Ideas and perspectives: How sediment archives can improve model projections of marine ecosystem change

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Abstract. Global warming is a major threat to marine biodiversity and ecosystem functioning, with consequences that are yet largely unknown. To frame these consequences, we need to understand how marine ecosystems respond to warming and related environmental changes. Ecosystem models have proven to be a valuable tool in this respect, but their projections vary considerably. A major limitation in current ecosystem models may be that they largely ignore evolutionary processes, which nonetheless can be relevant on the simulated time scales. In addition, ecosystem models are usually fit to contemporary data and used predictively afterwards, without further validation that they are equally applicable to past (and by inference, future) scenarios. A promising approach to validate evolutionary ecosystem models are biological archives such as natural sediments, which archive long-term ecosystem changes. Since the ecosystem changes present in sediment records are affected by evolution, evolution needs to be represented in ecosystem models not only to realistically simulate the future but also the sediment record itself. The sediment record, in turn, can provide the required constraints on long-term evolutionary changes, along with information on past environmental conditions, biodiversity, and relative abundances of taxa. Here, we present a framework to make use of such information to validate evolutionary ecosystem models and improve model projections of future ecosystem changes. Using the example of phytoplankton, key players in marine systems, we review existing literature and discuss (I) which data can be derived from ancient sedimentary archives, (II) how we can integrate these data into evolutionary ecosystem models to improve their projections of climate-driven ecosystem changes, and (III) future perspectives and aspects that remain challenging.

1 Introduction

Driven by the reality of global warming as a major threat to marine biodiversity and ecosystem functioning, ecosystem models are increasingly used to estimate future changes in marine ecosystems. However, projected changes differ notably between models (Laufkötter et al., 2015, 2016; Tittensor et al., 2021), which may be due to the fact that evolutionary processes are generally neglected, even though they can be of great importance on the simulated time scales (Irwin et al., 2015; Jin and Agustí, 2018). The reliability of current model projections

70 therefore remains questionable. Here, we propose to use data from sediment archives to
71 validate evolutionary ecosystem models before using them predictively and discuss how this
72 approach can improve model projections.

73   Compared with the period 1850–1900, global surface temperature has already increased
74 by 1.25 °C and, under the most extreme emissions scenario, is expected to increase by up to a
75 further 3.5 °C by the end of the century (IPCC scenario SSP5-8.5, Allan et al., (2021). The
76 current state of warming has already caused changes in marine communities (Peer and Miller,
77 2014; Poloczanska et al., 2013; Wasmund et al., 2019), which perform ecosystem functions
78 that are vital to human societies, including food production (Hollowed et al., 2013) and carbon
79 sequestration (Hain et al., 2014). The response of these ecosystem services under ongoing
80 global warming remains subject to great uncertainty, and there is a real but unknown risk of
81 positive feedbacks, irreversible tipping points, and ecosystem collapse (Lenton et al., 2008).
82 For example, IPCC models systematically underestimate the decline in Arctic summer sea ice,
83 which suggests that a tipping point may already have or may soon be passed (Lenton et al.,
84 2008; Stroeve et al., 2007). Passing this tipping point can cause strong nonlinear and long-term
85 changes in the system, such as amplified warming and sea ice loss through a positive albedo
86 feedback, and, in turn, major ecosystem change (Holland et al., 2006; Lenton et al., 2008).

87   Dynamic ecosystem models currently represent the best tool to understand complex
88 feedbacks between evolving ecosystems and their environment, but it is a considerable
89 challenge to develop models that would apply equally well to past, present, and future
90 scenarios. Despite their great potential, current models project diverging changes in ecosystem
91 functions like carbon cycling and net primary production (Laufkötter et al., 2015; 2016;
92 Tittensor et al., 2021). For example, a recent coupled model intercomparison showed a
93 variability of up to ± 10 % in projected global net primary production, depending on the
94 ecosystem model and earth system forcing used (Tittensor et al., 2021). This disagreement
95 between models illustrates how critical it is to assess the validity of model projections. Since
96 models hardly agree on the direction of change, the validity of current model projections
97 remains questionable.

98   To improve model projections, we need (I) to verify that allthe most relevant processes
99 are considered and (II) to validate projections with long-term data. Regarding (I), current
100 ecosystem models largely ignore a crucial process that can influence ecosystem responses to
101 environmental changes on perennial time scales – evolutionary adaptation (Hattich et al., 2024;

Irwin et al., 2015; O'Donnell et al., 2018). Some ecosystem models already consider adaptation, but only a small number have been compared to empirical data, both from experiments (Denman, 2017) and from sediment archives (Gibbs et al., 2020; Hinners et al., 2019). So far, however, testing against data has not been used to improve projections made by these models. With respect to (II), both experiments and marine monitoring studies cannot account for environmental changes on longer than decadal time scales, while experiments can hardly capture the complexity of real ecosystems. Natural archives such as sediments, however, allow ~~reconstructing~~the reconstruction of long-term ecosystem responses to past environmental changes (Capo et al., 2021; Ellegaard et al., 2020). Sediments preserve abiotic and biotic environmental proxies (Hillaire-Marcel and De Vernal, 2007), other organismal remains such as DNA (Alsos et al., 2022; Monchamp et al., 2016; Zimmermann et al., 2023), and dormant resting stages~~cells and seeds that~~. Dormant resting stages, which are formed by many phytoplankton and zooplankton taxa, are typically characterized by resistant, thick walls and the capacity to endure long phases of physiological dormancy (Ellegaard and Ribeiro, 2018). Similar to seeds, these resting stages can be resurrected and used for experiments (Bennington et al., 1991; Hinners et al., 2017; Isanta-Navarro et al., 2021). Since sediments can be dated, we can use the preserved information to derive long-term time series on past environmental conditions, biodiversity, relative taxa abundance, and adaptive changes in (functional) traits. Thus, sediment archives are well suited to constrain the long-term evolutionary changes needed to validate evolutionary ecosystem models. Evolution, in turn, needs to be represented in ecosystem models to simulate its impact on the sediment record.

