https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

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

Isabell Hochfeld[1], Ben A. Ward[2], Anke Kremp[3], Juliane Romahn[4,5,6], Alexandra Schmidt[7,8], Miklós Bálint[4,5,6], Lutz Becks[9], Jérôme Kaiser[3], Helge W. Arz[3], Sarah Bolius[3], Laura S. Epp[7], Markus Pfenninger[4], Christopher A. Klausmeier[10], Elena Litchman[10], and Jana Hinners[11]

[1]Institute of Marine Ecosystem and Fishery Science, University of Hamburg, Germany
[2]School of Ocean & Earth Science, University of Southampton Waterfront Campus, Southampton, United Kingdom
[3]Leibniz Institute for Baltic Sea Research Warnemünde IOW, Rostock, Germany
[4]Senckenberg Society for Nature Research, Frankfurt, Germany
[5]LOEWE Centre for Translational Biodiversity Genomics, Frankfurt, Germany
[6]Institute of Insect Biotechnology, Justus-Liebig University, Gießen, Germany
[7]Environmental Genomics, Department of Biology, University of Konstanz, Germany
[8]Max Planck Institute of Animal Behavior, Radolfzell, Germany
[9]Aquatic Ecology and Evolution, Department of Biology, University of Konstanz, Germany
[10]Kellogg Biological Station, Michigan State University, U.S.A.
[11]Hemholtz-Center Hereon, Geesthacht, Germany

Correspondence to: Isabell Hochfeld (isabell.hochfeld@uni-hamurg.de)

E-mail addresses and ORCIDs:
Isabell Hochfeld: isabell.hochfeld@uni-hamurg.de | 0000-0002-5705-0549
Ben A. Ward: b.a.ward@soton.ac.uk | 0000-0003-1290-8270
Anke Kremp: anke.kremp@io-warnemuende.de | 0000-0001-9484-6899
Juliane Romahn: juliane.romahn@senckenberg.de | 0009-0008-1464-8277
Alexandra Schmidt: alexandra.schmidt@uni-konstanz.de | 0000-0001-9262-0941
Miklós Bálint: miklos.balint@senckenberg.de | 0000-0003-0499-8536
Lutz Becks: lutz.becks@uni-konstanz.de | 0000-0002-3885-5253
Jérôme Kaiser: jerome.kaiser@io-warnemuende.de | 0000-0002-0290-9088
Helge W. Arz: helge.arz@io-warnemuende.de | 0000-0002-1997-1718
Sarah Bolius: sarah.bolius@io-warnemuende.de | 0000-0003-3542-6004
Laura S. Epp: laura.epp@uni-konstanz.de | 0000-0002-2230-9477
Markus Pfenninger: markus.pfenninger@senckenberg.de | 0000-0002-1547-7245
Christopher A. Klausmeier: klausme1@msu.edu | 0000-0002-6987-5871
Elena Litchman: litchman@msu.edu | 0000-0001-7736-6332
Jana Hinners: jana.hinners@hereon.de | 0000-0002-5145-2539

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

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 "collect" and 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), 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 therefore remains questionable. Here, we propose to use data from sediment archives to validate evolutionary

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

ecosystem models before using them predictively, and discuss how this approach can improve model projections.

Compared with the period 1850–1900, global surface temperature has already increased by 1.25 °C and, under the most extreme emissions scenario, is expected to increase by up to a further 3.5 °C by the end of the century (IPCC scenario SSP5-8.5, Allan et al., 2021). The current state of warming has already caused changes in marine communities (Peer and Miller, 2014; Poloczanska et al., 2013; Wasmund et al., 2019), which perform ecosystem functions that are vital to human societies, including food production (Hollowed et al., 2013) and carbon sequestration (Hain et al., 2013). The response of these ecosystem services under ongoing global warming remains subject to great uncertainty, and there is a real but unknown risk of positive feedbacks, irreversible tipping points, and ecosystem collapse (Lenton et al., 2008).

Dynamic ecosystem models currently represent the best tool to understand complex feedbacks between evolving ecosystems and their environment, but it is a considerable challenge to develop models that would apply equally well to past, present, and future scenarios. Despite their great potential, current models project diverging changes in ecosystem functions like carbon cycling and net primary production (Laufkötter et al., 2015, 2016). Since models hardly agree on the direction of change, the validity of current model projections remains questionable.

To improve model projections, we need (I) to verify that all relevant processes are considered and (II) to validate projections with long-term data. Regarding (I), current ecosystem models largely ignore a crucial process that can influence ecosystem responses to 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 (Beckmann et al., 2019; Le Gland et al., 2021; Sauterey et al., 2017), 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 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 & De Vernal,

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

2007), other organismal remains such as DNA (Alsos et al., 2022; Monchamp et al., 2016; Zimmermann et al., 2023), and dormant resting cells and seeds that 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 how the sediment record has been influenced by evolution.

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

2 Sediment archives – understanding phytoplankton responses to environmental change

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

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

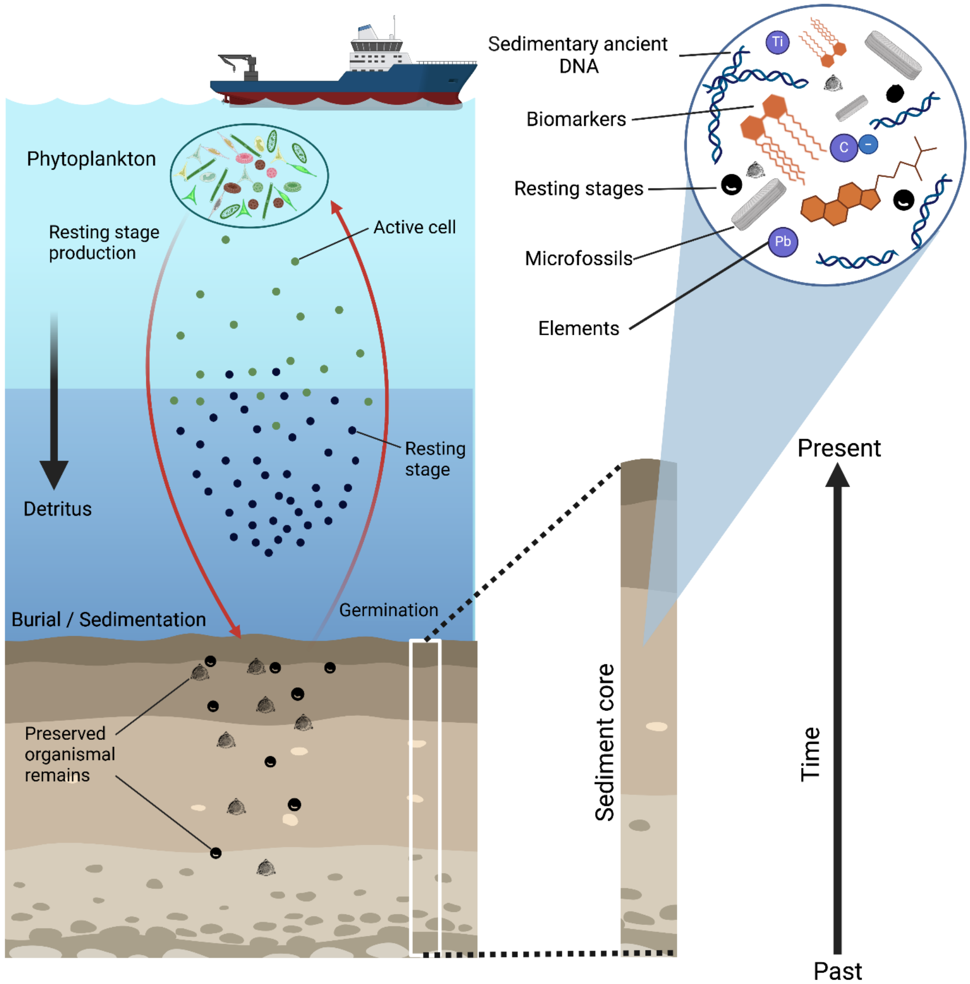

Figure 1: Overview of different types of data (environmental and biological) that can be obtained from sediment archives. **Left:** Schematic showing the deposition of organismal remains in the sediment. Red arrows indicate resting stage production, their deposition in the sediment, and the germination 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.

