

## PERSPECTIVE

# Developing model systems for dinoflagellates in the post-genomic era

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### Abstract

Dinoflagellates are a diverse group of eukaryotic microbes that are ubiquitous in aquatic environments. Largely photosynthetic, they encompass symbiotic, parasitic, and free-living lineages with a broad spectrum of trophism. Many free-living taxa can produce bioactive secondary metabolites such as biotoxins, some of which cause harmful algal blooms. In contrast, most symbiotic species are crucial for sustaining coral reef health. The year 2023 marked a decade since the first genome data of dinoflagellates became available. The growing genome-scale resources for these taxa are highlighting their remarkable evolutionary and genomic complexities. Here, we discuss the prospect of developing dinoflagellate models using the criteria of accessibility, tractability, resources, research support, and promise. Moving forward in the post-genomic era, we argue for the development of fit-to-purpose models that tailor to specific biological contexts, and that a one-size-fits-all model is inadequate for encapsulating the complex biology, ecology, and evolutionary history of dinoflagellates.

### KEYWORDS

dinoflagellate, model, phytoplankton, symbiosis

## INTRODUCTION

Dinoflagellates are a diverse group of unicellular eukaryotic microbes that are ubiquitous in marine and fresh waters. These taxa encompass free-living,

symbiotic, and parasitic lineages with a broad spectrum of trophism (Flynn et al., 2019). Photosynthetic and free-living dinoflagellates form the base of ocean food webs and sustain global aquatic ecosystems via primary production and cycling of organic carbon and

**Abbreviations:** HAB, harmful algal bloom; MYA, million years ago.

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nitrogen. Some free-living dinoflagellates produce marine biotoxins that cause harmful algal blooms (HABs) or “red tides” with diverse and serious ecosystem-wide impacts (Brown et al., 2020). Symbiotic dinoflagellates of the family Symbiodiniaceae represent essential endosymbionts in coral reefs (LaJeunesse et al., 2018). Breakdown of the coral-dinoflagellate symbiosis due to environmental stress can lead to coral bleaching and the eventual collapse of reef ecosystems (Suggett & Smith, 2020). Parasitic dinoflagellates can cause death in economically important crustaceans such as crabs and lobsters (Li et al., 2021).

With regard to systematics, dinoflagellates are classified as Alveolata (i.e., containing abutting alveolar vesicles—alveoli—under the plasma membrane), together with the parasitic apicomplexans, the heterotrophic ciliates, and other lineages, e.g., *Oxyrrhis marina*, Perkinsidae, and Colponemidia (Figure 1; Adl et al., 2019). Within the Dinoflagellata, three major clades are recognized (Adl et al., 2019; Hoppenrath, 2017): the largely parasitic Syndiniales, the Noctilucales, and the Dinophyceae (core dinoflagellates) that comprise ~2500 species in ~300 genera. Transcriptome data have clarified the phylogenetic relationships of key dinoflagellate taxa (Janouškovec et al., 2017; Price & Bhattacharya, 2017; Stephens et al., 2018). However, cryptic taxa are known: 48 new genera, 5 new families, and >200 species have been described over a 15-year period (Hoppenrath, 2017), highlighting the current underestimation of diversity. The phylogenetic position and vast diversity of dinoflagellates underscore their importance as study subjects for understanding the biology and evolution of microbial eukaryotes, specifically in the formation of algal blooms and the distinct lifestyles of cells that are free-living, occur in mutualistic symbiosis, or are parasitic. Dinoflagellates are also attractive targets for studies relative to climate change and anthropogenic impacts (Anderson et al., 2021) due in part to their cysts being common in the fossil record (Fensome, 1993).