Here, we discuss how we can use data from sediment archives to improve evolutionary ecosystem models and their projections of marine ecosystem change. Our approach focuses on phytoplankton, key players in marine ecosystems and respective models. Phytoplankton account for about half of global photosynthesis (Field et al., 1998), are the basis of the marine food web (Fenchel, 1988), represent an important component of biogeochemical cycles (Hutchins and Fu, 2017), and can even influence ocean physics (Hense, 2007; Sathyendranath et al., 1991). In addition, the large population sizes and short generation times of phytoplankton allow them to adapt quickly to changing environmental conditions (Aranguren-Gassis et al., 2019; Hattich et al., 2024; O'Donnell et al., 2018). All these factors, together with their long-lived dormant resting stages (Delebecq et al., 2020; Sanyal et al., 2022), make phytoplankton ideal model organisms for the approach we present here. Based on existing literature, we discuss which data we can obtain from sediment archives, how we can use these data to

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135 improve evolutionary ecosystem models and their projections, and remaining challenges and
136 future perspectives.

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2 Sediment archives – understanding phytoplankton responses to environmental change

140 Sediment archives provide information on past ecosystem status, including both environmental
141 and biological data (Fig. 1). Such data can be used to constrain evolutionary ecosystem models.

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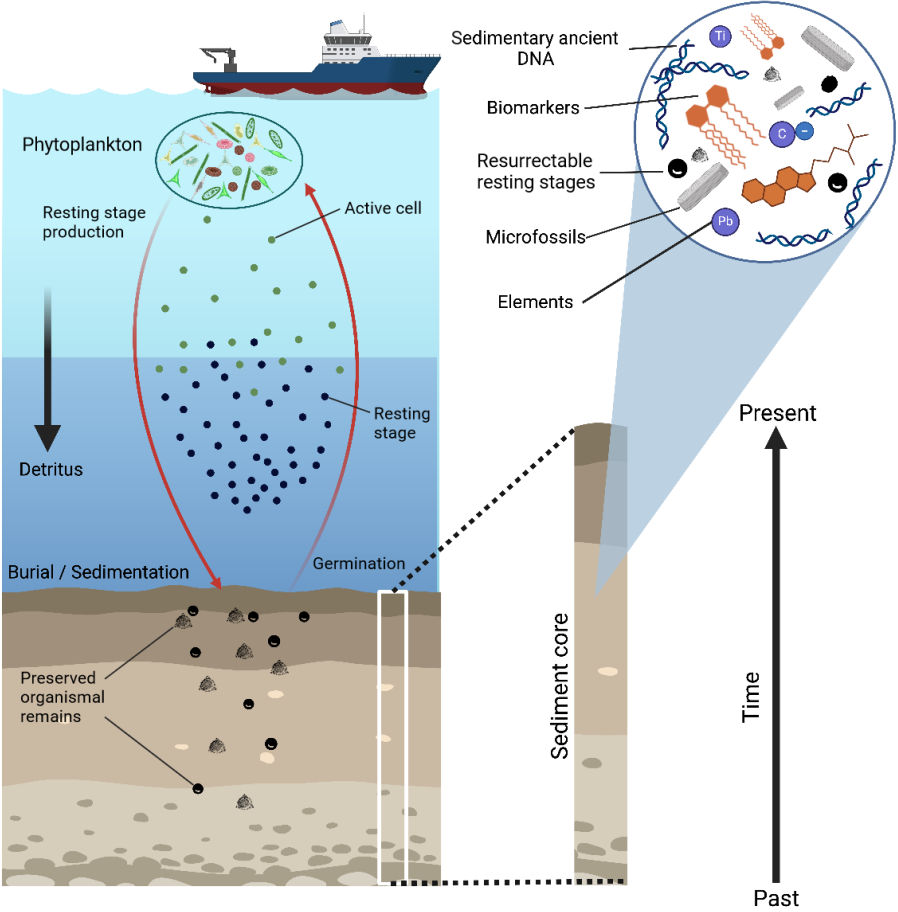


Figure 1: Overview of different types of data (environmental and biological) that can be obtained from sediment archives. **Left:** Schematic showing the deposition of organismal remains in the sediment. Red arrows indicate ~~resting stage production~~the production of dormant resting stages (thick-walled cells that can endure long phases of physiological dormancy), their deposition in the sediment, and the germination of resting stages from the sediment. The black arrow represents sinking of dead organic matter (detritus) to the seafloor. Preserved organismal remains, a mixture of resting stages and detritus, are shown in the sediment. **Right:** Close-up of the sediment core showing different types of data that can be obtained. The figure was created with BioRender.com.

2.1 Dating sediment archives

Before working with sediment archives, the sediments must be dated accurately to obtain a well-constrained relationship between age and sediment depth, a so-called age model. Common sediment dating methods include radiocarbon dating, lead isotope dating, and event stratigraphy. Radiocarbon (^{14}C) dating is based on ^{14}C half-life. Determining the amount of radioactive ^{14}C relative to the ^{12}C stable isotope allows estimating age ca. 50,000 years back in time (Hajdas et al., 2021). After 1950, radiocarbon dating is not applicable anymore due to the radiocarbon added artificially to the atmosphere by nuclear bomb tests. Therefore, sediments deposited after 1950 are dated using different methods such as lead isotope (^{210}Pb) dating and event stratigraphy. While the ^{210}Pb dating approach is based on the half-life of atmospheric ^{210}Pb (Appleby, 2001), event stratigraphy is based on the detection of specific events such as nuclear bomb tests, volcanic eruptions, and other distinct anthropogenic impacts that are registered in, for example, chemical parameters of the sediments (Hancock et al., 2011; Lowe and Alloway, 2015). By combining all the dating methods mentioned above, it is possible to obtain robust age models of sediment cores over the last ca. 50,000 years. Other stratigraphic methods, e.g., oxygen isotope stratigraphy, biostratigraphy, or paleomagnetic stratigraphy are applied to date older sediments deposited in aquatic environments (Bradley, 1999).

