupings of traits in the modern ocean, allowing us
- L. 464: and responses to
- L. 466: future, and thereby
- L. 471: the relationship~~s~~ between calcification and seawater carbon chemistry is unclear, limiting