The nuclear genomes of dinoflagellates are notorious for their immense sizes that exceed 200 Gbp based on early estimates (Hou & Lin, 2009; LaJeunesse et al., 2005) and their highly idiosyncratic features, e.g., non-canonical splice sites, *trans*-splicing of spliced-leader sequences in transcription, and permanently condensed chromosomes (Lin, 2011; Murray et al., 2016; Wisecaver & Hackett, 2011). Beyond

these peculiarities, the development of dinoflagellates as model organisms has been further impeded by the technical challenges and costs associated with genome-data generation. Since the first nuclear genome data from dinoflagellates were published (Shoguchi et al., 2013), genomic resources from other dinoflagellate taxa have become available (Figure 1) in parallel to the development of analytic workflows tailored for studying their atypical genome and gene features (Chen et al., 2020). These resources are elucidating the extensive genomic divergence of dinoflagellates relative to their evolutionary and ecological complexity (Dougan, González-Pech, et al., 2022; González-Pech et al., 2021).

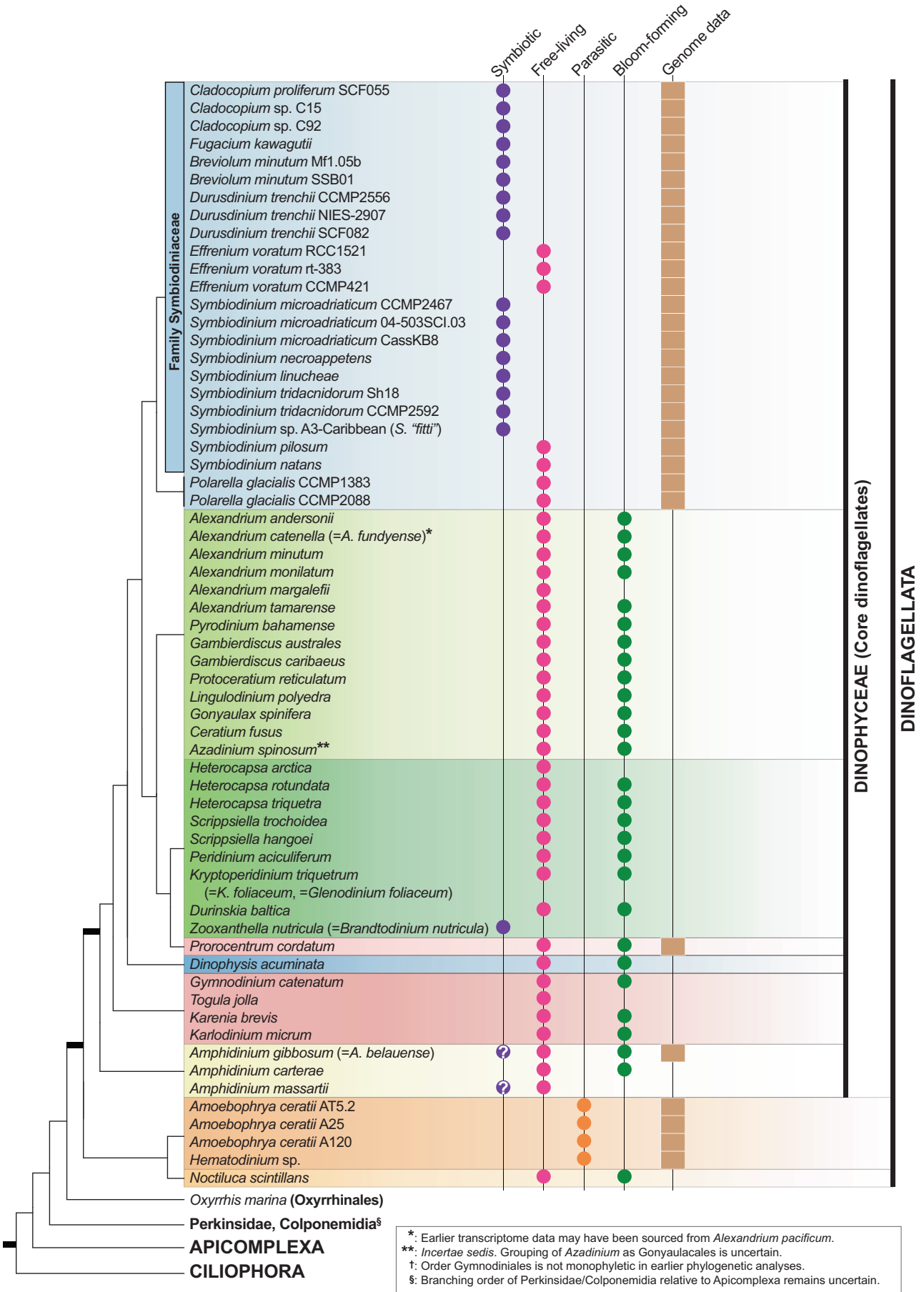
## WHAT ARE THE FEATURES OF A GOOD DINOFLAGELLATE MODEL?