2.2 Environmental data

171 Abiotic and biotic proxies, or indicators, preserved in sediment archives allow ~~reconstructing~~
172 the reconstruction of physicochemical characteristics of past marine and limnic environments.
173 For example, surface salinity can be estimated using lipids (alkenones) produced by micro-
174 phytoplankton species of the order Isochrysidales (Kaiser et al., 2017; Medlin et al., 2008;
175 Rosell-Melé, 1998). Some trace metals and their isotopes are indicators for past suboxic to
176 euxinic conditions in the water column and/or the sediments (Brumsack, 2006; Dellwig et al.,
177 2019). Relative assemblages of microfossils (e.g., resting stages of dinoflagellates, silica
178 frustules of diatoms, calcareous shells of foraminifera) and their shell geochemistry provide
179 important information not only on salinity, but also on pH, trophic state, and temperature, and
180 are therefore powerful proxies (Cléroux et al., 2008; Hillaire-Marcel and De Vernal, 2007; Lear
181 et al., 2002). Organic indexes based on biomarkers, e.g., alkenones (U^K_{37}, Prahl et al., (1988))
182 or other membrane lipids derived from archaea (TEX_{86}, Schouten et al., (2013)) can be used to
183 reconstruct surface and subsurface temperature. These and many other physical methods,
184 biological proxies, and geochemical tracers find their diverse applications in paleoceanography
185 (Hillaire-Marcel and De Vernal, 2007).

186 Proxy-based reconstructions must be considered carefully as they may be biased due to
187 preservation/degradation and influenced by local-to-regional environments. Using a
188 multiproxy approach and calibration depending on the environment is important for reliable
189 reconstructions. Reconstructed environmental conditions of the past can then be used as forcing
190 for ecosystem models.

191

2.3 Biological data

193 Apart from information on environmental conditions, sediment archives provide a wide variety
194 of biological information, such as biodiversity, relative taxa abundance, and trait adaptation.
195 This biological information is valuable for validating evolutionary ecosystem models.

196

2.3.1 Microfossils

198 Traditionally, the focus of research on sediment archives has been on fossilized plankton
199 remains. Fossil phytoplankton communities only represent species that consist of stable

mineral structures (e.g., of silica or carbonate) or contain specific fossilizable molecules such as sporopollenin. Among dinoflagellates, only a fraction of the community produces resting cysts (Limoges et al., 2020; Van Nieuwenhove et al., 2020), which are preserved over time and can be used for quantitative paleoecological reconstructions and biostratigraphy. Diatoms, on the other hand, are well-represented in the fossil record due to their resistant silica frustules with their diverse species-specific structures (Weckström, 2006). ~~Also s~~Some filamentous cyanobacteria also produce resistant resting stages, akinetes, constituting long-term records in brackish-marine and lake sediments (Wood et al., 2021). In lakes, chrysophyte cysts can provide long-term records that reveal group-specific phytoplankton dynamics over long time scales (Korkonen et al., 2017). While microfossil data provide continuous (semi-)quantitative records of the relative biomasses of the represented taxa and larger taxonomic groups (e.g., cyanobacteria, diatoms, and dinoflagellates) over geological time scales, their biodiversity information is limited. Only a fraction of taxa within the phytoplankton community is usually represented in the fossil record, and therefore, respective data are likely biased (Bálint et al., 2018). Nevertheless, for those taxa that are suitable and sufficiently represented, highly informative demographic data can be generated from microfossil and resting stage records (Cermeño et al., 2013; Kremp et al., 2018; Matul et al., 2018). Furthermore, data on the temporal distribution of larger taxonomic groups as obtained from microfossil records can provide general information on trait composition and function of phytoplankton communities through taxonomic identity (Blank and Sánchez-Baracaldo, 2010).

2.3.2 Sedimentary ancient DNA

To capture biodiversity dynamics of phytoplankton through time, recent advances in sedimentary ancient DNA approaches can increase taxonomic coverage and resolution. DNA can be preserved for thousands or even millions of years in natural sedimentary archives, such as limnic sediments (Capo et al., 2021; Clarke et al., 2019), marine sediments (Armbrecht et al., 2022; Coolen et al., 2009, 2013), paleosols (Frindte et al., 2020; Semenov et al., 2020) and permafrost (Kjær et al., 2022; Willerslev et al., 2003). Compared to microfossils, a distinctive characteristic of ancient DNA data lies in their capability for broad taxonomic coverage. Because every organism contains DNA and the differences between species are defined by their DNA, in theory, DNA could be used to identify any organism that became part of the sediment deposits (Bálint et al., 2018). Establishing relative abundances of organisms from

their DNA record is challenging though. While fossilized remains of certain phytoplankton taxa can inform us about cell counts, DNA records can be informative about copy numbers of particular genes (Mejbel et al., 2021). Since gene copy numbers can vary by orders of magnitude across species, inferences about abundance can be challenging with methods that target many taxa at once (Vasselon et al., 2018). If the focus is on a narrow set of taxa, gene copy number information provided by quantitative analyses (qPCR or ddPCR) might be more readily translated into abundance information, especially if the range of gene copy numbers per cell can be estimated for the focal species (Godhe et al., 2008). This approach potentially allows one to obtain demographic information on a targeted taxon in specific sediment horizons.

2.3.3 Resurrectable dormant resting stagesResurrection experiments

Living sediment archives are formed by temporal deposits of dormant resting stages, which can be obtained from organismsphytoplankton that produce long-lived resting cells/seeds (Härnström et al., 2011; Hinners et al., 2017) such as, but are also represented in organisms such as marine microbes (Lomstein et al., 2012; Wörmer et al., 2019), specificterrestrial plants (McGraw et al., 1991; Sallon et al., 2008), and zooplankton (Kerfoot and Weider, 2004; Pauwels et al., 2010)., and phytoplankton (Härnström et al., 2011; Hinners et al., 2017).

Laminated sediments, which form under anoxic conditions due to the absence of mixing by benthic fauna, contain distinct age cohorts of dormant or quiescent phytoplankton (Ellegaard et al., 2017). Such resting stages can germinate when exposed to oxygen, and cells start growing when suitable temperature, light, and nutrient conditions are provided. A number of studies have demonstrated the "resurrection" potential of different phytoplankton taxa after extended periods of resting, ranging from decades to millennia (Bolius et al., 2025; Härnström et al., 2011; Medwed et al., 2024; Sanyal et al., 2022).