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

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, 2015).

2.2 Environmental data

Abiotic and biotic proxies, or indicators, preserved in sediment archives allow reconstructing physicochemical characteristics of past marine and limnic environments. For example, surface salinity can be estimated using lipids (alkenones) produced by micro-phytoplankton species of the order Isochrysidales (Kaiser et al., 2017; Medlin et al., 2008; Rosell-Melé, 1998). Some trace metals and their isotopes are indicators for past suboxic to euxinic conditions in the water column and/or the sediments (Brumsack, 2006; Dellwig et al., 2019). Relative assemblages of microfossils (e.g., resting stages of dinoflagellates, silica frustules of diatoms, calcareous shells of foraminifera) and their shell geochemistry provide important information not only on salinity, but also on pH, trophic state, and temperature, and are therefore powerful proxies (Cléroux et al., 2008; Hillaire-Marcel & De Vernal, 2007; Lear et al., 2002). Organic indexes based on biomarkers, e.g., alkenones (U^{K}_{37}, Prahl et al., 1988) or other membrane lipids derived

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

from archaea (TEX_{86}, Schouten et al., 2013) can be used to reconstruct surface and subsurface temperature. These and many other physical methods, biological proxies, and geochemical tracers find their diverse applications in paleoceanography (Hillaire-Marcel & De Vernal, 2007).

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

2.3 Biological data

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

2.3.1 Microfossils

Traditionally, the focus of research on sediment archives has been on fossilized plankton 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 some filamentous cyanobacteria 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.,

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

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 to obtain demographic information on a targeted taxon in specific sediment horizons.

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

2.3.3 Resurrection experiments

Living sediment archives are formed by temporal deposits of dormant resting stages, which can be obtained from organisms that produce long-lived resting cells/seeds such as specific plants (McGraw et al., 1991; Sallon et al., 2008), 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 (Härnström et al., 2011; Kremp et al., 2018; 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). Comparison of trait values among temporal cohorts provides information on trait changes, their rates of change, and the mechanisms behind (Hattich et al., 2024). Different traits, e.g., 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.

Phenotypic trait data from resurrected cultures can also be linked to their genetic traits. 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. 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

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

method depends on several factors, including the quality of the phenotypic data and the accuracy of the genetic data.

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), 2022), current models vary widely in their formulations and predictions, with some models even disagreeing on the direction of change (Laufkötter et al., 2015, 2016). 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 perennial time scales (Aranguren-Gassis et al., 2019; Hattich et al., 2024;

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 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, 2024). Changes in phenology and relative taxa abundance, in turn, may have a direct impact on ecosystem functioning (Edwards and Richardson, 2004; 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.

Evolutionary adaptation can be integrated into ecosystem models by allowing for one or more phytoplankton traits to change on intergenerational time scales. In case of changing temperature, for example, phytoplankton thermal adaptation can be represented with an evolvable optimum temperature for growth (Beckmann et al., 2019; Kremer and Klausmeier, 2017). Different approaches exist to integrate adaptation into ecosystem models, with the most suitable approach depending on the research question. Overviews can be found in Beckmann et al. (2019) and Klausmeier et al. (2020b). However, integrating adaptation into ecosystem models brings new challenges, such as identifying the relevant traits and the associated limits and trade-offs (O'Donnell et al., 2018; Ward et al., 2019). One approach to obtain the necessary evolutionary information is represented by evolution experiments (Hinners et al., 2024; Ward et al., 2019). Since such experiments can neither replicate the complexity of real ecosystems nor long-term environmental change, we argue that sediment archives as "natural evolution experiments" represent a valuable complementary source of information, which we explain further below.

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

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

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.

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

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

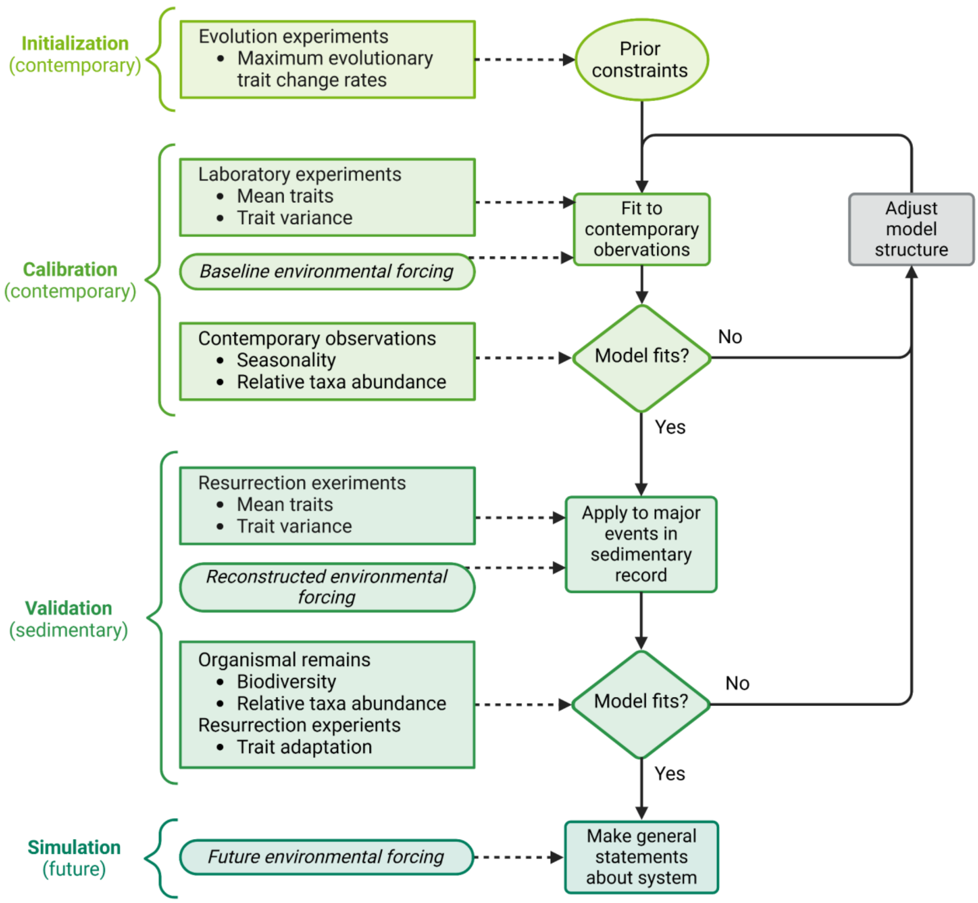

Figure 2: Conceptual framework for the development of an evolutionary ecosystem model that can be applied equally well to past, present, and future scenarios. Shown are the three different steps of model development (initialization, calibration, validation), the following application of the model (simulation),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

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

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

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., 2011; 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 (Lehtimäki et al., 1997; Vincent & 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.