The search for a dinoflagellate model has not been straightforward. Recently, 20 criteria for a model organism were proposed and grouped into five categories (Dietrich et al., 2020; Figure 2). Ideally, a model organism is widely accessible, readily tractable, has a rich knowledge base and resources available, has strong research support, and has strong promise through demonstrated translational and/or comparative potential. Although these criteria may not be generalizable across all systems, they present a good reference framework for identifying a model dinoflagellate. Here, we discuss the prospect of developing a dinoflagellate model in the post-genomic era, from the perspectives of three functional groups, with each representing a major ecological niche and/or key phylogenetic clade exhibiting specific evolutionary adaptations: (a) Symbiodiniaceae taxa that are predominantly symbiotic, (b) deep-branching Syndiniales taxa that are mostly parasitic, and (c) free-living taxa that form HABs.

### Symbiodiniaceae as model for marine algal symbiosis

Taxa of the family Symbiodiniaceae have the richest genomic resources available when compared to other dinoflagellates. This specialized family within order Suessiales diverged relatively recently (~160 million years ago (MYA); LaJeunesse et al., 2018) when

**FIGURE 1** Phylogeny of dinoflagellate taxa for which transcriptome and/or genome data are available. The topology does not address the full extent of dinoflagellate diversity. Taxa are organized by order following the latest systematic classification (Adl et al., 2019) relative to the key external taxonomic groupings of Alveolata. Branching order among taxa within each order is not shown. The relative positions of the orders follow the phylogeny in Stephens et al. (2018) where applicable; however, following Adl et al. (2019), Noctilucales is placed together with Syndiniales (external to Dinophyceae), the Oxyrrhinales is external to Dinoflagellata, and Gymnodiniales is shown as a monophyletic clade for simplicity. Classification of Family Symbiodiniaceae follows LaJeunesse et al. (2018). Vertical columns next to each taxon show its ecological niche (i.e., symbiotic, free-living, parasitic, and bloom-forming) and if genome data are available; a question mark indicates uncertainty. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