Phytoplankton strains that have been re-established from germinated resting stages of different temporal sediment layers can be characterized pheno- and genotypically (Härnström et al., 2011; Hinners et al., 2017; Medwed et al., 2024). Comparison of trait values among temporal cohorts provides information on trait changes, their rates of change, and the mechanisms behind those changes (Hattich et al., 2024). The general adaptive potential of phytoplankton has already been documented in resurrection experiments focusing on

dDifferent phytoplankton functional traits, e.g.,such as temperature-dependent growth and nutrient uptake (Hattich et al., 2024), resting stage formation (Hinners et al., 2017), and toxicity (Wood et al., 2021). have been measured in laboratory experiments on resurrected strains and resulting data have been used in ecosystem models (Hinners et al., 2019). Traits that are of particular interest for ecosystem modeling include growth characteristics dependent on environmental conditions (reaction norms), cell size, mortality rates, grazing rates (of zooplankton), toxicity, as well as triggers and rates of transition between life cycle stages. The structure of ecosystem models is often based on such phytoplankton functional traits, which describe the dependence of phytoplankton organisms on external factors (e.g., reaction norms), their life cycle (e.g., life cycle transitions), or interactions with other organisms (e.g., cell size, toxicity). To realistically assess the extent of adaptations to environmental changes and to use this information for future ecosystem models, it is therefore important to collect comprehensive information on changes in phytoplankton functional traits using resurrection experiments.

Phenotypic trait data from resurrected cultures can also be linked to their underlying genetic components. A common method for this is represented by genome-wide association studies (GWAS) (Hirschhorn and Daly, 2005; Uffelmann et al., 2021; Visscher et al., 2017). GWAS connect variations in the DNA sequence, known as single nucleotide polymorphisms (SNPs), to a specific trait. To do so, it is necessary to validate the candidate loci identified in GWAS by experiments that target the phenotypic functionality of these loci (Pfenninger, 2024). GWAS approaches can help to determine if certain functional groups of genes (e.g., those involved in oxidation or CO_2 fixation) were selected for or lost over time. In addition, GWAS approaches can help to determine whether the traits of interest are polygenic and can thus be adequately modeled as continuous quantitative traits. The success of this method depends on several factors, including the quality of the phenotypic data and the accuracy of the genetic data. Moreover, when co-analyzing compositional DNA data and quantitative phenotypic data, careful transformation, standardization, and the use of specialized statistical methods are essential to avoid misleading conclusions (Gloor et al., 2017).

3 Integration of data from sediment archives into evolutionary ecosystem models

Ecosystem models provide a powerful tool to study the functioning of marine ecosystems and their responses to environmental change. For example, ecosystem models can be used to understand global patterns of phytoplankton diversity (Dutkiewicz et al., 2020; Ward et al., 2012). In addition, they can help to identify potential feedback loops (e.g., between cyanobacteria and their environment (Hense, 2007) and trade-offs (e.g., between phytoplankton diversity and productivity, (Smith et al., 2016)). Finally, ecosystem models can simulate how phytoplankton (and zooplankton) respond to different biotic and abiotic factors, including viruses (Krishna et al., 2024; Weitz et al., 2015), eutrophication (Gustafsson et al., 2012), ocean acidification (Dutkiewicz et al., 2015), and temperature changes (Elliott et al., 2005; Lee et al., 2018).

3.1 The neglected role of evolutionary adaptation in ecosystem models

Over the past few years, ecosystem models have been increasingly used to estimate the impact of global warming on marine ecosystems and their functioning. Although the results of such studies are relevant for stakeholders (Intergovernmental Panel on Climate Change (IPCC), (Allan et al., 2021)), current models vary widely in their formulations and predictions, with some models even disagreeing on the direction of change (Laufkötter et al., 2015, 2016; Tittensor et al., 2021). We argue that a major uncertainty in current models is that they do not account for the high adaptive potential of phytoplankton.

Experiments and observations demonstrated that phytoplankton adaptation can be important on multi-year perennial time scales (Aranguren-Gassis et al., 2019; Hattich et al., 2024; O'Donnell et al., 2018) and may hence alter predicted ecosystem changes notably (Ward et al., 2019). Indeed, a recent modeling study revealed that adaptation can significantly reduce simulated warming-related changes in phytoplankton phenology and relative taxa abundance (Hochfeld and Hinners, 2024a). Changes in phenology and relative taxa abundance, in turn, may have a direct impact on ecosystem functioning (Edwards and Richardson, 2004; Hochfeld and Hinners, 2024b; Litchman et al., 2015). To conclude, it is becoming increasingly clear that adaptation cannot be neglected in global warming simulations, putting current models and their predictive ability into question.

322   Evolutionary adaptation can be integrated into ecosystem models by allowing for one
323 or more phytoplankton traits to change on intergenerational time scales. In case of changing
324 temperature, for example, phytoplankton thermal adaptation can be represented with an
325 evolvable optimum temperature for growth (Beckmann et al., 2019; Kremer and Klausmeier,
326 2017). Different approaches exist to integrate adaptation into ecosystem models, with the most
327 suitable approach depending on the research question, see Box 1 for details. Overviews can
328 also be found in Beckmann et al., (2019) and Klausmeier et al., (2020b). However, integrating
329 adaptation into ecosystem models brings new challenges, such as identifying the relevant traits
330 and the associated limits and trade-offs (O'Donnell et al., 2018; Ward et al., 2019). One
331 approach to obtain the necessary evolutionary information is represented by evolution
332 experiments, in which populations are kept under controlled environmental conditions for long
333 periods of time (weeks, months, or even years) in order to measure their evolutionary
334 adaptation to these environmental conditions (Hinners et al., 2024; O'Donnell et al., 2018;
335 Schaum et al., 2017). Since such experiments can neither replicate the complexity of real
336 ecosystems nor long-term environmental change, we argue that sediment archives as "natural
337 evolution experiments" represent a valuable complementary source of information, which we
338 explain further below.

339

340 **Box 1: Evolution in ecosystem models**

341 Different approaches exist to integrate evolutionary processes into ecosystem models. The
342 approaches differ in their biological complexity and their computational efficiency, which
343 makes them suitable for different applications (see Table 1). Thus, the mutational algorithm
344 should be chosen depending on the research question.