As the final step, model validation aims to test if the model is equally applicable to past, present, and (by implication) future scenarios by comparing the model output to independent validation data. We argue that data from sediment archives are ideally suited for validation, with a contemporarily calibrated model being successfully validated if it can represent major shifts in community structure and/or function that are present in the sediment record. As a first step, validation needs initial values for the mean and variance of the relevant traits. These parameters can be measured in the laboratory for resurrected organisms sampled from the sediment layer that corresponds to the beginning of the validation period. In addition, environmental conditions during the validation period must be reconstructed to create a forcing for the model. Extreme climate periods such as the Holocene thermal maximum (8,000–5,000 years ago, up to 5 °C above preindustrial levels) would be ideally suited to test the model’s validity in extreme and changing climates (Renssen et al., 2012; Tierney et al., 2020). The simulated biodiversity and relative taxa abundances can then be compared to organismal remains from different sediment layers throughout the validation period. Similarly, simulated

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

trait changes can be compared to results from resurrection experiments, which are performed with organisms from different sediment layers of the validation period. If the contemporarily calibrated model cannot reproduce major events in the sediment record, this implies that the model's structure and parameterization are not general to both contemporary and past systems and should therefore not be used to make predictions.

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

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.

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

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., 2005). 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 to sediment horizons being lost for analysis due to low concentrations of total organic carbon. Proxies for the reconstruction of environmental conditions and DNA also suffer from preservation/degradation biases and are therefore not independent from each other (Dommain et al., 2020; Mitchell et al., 2005; Wakeham and Canuel, 2006; Zonneveld et al., 2010). Preservation/degradation biases in biological data may lead to incomplete information on mean traits and trait variance. Resting stages that have been preserved in the sediment record and could be revived for experiments may not be representative of the entire population at the time of deposition, and therefore may not be representative of its traits. However, assuming that the fittest individuals of a population were most abundant in the past and hence are most abundant in the sediment, we should be able to measure representative mean trait values for the population. To obtain reliable estimates of trait variance, experimental studies on phytoplankton traits should aim to characterize as many strains as possible, e.g., using high-throughput methods (Argyle et al., 2021).

Evolutionary models require knowledge of how rapidly and how far the aforementioned traits can change from generation to generation, as well as of the trade-offs between traits (Levins, 1962; Litchman et al., 2007) and ultimate constraints on adaptation (Klausmeier et al., 2020b). Such information is available from evolution experiments (Hinners et al., 2024), but it is still unclear how applicable such information will be when moving from a highly simplified evolution experiment to a more complex community context. A major challenge is to link trait changes to changes in fitness. While the relationship between a fitness proxy and actual fitness may change over time (Collins et al., 2020), fitness is largely determined by species interactions (Schabhüttl et al., 2013). Based on the assumption that the fittest phytoplankton taxa are also the most abundant in the sediment, sediment archives make it possible to estimate the relative fitness of different taxa.

Despite limitations and knowledge gaps, sediment archives represent a valuable source of information that has the potential to advance ecosystem model development and hence

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

model projections of marine ecosystem change. As pointed out above, a crucial step in ecosystem model development is to make sure that models are equally applicable to past, present, and future scenarios before using them predictively. This requires validation data that are independent of the data used for calibration. Moreover, validation data need to cover the 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 zooplankton (Isanta-Navarro et al., 2021; Wersebe and Weider, 2023), viruses (Coolen, 2011), and terrestrial plants (Alsos et al., 2024).

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.

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

Author contribution

Isabell Hochfeld: Conceptualization; project administration; visualization; writing – original draft; writing – review and editing. **Ben A. Ward:** Conceptualization; writing - original draft; writing – review and editing. **Anke Kremp:** Conceptualization; writing – original draft; writing – review and editing. **Juliane Romahn:** Conceptualization; visualization; writing – original draft; writing – review and editing. **Alexandra Schmidt:** Conceptualization; visualization; writing – original draft; writing – review and editing. **Miklós Bálint:** Conceptualization; writing – original draft; writing – review and editing. **Lutz Becks:** Conceptualization; writing – original draft; writing – review and editing. **Jérôme Kaiser:** Conceptualization; writing – original draft; writing – review and editing. **Helge W. Arz:** Conceptualization; writing – review and editing. **Sarah Bolius:** Conceptualization; writing – review and editing. **Laura S. Epp:** Conceptualization; writing – review and editing. **Markus Pfenninger:** Conceptualization; writing – review and editing. **Christopher A. Klausmeier:** Conceptualization; writing – review and editing. **Elena Litchman:** Conceptualization; writing – review and editing. **Jana Hinners:** Conceptualization; project administration; writing - original draft; writing – review and editing.

Competing interests

The authors declare that they have no conflict of interest.

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

Acknowledgements

This work was made possible by the funding of the project PhytoArk (K314/2020) by the Leibniz Association. BAW was funded by a Royal Society University Research Fellowship. EL and CAK acknowledge US NSF grants 17-54250 and 21-24800. JR, MB, and MP acknowledge support by the LOEWE-Centre TBG funded by the Hessen State Ministry of Higher Education, Research, and the Arts (HMWK, grant number LOEWE/1/10/519/03/03.001(0014)/52).

References

Abrantes, F., Lebreiro, S., Rodrigues, T., Gil, I., Bartels-Jónsdóttir, H., Oliveira, P., Kissel, C., and Grimalt, J. O.: Shallow-marine sediment cores record climate variability and earthquake activity off Lisbon (Portugal) for the last 2000 years, Quaternary Science Reviews, 24, 2477–2494, https://doi.org/10.1016/j.quascirev.2004.04.009, 2005.

Allan, R. P., Cassou, C., Chen, D., Cherchi, A., Connors, L., Doblas-Reyes, F. J., Douville, H., Driouech, F., Edwards, T. L., Fischer, E., Flato, G. M., Forster, P., AchutaRao, K. M., Adhikary, B., Aldrian, E., and Armour, K.: Summary for Policymakers, IPCC, 2021.

Alsos, I. G., Rijal, D. P., Ehrich, D., Karger, D. N., Yoccoz, N. G., Heintzman, P. D., Brown, A. G., Lammers, Y., Pellissier, L., Alm, T., Bråthen, K. A., Coissac, E., Merkel, M. K. F., Alberti, A., Denoeud, F., Bakke, J., and PHYLONORWAY CONSORTIUM: Postglacial species arrival and diversity buildup of northern ecosystems took millennia, Science Advances, 8, eabo7434, https://doi.org/10.1126/sciadv.abo7434, 2022.

Alsos, I. G., Boussange, V., Rijal, D. P., Beaulieu, M., Brown, A. G., Herzschuh, U., Svenning, J.-C., and Pellissier, L.: Using ancient sedimentary DNA to forecast ecosystem trajectories under climate change, Philosophical Transactions of the Royal Society B: Biological Sciences, 379, 20230017, https://doi.org/10.1098/rstb.2023.0017, 2024.

Appleby, P. G.: Chronostratigraphic Techniques in Recent Sediments, in: Tracking Environmental Change Using Lake Sediments: Basin Analysis, Coring, and Chronological Techniques, edited by: Last, W. M. and Smol, J. P., Springer Netherlands, Dordrecht, 171–203, https://doi.org/10.1007/0-306-47669-X_9, 2001.

Aranguren-Gassis, M., Kremer, C. T., Klausmeier, C. A., and Litchman, E.: Nitrogen limitation inhibits marine diatom adaptation to high temperatures, Ecology Letters, 22, 1860–1869, https://doi.org/10.1111/ele.13378, 2019.

Argyle, P. A., Hinners, J., Walworth, N. G., Collins, S., Levine, N. M., and Doblin, M. A.: A High-Throughput Assay for Quantifying Phenotypic Traits of Microalgae, Front. Microbiol., 12, https://doi.org/10.3389/fmicb.2021.706235, 2021.

Armbrecht, L., Weber, M. E., Raymo, M. E., Peck, V. L., Williams, T., Warnock, J., Kato, Y., Hernández-Almeida, I., Hoem, F., Reilly, B., Hemming, S., Bailey, I., Martos, Y. M., Gutjahr, M., Percuoco, V., Allen, C., Brachfeld, S., Cardillo, F. G., Du, Z., Fauth, G., Fogwill, C., Garcia, M., Glüder, A., Guitard, M., Hwang, J.-H., Iizuka, M., Kenlee, B., O'Connell, S., Pérez, L. F., Ronge, T. A., Seki, O., Tauxe, L., Tripathi, S., and Zheng, X.: Ancient marine sediment DNA reveals diatom transition in Antarctica, Nat Commun, 13, 5787, https://doi.org/10.1038/s41467-022-33494-4, 2022.