Dinoflagellate group	Symbiodiniaceae (predominantly symbiotic)		Deep-branching taxa (parasitic Syndiniales)		Free-living bloom-formers	
	Lacking	Developing	Adequate	Lacking	Developing	Adequate
<b>Accessibility</b>	<ul style="list-style-type: none"> <li>Ease of supply</li> <li>Phenomenal access</li> <li>Ethical considerations</li> </ul>	<ul style="list-style-type: none"> <li>Limited geographical distribution</li> <li>Culturing limited to facultative symbionts</li> </ul>	<ul style="list-style-type: none"> <li>Broad distribution of dinoflagellate hosts</li> <li>Culturing is feasible</li> </ul>	<ul style="list-style-type: none"> <li>Global or broad distributions</li> <li>Culturing is feasible</li> </ul>		
<b>Tractability</b>	<ul style="list-style-type: none"> <li>Standardization</li> <li>Viability and durability</li> <li>Responsiveness</li> <li>Availability of methods and techniques</li> <li>Researcher risks</li> </ul>	<ul style="list-style-type: none"> <li>Limited methods for transformation and cryopreservation</li> <li>Small genome sizes (e.g. &lt; 3 Gbp)</li> </ul>	<ul style="list-style-type: none"> <li>Limited methods for transformation and cryopreservation</li> <li>Small genomes (~0.1 Gbp)</li> </ul>	<ul style="list-style-type: none"> <li>Limited methods for transformation and cryopreservation</li> <li>Large genomes (up to ~200 Gbp)</li> </ul>		
<b>Resources</b>	<ul style="list-style-type: none"> <li>Previous use</li> <li>Epistemic resources</li> <li>Training requirements</li> <li>Informational resources</li> </ul>	<ul style="list-style-type: none"> <li>Genome data available for 22 taxa so far</li> <li>Some transcriptome data available</li> </ul>	<ul style="list-style-type: none"> <li>Genome data of <i>Amoebophrya</i> available</li> <li>Some transcriptome data available</li> </ul>	<ul style="list-style-type: none"> <li>Very limited genome data available</li> <li>Some transcriptome data available</li> </ul>		
<b>Research support</b>	<ul style="list-style-type: none"> <li>Institutional support</li> <li>Financial considerations</li> <li>Community support</li> <li>Affective and cultural attributes</li> </ul>	<ul style="list-style-type: none"> <li>Synergy with coral reef research</li> <li>Impacts on tourism, fisheries, and reef ecology</li> </ul>	<ul style="list-style-type: none"> <li>Synergy with research in protist biology and marine parasitology</li> <li>Applications in aquaculture and fisheries</li> </ul>	<ul style="list-style-type: none"> <li>Synergy with research in marine toxicology and ecology</li> <li>Applications in aquaculture and fisheries</li> </ul>		
<b>Promise</b>	<ul style="list-style-type: none"> <li>Commercial and other applications</li> <li>Comparative potential</li> <li>Translational potential</li> <li>Novelty</li> </ul>	<ul style="list-style-type: none"> <li>Key for studying coral reef symbiosis</li> <li>Translations may require consideration of host and holobiont</li> </ul>	<ul style="list-style-type: none"> <li>Key for studying deep evolution</li> <li>Translation potential in biocontrol of HABs</li> </ul>	<ul style="list-style-type: none"> <li>Key for studying niche diversification and HAB ecology</li> <li>Translation potential in monitoring and mitigating HABs</li> </ul>		

**FIGURE 2** Assessing dinoflagellate models against the five categories of 20 criteria for a model organism (Dietrich et al., 2020) across the three broad functional groups: family Symbiodiniaceae that consists of predominantly symbiotic taxa, the deep-branching taxa of the parasitic Syndiniales, and the free-living bloom-forming taxa. For each group, each category of accessibility, tractability, resources, research support, and promise are assessed broadly as lacking, developing, or adequate. Images shown for each taxon group are purely examples for each functional group and are not to scale, and they do not reflect their potential as a model organism or species. Images of the two Symbiodiniaceae taxa were provided by Sarah Shah (The University of Queensland, Australia); the image of *Amoebophrya ceratii* was adapted from John et al. (2019); the three images of free-living dinoflagellates were supplied by Shauna A. Murray (University of Technology Sydney, Australia). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

compared to ancestral dinoflagellates that diverged ~650 MYA (Riding et al., 2023). Since the publication of the first dinoflagellate nuclear genome of the symbiodiniacean species, *Breviolum minutum* (Shoguchi et al., 2013), genomic resources from Symbiodiniaceae have grown significantly, representing 22 taxa as of July 31, 2023 (Figure 1). In addition to the ecological importance of Symbiodiniaceae to coral reef health, this development was driven in part by the smaller sizes of these sequenced genomes (1–3 Gbp) compared with other free-living dinoflagellates. Moreover, the major systematic revision of these taxa as family (LaJeunesse et al., 2018) and the continuing revisions of the various genera and clades (e.g., Butler et al., 2023) have greatly clarified their phylogenetic diversity. Both these efforts enhance the tractability and informational resources available for Symbiodiniaceae. However, accessibility of Symbiodiniaceae remains limited to