345   Individual-based models (IBMs) provide the most complex and most realistic
346 representation of evolutionary adaptation. IBMs simulate individual cells with their individual
347 phenotypic trait values (Beckmann et al., 2019; Clark et al., 2011; Collins, 2016); a prominent
348 approach was developed by (Beckmann et al., 2019), who assume that individual cells take up
349 nutrients, grow, divide, and die. Evolution is implemented through random mutations, which
350 occur every several hundred cell divisions (Lenski and Travisano, 1994). The new trait value
351 of the mutated daughter cell is sampled randomly from a normal distribution, which is centered
352 at the parental trait value with a prescribed standard deviation. Thus, small mutations are much

more likely than large mutations, while beneficial and deteriorating mutations are equally likely. With natural selection acting over time, the cells with the highest fitness that need the lowest time to divide again become dominant. Maladapted cells, on the contrary, die off eventually if their doubling rate is lower than stochastic losses like mortality and grazing, leading to progressive adaptation of the entire population.

Simulating natural populations with millions of individuals requires a lot of computational power. To reduce computational power demands, identical cells are often grouped into one model variable (Hellweger and Bucci, 2009), a so-called super-individual or agent. Due to the larger number of cells combined into one agent, mutations are assumed to occur more frequently but with a smaller step size (i.e., standard deviation) (Beckmann et al., 2019). Even though agent-based models require less computational power than IBMs, they are usually only integrated into 0-dimensional model environments.

A computationally much more efficient approach is provided by continuous trait-diffusion models (Chen and Smith, 2018; Le Gland et al., 2021; Smith et al., 2016), which do not resolve individual phenotypes as discrete entities. Instead, they compute the mean and variance of a trait for the entire phytoplankton compartment. Trait variance represents the diversity of ecotypes, with mutations adding new variance that can be selected. Selection, in this context, means that the mean trait increases when higher trait values are associated with higher net growth rates. Due to their low computational power requirements, continuous trait-diffusion models can be integrated into 1D or 3D model environments. Their simplistic representation of evolution, however, comes at a price: While the shape of the trait distribution must be prescribed, trade-offs between traits are difficult to implement, and evolutionary branching cannot be represented.

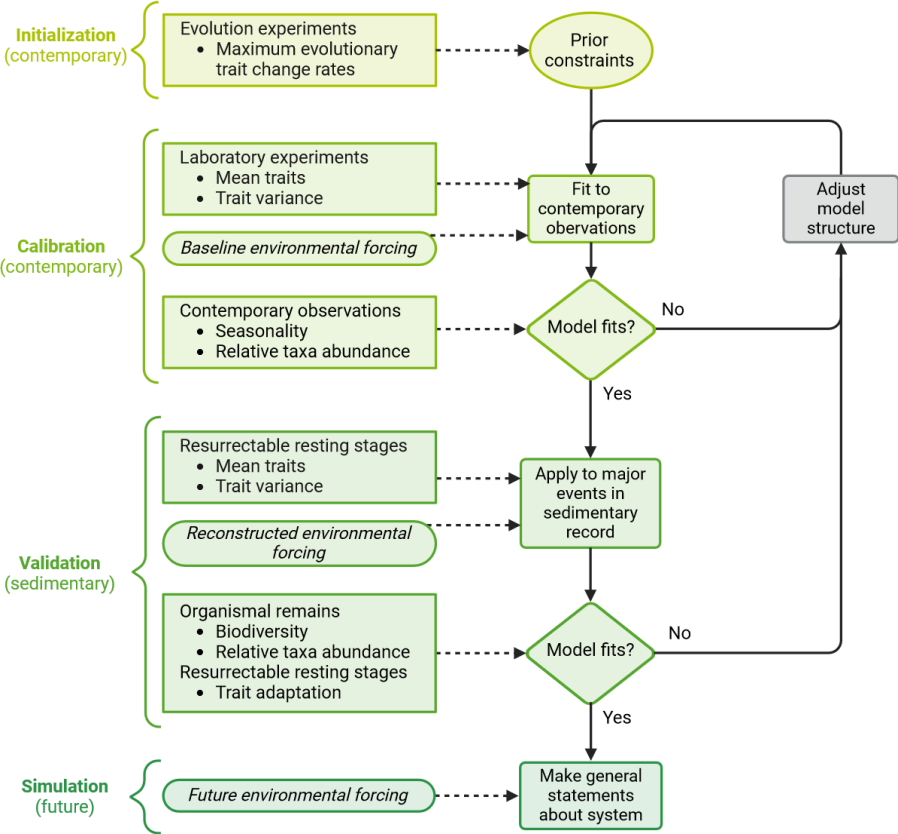
Multi-compartment trait-diffusion models can be described as the discretized version of continuous trait-diffusion models. The phytoplankton compartment is divided into multiple sub-compartments that differ slightly in one or more trait values (Hinners et al., 2019; Kremer and Klausmeier, 2013; Sauterey et al., 2017). Mutations are implemented as small, non-random fluxes of biomass between the sub-compartments. This approach is of intermediate biological complexity, which is also reflected in computational power demands. Multi-compartment trait-diffusion models require more power than continuous trait-diffusion models but less than IBMs or agent-based models and can hence be integrated into 1D model environments.

	IBM/Agent-based model	Continuous model	Multi-compartment model
Mutations	randomly drawn from normal distribution	small mutations	small mutations
Biological complexity	high	low	intermediate
Computational power requirements	high	low	intermediate
Applicability	0D models	0D to 1D to 3D models	0D to 1D models

Table 1: Summary of evolutionary modeling approaches and their applicability.

3.2 Building an evolutionary ecosystem model including data from sediment archives

It is a considerable challenge to develop ecosystem models that can be applied equally well to past, present, and future scenarios. Most state-of-the-art ecosystem models are developed in a two-step process that comprises the definition of prior estimates of parameter values (initialization) and the iterative fit to contemporary observations through parameter adjustment (calibration). We argue that this approach relies too heavily on how an ecosystem is structured in the present, so that models may no longer be applicable when ecosystem structure has changed in the future. To avoid these problems, models should represent fundamental processes that apply more generally instead of being tailored to a specific ecosystem. The general applicability of a model can be tested with an additional step during model development, validation, which makes use of data from sediment archives. While validation is already common for atmosphere and ocean models (Hollingsworth, 1994; Tonani et al., 2015), it has been largely ignored by the ecosystem modeling community. A recent study presented a validation approach for non-evolutionary terrestrial ecosystem models, which is mainly based on plant remains (Alsos et al., 2024). Our approach focuses on phytoplankton, key players in marine ecosystems and respective models. Due to the high evolutionary potential of phytoplankton, we additionally consider evolutionary processes.