Bálint, M., Pfenninger, M., Grossart, H.-P., Taberlet, P., Vellend, M., Leibold, M. A., Englund, G., and Bowler, D.: Environmental DNA Time Series in Ecology, Trends in Ecology & Evolution, 33, 945–957, https://doi.org/10.1016/j.tree.2018.09.003, 2018.

Beckmann, A., Schaum, C.-E., and Hense, I.: Phytoplankton adaptation in ecosystem models, Journal of Theoretical Biology, 468, 60–71, https://doi.org/10.1016/j.jtbi.2019.01.041, 2019.

Bennington, C. C., McGraw, J. B., and Vavrek, M. C.: Ecological Genetic Variation in Seed Banks. II. Phenotypic and Genetic Differences Between Young and Old Subpopulations of Luzula Parviflora, Journal of Ecology, 79, 627–643, https://doi.org/10.2307/2260658, 1991.

Blank, C. E. and Sánchez-Baracaldo, P.: Timing of morphological and ecological innovations in the cyanobacteria – a key to understanding the rise in atmospheric oxygen, Geobiology, 8, 1–23, https://doi.org/10.1111/j.1472-4669.2009.00220.x, 2010.

Bradley, R. S.: Paleoclimatology: reconstructing climates of the quaternary, Third edition., Elsevier, Academic Press, Amsterdam; Heidelberg, 675 pp., https://doi.org/10.1016/C2009-0-18310-1, 2015.

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

Brumsack, H.-J.: The trace metal content of recent organic carbon-rich sediments: Implications for Cretaceous black shale formation, Palaeogeography, Palaeoclimatology, Palaeoecology, 232, 344–361, https://doi.org/10.1016/j.palaeo.2005.05.011, 2006.

Capo, E., Giguet-Covex, C., Rouillard, A., Nota, K., Heintzman, P. D., Vuillemin, A., Ariztegui, D., Arnaud, F., Belle, S., Bertilsson, S., Bigler, C., Bindler, R., Brown, A. G., Clarke, C. L., Crump, S. E., Debroas, D., Englund, G., Ficetola, G. F., Garner, R. E., Gauthier, J., Gregory-Eaves, I., Heinecke, L., Herzschuh, U., Ibrahim, A., Kisand, V., Kjær, K. H., Lammers, Y., Littlefair, J., Messager, E., Monchamp, M.-E., Olajos, F., Orsi, W., Pedersen, M. W., Rijal, D. P., Rydberg, J., Spanbauer, T., Stoof-Leichsenring, K. R., Taberlet, P., Talas, L., Thomas, C., Walsh, D. A., Wang, Y., Willerslev, E., van Woerkom, A., Zimmermann, H. H., Coolen, M. J. L., Epp, L. S., Domaizon, I., G. Alsos, I., and Parducci, L.: Lake Sedimentary DNA Research on Past Terrestrial and Aquatic Biodiversity: Overview and Recommendations, Quaternary, 4, 6, https://doi.org/10.3390/quat4010006, 2021.

Cermeño, P., Marañón, E., and Romero, O. E.: Response of marine diatom communities to Late Quaternary abrupt climate changes, Journal of Plankton Research, 35, 12–21, https://doi.org/10.1093/plankt/fbs073, 2013.

Clarke, C. L., Edwards, M. E., Brown, A. G., Gielly, L., Lammers, Y., Heintzman, P. D., Ancin-Murguzur, F. J., Bråthen, K.-A., Goslar, T., and Alsos, I. G.: Holocene floristic diversity and richness in northeast Norway revealed by sedimentary ancient DNA (sedaDNA) and pollen, Boreas, 48, 299–316, https://doi.org/10.1111/bor.12357, 2019.

Cléroux, C., Cortijo, E., Anand, P., Labeyrie, L., Bassinot, F., Caillon, N., and Duplessy, J.-C.: Mg/Ca and Sr/Ca ratios in planktonic foraminifera: Proxies for upper water column temperature reconstruction, Paleoceanography, 23, https://doi.org/10.1029/2007PA001505, 2008.

Collins, S. and Bell, G.: Phenotypic consequences of 1,000 generations of selection at elevated CO2 in a green alga, Nature, 431, 566–569, https://doi.org/10.1038/nature02945, 2004.

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

Collins, S., Boyd, P. W., and Doblin, M. A.: Evolution, Microbes, and Changing Ocean Conditions, Annual Review of Marine Science, 12, 181–208, https://doi.org/10.1146/annurev-marine-010318-095311, 2020.

Coolen, M. J. L.: 7000 Years of Emiliania huxleyi Viruses in the Black Sea, Science, 333, 451–452, https://doi.org/10.1126/science.1200072, 2011.

Coolen, M. J. L., Saenz, J. P., Giosan, L., Trowbridge, N. Y., Dimitrov, P., Dimitrov, D., and Eglinton, T. I.: DNA and lipid molecular stratigraphic records of haptophyte succession in the Black Sea during the Holocene, Earth and Planetary Science Letters, 284, 610–621, https://doi.org/10.1016/j.epsl.2009.05.029, 2009.

Coolen, M. J. L., Orsi, W. D., Balkema, C., Quince, C., Harris, K., Sylva, S. P., Filipova-Marinova, M., and Giosan, L.: Evolution of the plankton paleome in the Black Sea from the Deglacial to Anthropocene, Proceedings of the National Academy of Sciences, 110, 8609–8614, https://doi.org/10.1073/pnas.1219283110, 2013.

Delebecq, G., Schmidt, S., Ehrhold, A., Latimier, M., and Siano, R.: Revival of Ancient Marine Dinoflagellates Using Molecular Biostimulation, Journal of Phycology, 56, 1077–1089, https://doi.org/10.1111/jpy.13010, 2020.

Dellwig, O., Wegwerth, A., Schnetger, B., Schulz, H., and Arz, H. W.: Dissimilar behaviors of the geochemical twins W and Mo in hypoxic-euxinic marine basins, Earth-Science Reviews, 193, 1–23, https://doi.org/10.1016/j.earscirev.2019.03.017, 2019.

Denman, K. L.: A Model Simulation of the Adaptive Evolution through Mutation of the Coccolithophore Emiliania huxleyi Based on a Published Laboratory Study, Frontiers in Marine Science, 3, 2017.

Dommain, R., Andama, M., McDonough, M. M., Prado, N. A., Goldhammer, T., Potts, R., Maldonado, J. E., Nkurunungi, J. B., and Campana, M. G.: The Challenges of Reconstructing Tropical Biodiversity With Sedimentary Ancient DNA: A 2200-Year-Long Metagenomic Record From Bwindi Impenetrable Forest, Uganda, Front. Ecol. Evol., 8, https://doi.org/10.3389/fevo.2020.00218, 2020.

Dutkiewicz, S., Morris, J. J., Follows, M. J., Scott, J., Levitan, O., Dyhrman, S. T., and Berman-Frank, I.: Impact of ocean acidification on the structure of future phytoplankton communities, Nature Clim Change, 5, 1002–1006, https://doi.org/10.1038/nclimate2722, 2015.

Dutkiewicz, S., Cermeno, P., Jahn, O., Follows, M. J., Hickman, A. E., Taniguchi, D. A. A., and Ward, B. A.: Dimensions of marine phytoplankton diversity, Biogeosciences, 17, 609–634, https://doi.org/10.5194/bg-17-609-2020, 2020.

Edwards, M. and Richardson, A. J.: Impact of climate change on marine pelagic phenology and trophic mismatch, Nature, 430, 881–884, https://doi.org/10.1038/nature02808, 2004.