facultative symbionts that can be readily maintained as monoclonal cultures and subjected to experimental manipulation. The geographical distribution of these taxa is restricted, e.g., *Cladocopium* taxa are abundant in the Pacific, whereas *Symbiodinium* is more common in the Atlantic, except for the thermotolerant *Durusdinium trenchii*, which may be invasive (Pettay et al., 2015). Living cells of host-specific or (potentially) obligate symbionts remain challenging to isolate and maintain in cultures due to their specialized growth requirements (Krueger & Gates, 2012).

The broad spectrum of symbiotic associations or “facultativeness” presents not only a challenge but also an opportunity for studying Symbiodiniaceae ecology. On the one hand, the putative obligate symbionts, due to prolonged spatial confinement, are hypothesized to have smaller genome sizes and a lower prevalence of structural rearrangements, mobile elements, and



pseudogenes when compared to facultative symbionts (González-Pech et al., 2019). On the other hand, Symbiodiniaceae taxa that have not been associated with any hosts exhibit genomic features similar to other free-living dinoflagellates as would be expected for the ancestor of Symbiodiniaceae (Shah, Dougan, Chen, Lo, et al., 2023). Recent studies have revealed high genomic divergence even among isolates of the same species (González-Pech et al., 2021; Shah, Dougan, Chen, Bhattacharya, et al., 2023) and have clarified how whole-genome duplication has uniquely enhanced the efficiency of *Durusdinium trenchii* as a coral symbiont (Dougan, Bellantuono, et al., 2022). This body of research highlights the potential offered by these taxa for understanding how symbiogenesis arose in the origin and diversification of Symbiodiniaceae, which underpins the health of biodiverse coral reefs. However, current research also demonstrates the limits of generalizing knowledge and the translational potential of Symbiodiniaceae as a model, which is tightly linked to their interactions with the host and other microbes, and how they function as an ecological unit, e.g., in the coral holobiont (Voolstra et al., 2021). Therefore, a model based on a facultative symbiont may be inadequate compared to models that are specific to types of symbiotic associations, localities, and/or hosts (Figure 2).

### Deep-branching syndiniales as model for understanding dinoflagellate origin

The order Syndiniales largely comprises parasitic dinoflagellates and is a deep-branching lineage that split prior to the diversification of the monophyletic Dinophyceae (Figure 1). Genomic resources are available primarily from *Amoebophrya ceratii* (Farhat et al., 2021; John et al., 2019) and *Hematodinium* sp. (Gornik et al., 2015). *Amoebophrya ceratii* is an endoparasite that infects other dinoflagellates (Guillou et al., 2023). Genomes of *A. ceratii* (120–131 Mbp) are the smallest described for any dinoflagellate (Farhat et al., 2021; John et al., 2019) as would be expected in highly reduced genomes among intracellular parasites (Husnik & Keeling, 2019). This is explained by the loss of genes not needed for the parasitic lifestyle and by their dependence on the host for survival. In comparison, *Hematodinium* sp., the crustacean parasite known to be robust in culture without the host (Li et al., 2011), exhibits a nearly 40-fold larger genome (~4.8 Gbp; Gornik et al., 2015), similar to free-living taxa. Interestingly, *A. ceratii*, due to its infection of HAB species, provides an attractive biocontrol agent for these bloom events (Alves-de-Souza et al., 2015).

The ancestor of dinoflagellates and apicomplexans is thought to be photosynthetic (Janouškovec et al., 2010). The highly reduced and fragmented plastid genomes of dinoflagellates are organized in mini-circles (Howe

et al., 2008), and the mitochondrial genomes, in general, harbor only three protein-coding genes and fragments of ribosomal RNAs (Waller & Jackson, 2009). In contrast to all other dinoflagellates—including another parasitic lineage of Blastodinales (Skovgaard et al., 2012) within Dinophyceae—Synidinales taxa lack plastids, and *A. ceratii* potentially also lacks mitochondria (John et al., 2019; Kayal & Smith, 2021).