411   The development approach for evolutionary ecosystem models that we propose here
412   comprises three different steps: initialization, calibration, and validation (Fig. 2). Both
413   initialization and calibration are performed using contemporary data, while validation requires
414   data from sediment archives. Only when all three steps have been completed should a model
415   be used to simulate future ecosystem changes.

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417   **Figure 2:** Conceptual framework for the development of an evolutionary ecosystem model that can be
418   applied equally well to past, present, and future scenarios. Shown are the three different steps of model
419   development (initialization, calibration, validation), the following application of the model (simulation),
420   and the data required for each step. The figure was created with BioRender.com.

421

Initialization requires prior estimates of parameter values that need to be valid regardless of the simulated environmental scenario. Such parameters include constraints on adaptation, such as maximum evolutionary trait change rates, which are, however, difficult to assess. For example, evolutionary trait change rates can be assessed by comparing ancestral trait values to those from populations evolved in a new environment for a specific time after accounting for plastic responses (Collins and Bell, 2004; Hutchins et al., 2015; Listmann et al., 2016). In addition, it is possible to measure changes in fitness proxies, most commonly population growth rate or lineage competitive ability (Elena and Lenski, 2003). However, interpretation is not straightforward since the relationship between fitness and its proxies may change over time (Collins et al., 2020). Finally, genetic mutation rates can be estimated via genome sequencing (e.g., (Krasovec et al., 2019), but genetic mutation does not necessarily translate into trait changes. While functional traits may depend on multiple genes (epistasis), one gene may affect multiple traits (pleiotropy) (Lässig et al., 2017; Østman et al., 2012; Tyler et al., 2009). To conclude, evolutionary trait change rates can only be assessed roughly and require further adjustment in the next steps of model development.

The goal of model calibration is to fine tune the model parameters and the model structure until the model reproduces contemporary observations. To do so, initial values for mean traits and trait variance are required (Fig. 2). These parameters can be measured in the laboratory for recently sampled organisms (Lehtimaki et al., 1997; Vincent and Silvester, 1979). The model is then forced with a baseline environmental forcing, usually a steady seasonal forcing that represents present-day conditions. Using this forcing, the model is run until it reaches a steady state, where phenology and taxa abundances repeat each season. Simulated phenology and taxa abundances are then compared to contemporary observations from seagoing research and remote sensing. If the model does not reproduce the observations, model parameters and structure are adjusted iteratively until model output and observations match. When adjusting parameter values, care must be taken to keep all values within a realistic range, especially when such a range can be constrained by measurements e.g., for traits like half-saturation constants and maximum growth rates (Eppley et al., 1969; Hinners et al., 2017). When adjusting the model structure, on the other hand, it should be reconsidered whether the most relevant processes (e.g., life cycle transitions, mortality, ecological interactions such as grazing) are included and described realistically.

453   As the final step, model validation aims to test if the model is equally applicable to past,
454   present, and (by implication) future scenarios by comparing the model output to independent
455   validation data. We argue that data from sediment archives are ideally suited for validation,
456   with a contemporarily calibrated model being successfully validated if it can represent major
457   shifts in community structure and/or function that are present in the sediment record. As a first
458   step, validation needs initial values for the mean and variance of the relevant traits. These
459   parameters can be measured in the laboratory for resurrected organisms sampled from the
460   sediment layer that corresponds to the beginning of the validation period. In addition,
461   environmental conditions during the validation period must be reconstructed to create a forcing
462   for the model. Extreme climate periods such as the Pliocene (5.3-2.6 million years ago), when
463   the global mean surface temperature was ~2°C higher than today and more than 10°C higher
464   at high latitudes (Ballantyne et al., 2010; Haywood et al., 2000; Salzmann et al., 2008), or the
465   last interglacial period (128,000-116,000 years ago, Muhs, 2002; Stirling et al., 1998), when
466   temperatures in the Arctic were up to 5°C higher than today (North Greenland Ice Core Project
467   members, 2004)Holocene thermal maximum (8,000-5,000 years ago, up to 5 °C above
468   preindustrial levels) would be ideally suited to test the model's validity in extreme and
469   changing climates (Renssen et al., 2012; Tierney et al., 2020). The simulated biodiversity and
470   relative taxa abundances can then be compared to organismal remains from different sediment
471   layers throughout the validation period. Similarly, simulated trait changes can be compared to
472   results from resurrection experiments, which are performed with organisms from different
473   sediment layers of the validation period. If the contemporarily calibrated model cannot
474   reproduce major events in the sediment record, this implies that the model's structure and
475   parameterization are not general to both contemporary and past systems and should therefore
476   not be used to make predictions.

477   For example, (Gibbs et al., 2020) used an evolutionary ecosystem model that was
478   parameterized in accordance with contemporary laboratory measurements to reproduce an
479   observed shift in the trophic status of coccolithophores after the end-Cretaceous mass
480   extinction. However, while the model produced an evolutionary response that was qualitatively
481   consistent with the sediment record, the simulated evolutionary response progressed at a rate
482   that was orders of magnitude too fast. This indicates that the model structure would require
483   further adjustments until both contemporary and sedimentary data are reproduced before the
484   model could be used predictively. This indicates that the model would require further

adjustments to allow reproduction of both contemporary and sedimentary data before the model could be used predictively.

While such a model could be recalibrated to fit the past data, we do not recommend this approach, because the ad hoc adjustment of the model parameters does not fix the underlying problem. In addition, calibration is not possible when making predictions. Therefore, instead of recalibrating the model to past data, we advocate refining the model structure to better represent processes that do apply generally, across past, present, and future systems. After recalibration to contemporary data, the refined model could be tested again against past data. Repeating this process iteratively until both contemporary and past data can be reproduced with the same model assures that the model can provide meaningful statements about an ecosystem's possible response to future climate changes.