Elena, S. F. and Lenski, R. E.: Evolution experiments with microorganisms: the dynamics and genetic bases of adaptation, Nat Rev Genet, 4, 457–469, https://doi.org/10.1038/nrg1088, 2003.

Ellegaard, M., Dale, B., Mertens, K. N., Pospelova, V., and Ribeiro, S.: Dinoflagellate Cysts as Proxies for Holocene Environmental Change in Estuaries: Diversity, Abundance and Morphology, in: Applications of Paleoenvironmental Techniques in Estuarine Studies, edited by: Weckström, K., Saunders, K. M., Gell, P. A., and Skilbeck, C. G., Springer Netherlands, Dordrecht, 295–312, https://doi.org/10.1007/978-94-024-0990-1_12, 2017.

Ellegaard, M., Clokie, M. R. J., Czypionka, T., Frisch, D., Godhe, A., Kremp, A., Letarov, A., McGenity, T. J., Ribeiro, S., and John Anderson, N.: Dead or alive: sediment DNA archives as tools for tracking aquatic evolution and adaptation, Commun Biol, 3, 1–11, https://doi.org/10.1038/s42003-020-0899-z, 2020.

Elliott, J. A., Thackeray, S. J., Huntingford, C., and Jones, R. G.: Combining a regional climate model with a phytoplankton community model to predict future changes in phytoplankton in lakes, Freshwater Biology, 50, 1404–1411, https://doi.org/10.1111/j.1365-2427.2005.01409.x, 2005.

Fenchel, T.: Marine Plankton Food Chains, Annual Review of Ecology and Systematics, 19, 19–38, https://doi.org/10.1146/annurev.es.19.110188.000315, 1988.

Field, C. B., Behrenfeld, M. J., Randerson, J. T., and Falkowski, P.: Primary Production of the Biosphere: Integrating Terrestrial and Oceanic Components, Science, 281, 237–240, https://doi.org/10.1126/science.281.5374.237, 1998.

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

Frindte, K., Lehndorff, E., Vlaminck, S., Werner, K., Kehl, M., Khormali, F., and Knief, C.: Evidence for signatures of ancient microbial life in paleosols, Sci Rep, 10, 16830, https://doi.org/10.1038/s41598-020-73938-9, 2020.

Gibbs, S. J., Bown, P. R., Ward, B. A., Alvarez, S. A., Kim, H., Archontikis, O. A., Sauterey, B., Poulton, A. J., Wilson, J., and Ridgwell, A.: Algal plankton turn to hunting to survive and recover from end-Cretaceous impact darkness, Science Advances, 6, eabc9123, https://doi.org/10.1126/sciadv.abc9123, 2020.

Godhe, A., Asplund, M. E., Härnström, K., Saravanan, V., Tyagi, A., and Karunasagar, I.: Quantification of Diatom and Dinoflagellate Biomasses in Coastal Marine Seawater Samples by Real-Time PCR, Applied and Environmental Microbiology, 74, 7174–7182, https://doi.org/10.1128/AEM.01298-08, 2008.

Gustafsson, B. G., Schenk, F., Blenckner, T., Eilola, K., Meier, H. E. M., Müller-Karulis, B., Neumann, T., Ruoho-Airola, T., Savchuk, O. P., and Zorita, E.: Reconstructing the Development of Baltic Sea Eutrophication 1850–2006, AMBIO, 41, 534–548, https://doi.org/10.1007/s13280-012-0318-x, 2012.

Hain, M. P., Sigman, D. M., and Haug, G. H.: The Biological Pump in the Past, in: The Oceans and Marine Geochemistry, Elsevier Inc., 485–517, https://doi.org/10.1016/B978-0-08-095975-7.00618-5, 2013.

Hajdas, I., Ascough, P., Garnett, M. H., Fallon, S. J., Pearson, C. L., Quarta, G., Spalding, K. L., Yamaguchi, H., and Yoneda, M.: Radiocarbon dating, Nat Rev Methods Primers, 1, 1–26, https://doi.org/10.1038/s43586-021-00058-7, 2021.

Hancock, G. J., Leslie, C., Everett, S. E., Tims, S. G., Brunskill, G. J., and Haese, R.: Plutonium as a chronomarker in Australian and New Zealand sediments: a comparison with 137Cs, Journal of Environmental Radioactivity, 102, 919–929, https://doi.org/10.1016/j.jenvrad.2009.09.008, 2011.

Härnström, K., Ellegaard, M., Andersen, T. J., and Godhe, A.: Hundred years of genetic structure in a sediment revived diatom population, Proceedings of the National Academy of Sciences, 108, 4252–4257, https://doi.org/10.1073/pnas.1013528108, 2011.

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

Hattich, G. S. I., Jokinen, S., Sildever, S., Gareis, M., Heikkinen, J., Junghardt, N., Segovia, M., Machado, M., and Sjöqvist, C.: Temperature optima of a natural diatom population increases as global warming proceeds, Nat. Clim. Chang., 1–8, https://doi.org/10.1038/s41558-024-01981-9, 2024.

Hense, I.: Regulative feedback mechanisms in cyanobacteria-driven systems: a model study, Marine Ecology Progress Series, 339, 41–47, https://doi.org/10.3354/meps339041, 2007.

Hillaire-Marcel, C. and De Vernal, A.: Proxies in Late Cenozoic Paleoceanography, Elsevier, 863 pp., 2007.

Hinners, J., Kremp, A., and Hense, I.: Evolution in temperature-dependent phytoplankton traits revealed from a sediment archive: do reaction norms tell the whole story?, Proceedings of the Royal Society B: Biological Sciences, 284, 20171888, https://doi.org/10.1098/rspb.2017.1888, 2017.

Hinners, J., Hense, I., and Kremp, A.: Modelling phytoplankton adaptation to global warming based on resurrection experiments, Ecological Modelling, 400, 27–33, https://doi.org/10.1016/j.ecolmodel.2019.03.006, 2019.

Hinners, J., Argyle, P. A., Walworth, N. G., Doblin, M. A., Levine, N. M., and Collins, S.: Multi-trait diversification in marine diatoms in constant and warmed environments, Proceedings of the Royal Society B: Biological Sciences, 291, 20232564, https://doi.org/10.1098/rspb.2023.2564, 2024.

Hirschhorn, J. N. and Daly, M. J.: Genome-wide association studies for common diseases and complex traits, Nat Rev Genet, 6, 95–108, https://doi.org/10.1038/nrg1521, 2005.

Hochfeld, I. and Hinners, J.: Evolutionary adaptation to steady or changing environments affects competitive outcomes in marine phytoplankton, Limnology and Oceanography, 69, 1172–1186, https://doi.org/10.1002/lno.12559, 2024.

Hollingsworth, A.: Validation and diagnosis of atmospheric models, Dynamics of Atmospheres and Oceans, 20, 227–246, https://doi.org/10.1016/0377-0265(94)90019-1, 1994.

Hollowed, A. B., Barange, M., Beamish, R. J., Brander, K., Cochrane, K., Drinkwater, K., Foreman, M. G. G., Hare, J. A., Holt, J., Ito, S., Kim, S., King, J. R., Loeng, H., MacKenzie, B. R., Mueter, F. J., Okey, T. A., Peck, M. A., Radchenko, V. I., Rice, J. C., Schirripa, M. J., Yatsu, A., and Yamanaka, Y.: Projected impacts of climate change on marine fish and fisheries, ICES Journal of Marine Science, 70, 1023–1037, https://doi.org/10.1093/icesjms/fst081, 2013.

Hutchins, D. A. and Fu, F.: Microorganisms and ocean global change, Nat Microbiol, 2, 1–11, https://doi.org/10.1038/nmicrobiol.2017.58, 2017.

Hutchins, D. A., Walworth, N. G., Webb, E. A., Saito, M. A., Moran, D., McIlvin, M. R., Gale, J., and Fu, F.-X.: Irreversibly increased nitrogen fixation in Trichodesmium experimentally adapted to elevated carbon dioxide, Nat Commun, 6, 8155, https://doi.org/10.1038/ncomms9155, 2015.

Intergovernmental Panel on Climate Change (IPCC): Climate Change 2022 – Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, 1st ed., Cambridge University Press, https://doi.org/10.1017/9781009325844, 2022.

Irwin, A. J., Finkel, Z. V., Müller-Karger, F. E., and Troccoli Ghinaglia, L.: Phytoplankton adapt to changing ocean environments, Proceedings of the National Academy of Sciences, 112, 5762–5766, https://doi.org/10.1073/pnas.1414752112, 2015.

Isanta-Navarro, J., Hairston, N. G., Beninde, J., Meyer, A., Straile, D., Möst, M., and Martin-Creuzburg, D.: Reversed evolution of grazer resistance to cyanobacteria, Nat Commun, 12, 1945, https://doi.org/10.1038/s41467-021-22226-9, 2021.

Jin, P. and Agustí, S.: Fast adaptation of tropical diatoms to increased warming with trade-offs, Sci Rep, 8, 17771, https://doi.org/10.1038/s41598-018-36091-y, 2018.

Kaiser, J., van der Meer, M. T. J., and Arz, H. W.: Long-chain alkenones in Baltic Sea surface sediments: New insights, Organic Geochemistry, 112, 93–104, https://doi.org/10.1016/j.orggeochem.2017.07.002, 2017.

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

Kerfoot, W. C. and Weider, L. J.: Experimental paleoecology (resurrection ecology): Chasing Van Valen's Red Queen hypothesis, Limnology and Oceanography, 49, 1300–1316, https://doi.org/10.4319/lo.2004.49.4_part_2.1300, 2004.

Kjær, K. H., Winther Pedersen, M., De Sanctis, B., De Cahsan, B., Korneliussen, T. S., Michelsen, C. S., Sand, K. K., Jelavić, S., Ruter, A. H., Schmidt, A. M. A., Kjeldsen, K. K., Tesakov, A. S., Snowball, I., Gosse, J. C., Alsos, I. G., Wang, Y., Dockter, C., Rasmussen, M., Jørgensen, M. E., Skadhauge, B., Prohaska, A., Kristensen, J. Å., Bjerager, M., Allentoft, M. E., Coissac, E., Rouillard, A., Simakova, A., Fernandez-Guerra, A., Bowler, C., Macias-Fauria, M., Vinner, L., Welch, J. J., Hidy, A. J., Sikora, M., Collins, M. J., Durbin, R., Larsen, N. K., and Willerslev, E.: A 2-million-year-old ecosystem in Greenland uncovered by environmental DNA, Nature, 612, 283–291, https://doi.org/10.1038/s41586-022-05453-y, 2022.

Klausmeier, C. A., Osmond, M. M., Kremer, C. T., and Litchman, E.: Ecological limits to evolutionary rescue, Philosophical Transactions of the Royal Society B: Biological Sciences, 375, 20190453, https://doi.org/10.1098/rstb.2019.0453, 2020a.

Klausmeier, C. A., Kremer, C. T., and Koffel, T.: Trait-based ecological and eco-evolutionary theory, in: Theoretical Ecology: concepts and applications, edited by: McCann, K. S. and Gellner, G., Oxford University Press, 0, https://doi.org/10.1093/oso/9780198824282.003.0011, 2020b.

Korkonen, S. T., Ojala, A. E. K., Kosonen, E., and Weckström, J.: Seasonality of chrysophyte cyst and diatom assemblages in varved Lake Nautajärvi – implications for palaeolimnological studies, Journal of Limnology, 76, https://doi.org/10.4081/jlimnol.2017.1473, 2017.

Krasovec, M., Sanchez-Brosseau, S., and Piganeau, G.: First Estimation of the Spontaneous Mutation Rate in Diatoms, Genome Biology and Evolution, 11, 1829–1837, https://doi.org/10.1093/gbe/evz130, 2019.

Kremer, C. T. and Klausmeier, C. A.: Species packing in eco-evolutionary models of seasonally fluctuating environments, Ecology Letters, 20, 1158–1168, https://doi.org/10.1111/ele.12813, 2017.

Kremp, A., Hinners, J., Klais, R., Leppänen, A.-P., and Kallio, A.: Patterns of vertical cyst distribution and survival in 100-year-old sediment archives of three spring dinoflagellate species from the Northern Baltic Sea, European Journal of Phycology, 53, 135–145, https://doi.org/10.1080/09670262.2017.1386330, 2018.

Krishna, S., Peterson, V., Listmann, L., and Hinners, J.: Interactive effects of viral lysis and warming in a coastal ocean identified from an idealized ecosystem model, Ecological Modelling, 487, 110550, https://doi.org/10.1016/j.ecolmodel.2023.110550, 2024.

Lässig, M., Mustonen, V., and Walczak, A. M.: Predicting evolution, Nat Ecol Evol, 1, 1–9, https://doi.org/10.1038/s41559-017-0077, 2017.

Laufkötter, C., Vogt, M., Gruber, N., Aita-Noguchi, M., Aumont, O., Bopp, L., Buitenhuis, E., Doney, S. C., Dunne, J., Hashioka, T., Hauck, J., Hirata, T., John, J., Le Quéré, C., Lima, I. D., Nakano, H., Seferian, R., Totterdell, I., Vichi, M., and Völker, C.: Drivers and uncertainties of future global marine primary production in marine ecosystem models, Biogeosciences, 12, 6955–6984, https://doi.org/10.5194/bg-12-6955-2015, 2015.

Laufkötter, C., Vogt, M., Gruber, N., Aumont, O., Bopp, L., Doney, S. C., Dunne, J. P., Hauck, J., John, J. G., Lima, I. D., Seferian, R., and Völker, C.: Projected decreases in future marine export production: the role of the carbon flux through the upper ocean ecosystem, Biogeosciences, 13, 4023–4047, https://doi.org/10.5194/bg-13-4023-2016, 2016.

Le Gland, G., Vallina, S. M., Smith, S. L., and Cermeño, P.: SPEAD 1.0 – Simulating Plankton Evolution with Adaptive Dynamics in a two-trait continuous fitness landscape applied to the Sargasso Sea, Geoscientific Model Development, 14, 1949–1985, https://doi.org/10.5194/gmd-14-1949-2021, 2021.

Lear, C. H., Rosenthal, Y., and Slowey, N.: Benthic foraminiferal Mg/Ca-paleothermometry: a revised core-top calibration, Geochimica et Cosmochimica Acta, 66, 3375–3387, https://doi.org/10.1016/S0016-7037(02)00941-9, 2002.

Lee, S., Hofmeister, R., and Hense, I.: The role of life cycle processes on phytoplankton spring bloom composition: a modelling study applied to the Gulf of Finland, Journal of Marine Systems, 178, 75–85, https://doi.org/10.1016/j.jmarsys.2017.10.010, 2018.

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

Lehtimaki, J., Moisander, P., Sivonen, K., and Kononen, K.: Growth, nitrogen fixation, and nodularin production by two baltic sea cyanobacteria, Applied and Environmental Microbiology, 63, 1647–1656, https://doi.org/10.1128/aem.63.5.1647-1656.1997, 1997.

Lenton, T. M., Held, H., Kriegler, E., Hall, J. W., Lucht, W., Rahmstorf, S., and Schellnhuber, H. J.: Tipping elements in the Earth's climate system, Proceedings of the National Academy of Sciences, 105, 1786–1793, https://doi.org/10.1073/pnas.0705414105, 2008.