To estimate remaining model uncertainties, the uncertainties in parameter values and environmental forcing can be used for sensitivity experiments. The extent to which the model structure influences the results can be assessed by comparing the model results before and after the structural change.

3.3. Exemplary implementation

Below, we describe an exemplary implementation of our approach using the following research question: How did and will the phytoplankton community in the Baltic Sea change during the past and future 100 years, and what role does thermal adaptation play in these changes?

For our exemplary implementation, we assume that sediment cores have already been collected and analyzed. Thus, it is known which temperature-dependent traits have changed over the past 100 years before our approach is implemented. In this example, we assume that an adaptive response in the optimum temperature is evident in the sediment record, as reported in e.g., Hattich et al. (2024).

1. Ecosystem model setup and initialization:

As a first step, the evolutionary ecosystem model structure is built. The model structure mathematically describes the dynamics and interactions between components of the Baltic Sea ecosystem that are considered relevant for answering the research question. In this case, the

model structure includes equations for nutrients, the most relevant phytoplankton functional groups in the Baltic Sea (dinoflagellates, diatoms, and cyanobacteria), and dead organic matter (detritus). For each phytoplankton functional group, a growth equation is formulated, including a limitation function for nutrients. In addition, functions for life cycle transitions (e.g., following (Hochfeld and Hinners, 2024a) and mortality are implemented. The respective formulations and parameters (i.e., half- saturation constants, basic transition rates in life cycle transition functions, basic mortality rates in mortality functions) are adopted from literature (e.g., Eppley et al., 1969; Hense and Beckmann, 2006; Hinners et al., 2019). A 1-dimensional water column model is used for the simulations (e.g., GOTM, Li et al., 2021; Umlauf et al., 2005), evolution is enabled using a multi-compartment model (e.g., Hinners et al., 2019). The evolutionary algorithm is initialized with experimentally derived evolutionary trait change rates for optimum temperature, which can be obtained from literature (e.g., Jin and Agustí, 2018; Listmann et al., 2016).

2. Model calibration:

For calibration, the model needs to be complemented by temperature limitation functions for the simulated taxa. These temperature limitation functions are established from the thermal reaction norms of resurrected resting stages from the uppermost sediment layer, including the mean and the variance of the optimum temperature. In addition, a baseline temperature forcing is created to represent recent annual temperature fluctuations in the Baltic Sea, e.g., by using temperature data from the Copernicus database (https://resources.marine.copernicus.eu/products). The model is then run with the baseline forcing until a steady state is reached, where the simulated dynamics repeat each season. Finally, the model output is compared to existing, recent data on the relative abundances and seasonal dynamics of the simulated phytoplankton taxa (e.g., Hjerne et al., 2019). If the model does not reproduce the data, both the model structure, i.e., the functions for nutrient limitation, life cycle transitions, and mortality, as well as the corresponding parameters initialized in step 1 are adjusted until the model output fits the data.

3. Model validation:

For validation, the model is initialized with mean optimum temperatures and variances from 100 years ago. For this purpose, data from resurrection experiments with resting stages from the historic sediment layer are used (e.g., Hattich et al., 2024). A hindcast temperature forcing

for the last 100 years is reconstructed from the sedimentary record using biotic proxies such as microfossils and biomarkers (e.g., Kabel et al., 2012; Wittenborn et al., 2022). After applying the hindcast forcing to the model, model performance is evaluated based on a biological sediment assessment of changes in relative taxa abundance (using genetic analyses and the assessment of resting stages across the sediment, e.g., Kremp et al., 2018; Schmidt et al., 2024), and changes in the optimum temperatures of these taxa (using resurrection experiments, e.g., Hattich et al., 2024). If the model is not able to reproduce changes in relative taxa abundances and past adaptation of the optimum temperature, its structure needs to be refined. For example, the simulated evolutionary response may be less pronounced than the one derived from the sedimentary record. This issue could be fixed by increasing the evolutionary trait change rates until the model reproduces the observed evolutionary changes, which may result in unrealistically high evolutionary trait change rates. Instead of simply adjusting parameters, it may therefore be necessary to consider other hitherto disregarded processes that may exert an additional selection pressure, for example, a temperature-dependent cyst mortality (Hinners et al., 2019). If the model reproduces past adaptive changes and taxa abundances with the new cyst mortality function, model performance is tested again for the baseline environmental forcing. If the revised model still reproduces the calibration data, it is equally applicable to the past 100 years and the present and can therefore be used for the intended simulations of future climate change.

4 Challenges and potential of using data from sediment archives for evolutionary ecosystem modeling

Our approach has the potential to increase the informative value of model projections of future changes in marine ecosystems. However, there are still some challenges associated with it.

A major challenge is posed by the low temporal resolution of sediment records, which can range from multi-centennial to annual depending on the sedimentation rate (Abrantes et al., 2005; Maslin et al., 2003). Thus, phenological information is missing even in high-resolution records, meaning that simulated phenology cannot be validated using data from sediment archives. Instead, simulated phenology can be validated using monitoring data, which may go back several decades (Wasmund et al., 2019). In addition, preservation issues can lead

575 ~~to sediment horizons being lost for analysis due to low concentrations of total organic carbon.~~
576 ~~Proxies for the reconstruction of environmental conditions and DNA also suffer from~~
577 ~~preservation/degradation biases and are therefore not independent from each other (Dommain~~
578 ~~et al., 2020; Mitchell et al., 2005; Wakeham and Canuel, 2006; Zonneveld et al., 2010).~~
579 ~~Preservation/degradation biases in biological data may lead to incomplete information on mean~~
580 ~~traits and trait variance.~~