Levins, R.: Theory of Fitness in a Heterogeneous Environment. I. The Fitness Set and Adaptive Function, The American Naturalist, 96, 361–373, https://doi.org/10.1086/282245, 1962.

Limoges, A., Van Nieuwenhove, N., Head, M. J., Mertens, K. N., Pospelova, V., and Rochon, A.: A review of rare and less well known extant marine organic-walled dinoflagellate cyst taxa of the orders Gonyaulacales and Suessiales from the Northern Hemisphere, Marine Micropaleontology, 159, 101801, https://doi.org/10.1016/j.marmicro.2019.101801, 2020.

Listmann, L., LeRoch, M., Schlüter, L., Thomas, M. K., and Reusch, T. B. H.: Swift thermal reaction norm evolution in a key marine phytoplankton species, Evolutionary Applications, 9, 1156–1164, https://doi.org/10.1111/eva.12362, 2016.

Litchman, E., Klausmeier, C. A., Schofield, O. M., and Falkowski, P. G.: The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level, Ecology Letters, 10, 1170–1181, https://doi.org/10.1111/j.1461-0248.2007.01117.x, 2007.

Litchman, E., de Tezanos Pinto, P., Edwards, K. F., Klausmeier, C. A., Kremer, C. T., and Thomas, M. K.: Global biogeochemical impacts of phytoplankton: a trait-based perspective, Journal of Ecology, 103, 1384–1396, https://doi.org/10.1111/1365-2745.12438, 2015.

Lowe, D. J. and Alloway, B. V.: Tephrochronology, in: Encyclopedia of Scientific Dating Methods, Springer, Dordrecht, 783–799, 2015.

Maslin, M., Pike, J., Stickley, C., and Ettwein, V.: Evidence of Holocene Climate Variability in Marine Sediments, in: Global Change in the Holocene, Routledge, 2005.

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

Matul, A., Spielhagen, R. F., Kazarina, G., Kruglikova, S., Dmitrenko, O., and Mohan, R.: Warm-water events in the eastern Fram Strait during the last 2000 years as revealed by different microfossil groups, Polar Research, 2018.

McGraw, J. B., Vavrek, M. C., and Bennington, C. C.: Ecological Genetic Variation in Seed Banks I. Establishment of a Time Transect, Journal of Ecology, 79, 617–625, https://doi.org/10.2307/2260657, 1991.

Medlin, L. K., Sáez, A. G., and Young, J. R.: A molecular clock for coccolithophores and implications for selectivity of phytoplankton extinctions across the K/T boundary, Marine Micropaleontology, 67, 69–86, https://doi.org/10.1016/j.marmicro.2007.08.007, 2008.

Mejbel, H. S., Dodsworth, W., Baud, A., Gregory-Eaves, I., and Pick, F. R.: Comparing Quantitative Methods for Analyzing Sediment DNA Records of Cyanobacteria in Experimental and Reference Lakes, Front. Microbiol., 12, https://doi.org/10.3389/fmicb.2021.669910, 2021.

Mitchell, D., Willerslev, E., and Hansen, A.: Damage and repair of ancient DNA, Mutation Research/Fundamental and Molecular Mechanisms of Mutagenesis, 571, 265–276, https://doi.org/10.1016/j.mrfmmm.2004.06.060, 2005.

Monchamp, M.-E., Walser, J.-C., Pomati, F., and Spaak, P.: Sedimentary DNA Reveals Cyanobacterial Community Diversity over 200 Years in Two Perialpine Lakes, Applied and Environmental Microbiology, 82, 6472–6482, https://doi.org/10.1128/AEM.02174-16, 2016.

O’Donnell, D. R., Hamman, C. R., Johnson, E. C., Kremer, C. T., Klausmeier, C. A., and Litchman, E.: Rapid thermal adaptation in a marine diatom reveals constraints and trade-offs, Global Change Biology, 24, 4554–4565, https://doi.org/10.1111/gcb.14360, 2018.

Østman, B., Hintze, A., and Adami, C.: Impact of epistasis and pleiotropy on evolutionary adaptation, Proceedings of the Royal Society B: Biological Sciences, 279, 247–256, https://doi.org/10.1098/rspb.2011.0870, 2011.

Pauwels, K., De Meester, L., Put, S., Decaestecker, E., Decaestecker, E., and Stoks, R.: Rapid evolution of phenoloxidase expression, a component of innate immune function, in a natural population of Daphnia magna, Limnology and Oceanography, 55, 1408–1413, https://doi.org/10.4319/lo.2010.55.3.1408, 2010.

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

Peer, A. C. and Miller, T. J.: Climate Change, Migration Phenology, and Fisheries Management Interact with Unanticipated Consequences, North American Journal of Fisheries Management, 34, 94–110, https://doi.org/10.1080/02755947.2013.847877, 2014.

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A., and Richardson, A. J.: Global imprint of climate change on marine life, Nature Clim Change, 3, 919–925, https://doi.org/10.1038/nclimate1958, 2013.

Prahl, F. G., Muehlhausen, L. A., and Zahnle, D. L.: Further evaluation of long-chain alkenones as indicators of paleoceanographic conditions, Geochimica et Cosmochimica Acta, 52, 2303–2310, https://doi.org/10.1016/0016-7037(88)90132-9, 1988.

Renssen, H., Seppä, H., Crosta, X., Goosse, H., and Roche, D. M.: Global characterization of the Holocene Thermal Maximum, Quaternary Science Reviews, 48, 7–19, https://doi.org/10.1016/j.quascirev.2012.05.022, 2012.

Rosell-Melé, A.: Interhemispheric appraisal of the value of alkenone indices as temperature and salinity proxies in high-latitude locations, Paleoceanography, 13, 694–703, https://doi.org/10.1029/98PA02355, 1998.

Sallon, S., Solowey, E., Cohen, Y., Korchinsky, R., Egli, M., Woodhatch, I., Simchoni, O., and Kislev, M.: Germination, Genetics, and Growth of an Ancient Date Seed, Science, 320, 1464–1464, https://doi.org/10.1126/science.1153600, 2008.

Sanyal, A., Larsson, J., van Wirdum, F., Andrén, T., Moros, M., Lönn, M., and Andrén, E.: Not dead yet: Diatom resting spores can survive in nature for several millennia, American Journal of Botany, 109, 67–82, https://doi.org/10.1002/ajb2.1780, 2022.

Sathyendranath, S., Gouveia, A. D., Shetye, S. R., Ravindran, P., and Platt, T.: Biological control of surface temperature in the Arabian Sea, Nature, 349, 54–56, https://doi.org/10.1038/349054a0, 1991.

Sauterey, B., Ward, B., Rault, J., Bowler, C., and Claessen, D.: The Implications of Eco-Evolutionary Processes for the Emergence of Marine Plankton Community Biogeography, The American Naturalist, 190, 116–130, https://doi.org/10.1086/692067, 2017.

Schabhüttl, S., Hingsamer, P., Weigelhofer, G., Hein, T., Weigert, A., and Striebel, M.: Temperature and species richness effects in phytoplankton communities, Oecologia, 171, 527–536, https://doi.org/10.1007/s00442-012-2419-4, 2013.

Schouten, S., Hopmans, E. C., and Sinninghe Damsté, J. S.: The organic geochemistry of glycerol dialkyl glycerol tetraether lipids: A review, Organic Geochemistry, 54, 19–61, https://doi.org/10.1016/j.orggeochem.2012.09.006, 2013.

Semenov, M. V., Chernov, T. I., Zhelezova, A. D., Nikitin, D. A., Tkhakakhova, A. K., Ivanova, E. A., Xenofontova, N. A., Sycheva, S. A., Kolganova, T. V., and Kutovaya, O. V.: Microbial Communities of Interglacial and Interstadial Paleosols of the Late Pleistocene, Eurasian Soil Sc., 53, 772–779, https://doi.org/10.1134/S1064229320060101, 2020.