581 Assuming that evolutionary change in phytoplankton can occur on a decadal time scale
582 (Irwin et al., 2015), sediments that accumulate at similar or even higher rates, which is usually
583 the case in lakes and marginal seas, should allow the detection of evolutionary change (based
584 on resurrection experiments or genetic analyses). At sites with lower sedimentation rates, rates
585 of evolutionary change may be underestimated. It is therefore recommended to work in
586 environments with high sedimentation rates (e.g., $\geq$ 1 mm/year) to investigate evolutionary
587 changes. In addition, the age model uncertainty, which increases with the age of the sediments,
588 can lead to inaccuracies in the determined rates of evolutionary change. Depending on the
589 depositional environment, preservation rates (decomposition rates) of organic matter vary
590 greatly (Canfield, 1994; Hedges and Keil, 1995; Wakeham and Canuel, 2006). Preservation is
591 lowest in oxic environments with low sedimentation rates and highest in anoxic environments
592 with high sedimentation rates (Canfield, 1994). Differential preservation may also bias
593 estimates of relative abundance, although structurally similar organic compounds are expected
594 to be similarly preserved (Wakeham and Canuel, 2006). To determine possible effects of
595 preservation on the estimates of (relative) abundance and evolutionary changes, it is important
596 to estimate the content of total organic carbon in the sediment. For the investigation of
597 evolutionary changes, it is therefore recommended to work in environments with high
598 sedimentation rates, low age model uncertainty, and hypoxic to anoxic conditions. Among
599 others, the Baltic Sea, the Black Sea, the Cariaco Basin, and many lakes represent such suitable
600 environments.

601 Dormant rResting stages that have been preserved in the sediment record and could be
602 revived for experiments may not be representative of the entire population at the time of
603 deposition, and therefore may not be representative of its traits. However, assuming that the
604 fittest individuals of a population were most abundant in the past and hence are most abundant
605 in the sediment, we should be able to measure representative mean trait values for the
606 population. Nevertheless, we cannot rule out that storage in the sediment may have distorted

607 the measurable characteristics of a population. To obtain reliable estimates of trait variance,

608 experimental studies on phytoplankton traits should therefore aim to characterize as many

609 strains as possible, e.g., using high-throughput methods (Argyle et al., 2021). Proxies for the

610 reconstruction of environmental conditions and DNA can also suffer from

611 preservation/degradation biases and are therefore not independent from each other (Dommain

612 et al., 2020; Mitchell et al., 2005; Wakeham and Canuel, 2006; Zonneveld et al., 2010).

613 Evolutionary models require knowledge of how rapidly and how far the aforementioned

614 traits can change from generation to generation, as well as of the trade-offs between traits

615 (Levins, 1962; Litchman et al., 2007) and ultimate constraints on adaptation (Klausmeier et al.,

616 2020a). Such information is available from evolution experiments (Hinners et al., 2024), but it

617 is still unclear how applicable such information will be when moving from a highly simplified

618 evolution experiment to a more complex community context. A major challenge is to link trait

619 changes to changes in fitness. While the relationship between a fitness proxy and actual fitness

620 may change over time (Collins et al., 2020), fitness is largely determined by species interactions

621 (Schabhüttl et al., 2013). Based on the assumption that the fittest phytoplankton taxa are also

622 the most abundant in the sediment, sediment archives make it possible to estimate the relative

623 fitness of different taxa. However, the validity of this assumption might be challenged by

624 ecological and evolutionary complexities, and possible preservation differences between

625 taxa. Preservation differences might be evaluated by synthesizing information from different

626 proxies of abundance (e.g., biomarkers and sedimentary ancient DNA). Knowledge on species’

627 biology and ecology should be informative about the confounding effects of ecological and

628 evolutionary complexities, such as demographic trade-offs, differential responses to

629 environmental fluctuations (Melbinger and Vergassola, 2015), temporal trade-offs (Betini et

630 al., 2017), etc. Consequently, the validity of the fitness = abundance assumption should be

631 tested in each individual case.

632 Despite limitations and knowledge gaps, sediment archives represent a valuable source

633 of information that has the potential to advance ecosystem model development and hence

634 model projections of marine ecosystem change. As pointed out above, a crucial step in

635 ecosystem model development is to make sure that models are equally applicable to past,

636 present, and future scenarios before using them predictively. This requires validation data that

637 are independent of the data used for calibration. Moreover, validation data need to cover the

638 complexity of marine ecosystems and long-term environmental changes over hundreds to

thousands of years. While data from laboratory, mesocosm, or marine monitoring studies only partly fulfill these criteria, sediment archives fulfill all of them. Furthermore, the approach presented here is not limited to phytoplankton, but can be applied to other organisms that are well-represented in the sediment record, such as marine microbes (Wörmer et al., 2019), zooplankton (Isanta-Navarro et al., 2021; Wersebe and Weider, 2023), viruses (Coolen, 2011), and terrestrial plants (Alsos et al., 2024). Depending on the chosen group of organisms, its applicability for evolution experiments, and its potential to survive in the sediment or to be identified by microfossils or DNA, our described approach may require adjustment.

5 Conclusions

Marine communities perform functions that are essential for the environment and for humanity. However, it is largely unknown how these functions will change under global warming, and the possibility of positive feedbacks, irreversible tipping points, and ecosystem collapse must be considered. It is therefore crucial to develop tools that provide reliable estimates of future changes in marine ecosystems.

Ecosystem models represent a promising tool for predicting marine ecosystem change, but their current projections are largely inconsistent. Here, we present a promising approach that can increase the informative value of ecosystem model projections. We argue that a major uncertainty in current ecosystem models is that they largely ignore evolutionary processes, which can be highly relevant on perennial time scales. In addition, current ecosystem models are typically calibrated to contemporary data and then used for projections without validating that they are equally applicable to past (and by implication, future) scenarios. We suggest not only to calibrate evolutionary ecosystem models against contemporary observations, but also to validate the calibrated models against major evolutionary ecosystem changes that are present in sediment records. Compared to data from conventional experiments and marine monitoring, sediment records make it possible to map the complexity of real ecosystems and long-term environmental changes. Only if a contemporarily calibrated evolutionary ecosystem model can reproduce observations from sediment records, can we have some confidence in its projections of future ecosystem change.

668   Some challenges remain, especially regarding the low temporal resolution of sediment
669   archives and potential biases due to preservation differences.~~their partly biased information.~~
670   Nevertheless, data from sediment archives provide a unique opportunity to learn from the past
671   and hence have the potential to take ecosystem models and their projections of future ecosystem
672   change a crucial step forward. The approach presented here is not limited to phytoplankton, but
673   can be applied to other organisms and ecosystems.

674

Author contribution

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691

Competing interests

693   The authors declare that they have no conflict of interest.

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