Smith, S. L., Vallina, S. M., and Merico, A.: Phytoplankton size-diversity mediates an emergent trade-off in ecosystem functioning for rare versus frequent disturbances, Sci Rep, 6, 34170, https://doi.org/10.1038/srep34170, 2016.

Tierney, J. E., Poulsen, C. J., Montañez, I. P., Bhattacharya, T., Feng, R., Ford, H. L., Hönisch, B., Inglis, G. N., Petersen, S. V., Sagoo, N., Tabor, C. R., Thirumalai, K., Zhu, J., Burls, N. J., Foster, G. L., Goddéris, Y., Huber, B. T., Ivany, L. C., Kirtland Turner, S., Lunt, D. J., McElwain, J. C., Mills, B. J. W., Otto-Bliesner, B. L., Ridgwell, A., and Zhang, Y. G.: Past climates inform our future, Science, 370, eaay3701, https://doi.org/10.1126/science.aay3701, 2020.

Tonani, M., Balmaseda, M., Bertino, L., Blockley, E., Brassington, G., Davidson, F., Drillet, Y., Hogan, P., Kuragano, T., Lee, T., Mehra, A., Paranathara, F., Tanajura, C. A. S., and Wang, H.: Status and future of global and regional ocean prediction systems, Journal of Operational Oceanography, 8, s201–s220, https://doi.org/10.1080/1755876X.2015.1049892, 2015.

Tyler, A. L., Asselbergs, F. W., Williams, S. M., and Moore, J. H.: Shadows of complexity: what biological networks reveal about epistasis and pleiotropy, BioEssays, 31, 220–227, https://doi.org/10.1002/bies.200800022, 2009.

Uffelmann, E., Huang, Q. Q., Munung, N. S., de Vries, J., Okada, Y., Martin, A. R., Martin, H. C., Lappalainen, T., and Posthuma, D.: Genome-wide association studies, Nat Rev Methods Primers, 1, 1–21, https://doi.org/10.1038/s43586-021-00056-9, 2021.

Van Nieuwenhove, N., Head, M. J., Limoges, A., Pospelova, V., Mertens, K. N., Matthiessen, J., De Schepper, S., de Vernal, A., Eynaud, F., Londeix, L., Marret, F., Penaud, A., Radi, T., and Rochon, A.: An overview and brief description of common marine organic-walled dinoflagellate cyst taxa occurring in surface sediments of the Northern Hemisphere, Marine Micropaleontology, 159, 101814, https://doi.org/10.1016/j.marmicro.2019.101814, 2020.

Vasselon, V., Bouchez, A., Rimet, F., Jacquet, S., Trobajo, R., Corniquel, M., Tapolczai, K., and Domaizon, I.: Avoiding quantification bias in metabarcoding: Application of a cell biovolume correction factor in diatom molecular biomonitoring, Methods in Ecology and Evolution, 9, 1060–1069, https://doi.org/10.1111/2041-210X.12960, 2018.

Vincent, W. F. and Silvester, W. B.: Growth of blue-green algae in the Manukau (New Zealand) oxidation ponds—I. Growth potential of oxidation pond water and comparative optima for blue-green and green algal growth, Water Research, 13, 711–716, https://doi.org/10.1016/0043-1354(79)90234-3, 1979.

Visscher, P. M., Wray, N. R., Zhang, Q., Sklar, P., McCarthy, M. I., Brown, M. A., and Yang, J.: 10 Years of GWAS Discovery: Biology, Function, and Translation, The American Journal of Human Genetics, 101, 5–22, https://doi.org/10.1016/j.ajhg.2017.06.005, 2017.

Wakeham, S. G. and Canuel, E. A.: Degradation and Preservation of Organic Matter in Marine Sediments, in: Marine Organic Matter: Biomarkers, Isotopes and DNA, edited by: Volkman, J. K., Springer, Berlin, Heidelberg, 295–321, https://doi.org/10.1007/698_2_009, 2006.

Ward, B. A., Dutkiewicz, S., Jahn, O., and Follows, M. J.: A size-structured food-web model for the global ocean, Limnology and Oceanography, 57, 1877–1891, https://doi.org/10.4319/lo.2012.57.6.1877, 2012.

Ward, B. A., Collins, S., Dutkiewicz, S., Gibbs, S., Bown, P., Ridgwell, A., Sauterey, B., Wilson, J. D., and Oschlies, A.: Considering the Role of Adaptive Evolution in Models of the

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

Ocean and Climate System, Journal of Advances in Modeling Earth Systems, 11, 3343–3361, https://doi.org/10.1029/2018MS001452, 2019.

Wasmund, N., Nausch, G., Gerth, M., Busch, S., Burmeister, C., Hansen, R., and Sadkowiak, B.: Extension of the growing season of phytoplankton in the western Baltic Sea in response to climate change, Marine Ecology Progress Series, 622, 1–16, https://doi.org/10.3354/meps12994, 2019.

Weckström, K.: Assessing Recent Eutrophication in Coastal Waters of the Gulf of Finland (Baltic Sea) using Subfossil Diatoms, J Paleolimnol, 35, 571–592, https://doi.org/10.1007/s10933-005-5264-1, 2006.

Weitz, J. S., Stock, C. A., Wilhelm, S. W., Bourouiba, L., Coleman, M. L., Buchan, A., Follows, M. J., Fuhrman, J. A., Jover, L. F., Lennon, J. T., Middelboe, M., Sonderegger, D. L., Suttle, C. A., Taylor, B. P., Frede Thingstad, T., Wilson, W. H., and Eric Wommack, K.: A multitrophic model to quantify the effects of marine viruses on microbial food webs and ecosystem processes, ISME J, 9, 1352–1364, https://doi.org/10.1038/ismej.2014.220, 2015.

Wersebe, M. J. and Weider, L. J.: Resurrection genomics provides molecular and phenotypic evidence of rapid adaptation to salinization in a keystone aquatic species, Proceedings of the National Academy of Sciences, 120, e2217276120, https://doi.org/10.1073/pnas.2217276120, 2023.

Willerslev, E., Hansen, A. J., Binladen, J., Brand, T. B., Gilbert, M. T. P., Shapiro, B., Bunce, M., Wiuf, C., Gilichinsky, D. A., and Cooper, A.: Diverse Plant and Animal Genetic Records from Holocene and Pleistocene Sediments, Science, 300, 791–795, https://doi.org/10.1126/science.1084114, 2003.

Wood, S. M., Kremp, A., Savela, H., Akter, S., Vartti, V.-P., Saarni, S., and Suikkanen, S.: Cyanobacterial Akinete Distribution, Viability, and Cyanotoxin Records in Sediment Archives From the Northern Baltic Sea, Front. Microbiol., 12, https://doi.org/10.3389/fmicb.2021.681881, 2021.

Zimmermann, H. H., Stoof-Leichsenring, K. R., Dinkel, V., Harms, L., Schulte, L., Hütt, M.-T., Nürnberg, D., Tiedemann, R., and Herzschuh, U.: Marine ecosystem shifts with deglacial

https://doi.org/10.5194/egusphere-2024-3297
Preprint. Discussion started: 23 October 2024

sea-ice loss inferred from ancient DNA shotgun sequencing, Nat Commun, 14, 1650, https://doi.org/10.1038/s41467-023-36845-x, 2023.

Zonneveld, K. a. F., Versteegh, G. J. M., Kasten, S., Eglinton, T. I., Emeis, K.-C., Huguet, C., Koch, B. P., de Lange, G. J., de Leeuw, J. W., Middelburg, J. J., Mollenhauer, G., Prahl, F. G., Rethemeyer, J., and Wakeham, S. G.: Selective preservation of organic matter in marine environments; processes and impact on the sedimentary record, Biogeosciences, 7, 483–511, https://doi.org/10.5194/bg-7-483-2010, 2010.