Deep-branching lineages of the Dinoflagellata such as *A. ceratii* and their close relatives, e.g., *Oxyrrhis marina*, a proposed model for protist biology (Montagnes et al., 2011), provide important references in comparative studies for understanding the origin and early evolution of dinoflagellates (Figure 2). Traits of interest include the origin of phototrophy and mixotrophy (or the escape from parasitism), the origin of bloom-forming taxa, and the complexity of organelle evolution, particularly of plastid evolution that is impacted by multiple endosymbiosis events (Waller & Kořený, 2017; Yoon et al., 2005).

### Free-living, bloom-forming taxa as models for HABS

Most described dinoflagellate taxa are free-living and occur in diverse habitats, including planktonic, epiphytic, and epibenthic habitats, in both marine and freshwater environments. Central to ocean biogeochemical cycling processes, these dinoflagellates can numerically dominate marine habitats (de Vargas et al., 2015). Some are secondarily symbiotic, e.g., *Zooxanthella nutricula* (Gottschling & McLean, 2013), but most have remained free-living. Many free-living taxa are heterotrophic or mixotrophic and can form blooms under favorable conditions (e.g., episodic increased availability of nutrients and/or temperature in the environment) that may cause HABS. Free-living dinoflagellates often have broad geographic distributions at the shelves, coasts, and open oceans, with some exceptions. Recent data have suggested poleward movement of species and HABS due to warming oceans (Gobler, 2020). Bloom-forming taxa often exhibit high levels of intraspecific genetic variation upon which natural selection can act, reflected in wide-ranging phenotypes, such as growth rate, toxin production and photosynthetic efficiency, and genetic structure of populations at different geographic scales (Brandenburg et al., 2021; Nagai et al., 2007; Verma et al., 2020).

Relative to their prevalence in the environment and their importance, free-living dinoflagellates have the least genomic resources, with only a few draft genomes available (Figure 1). The large genome sizes of HAB taxa present a major hurdle for data generation. Most available genome-scale data have been limited to transcriptome datasets (Figure 1), with a strong research focus on polyketide synthase genes

involved in the toxin biosynthesis of HAB species (Van Dolah et al., 2017; Verma et al., 2019). Furthermore, gene dosage is known to regulate the amount of paralytic shellfish toxins produced by *Alexandrium* spp. during blooms (Murray et al., 2011, 2019); these are the only marine toxins to be declared a weapon by the Chemical Weapons Convention (Sierra & Martínez-Álvarez, 2020). A recent multi-omic analysis of *Prorocentrum cordatum* revealed extensive gene duplication and RNA editing that act as mechanisms to generate gene-function plasticity (Dogan, Deng, et al., 2022). Although these results are useful, the lack of genome data for most HAB species presents a significant knowledge gap. Comparative analysis of these data is necessary for determining the evolutionary, molecular, and ecological mechanisms that underpin the population dynamics of blooms, which will guide the formulation of effective strategies for predicting and managing HABs (Figure 2).

## WHERE DO WE GO FROM HERE?

Given the vast ecological, phylogenetic, and genomic diversity of dinoflagellates, we argue in favor of context-specific models, at least one for each of the three functional groups we discuss above. Taxa that satisfy all five categories of criteria (Figure 2) are yet to be identified, with tractability and informational resources being the two key limitations.

A desirable trait for a model unicellular organism is the availability of cryopreserved cells that enables robust standardization and reproducibility of experiments while minimizing the impact of morphological, physiological, and genetic alterations that could accumulate during long-term cultivation. Although monoclonal cultures are available from major culture collections, most dinoflagellate strains are cryo-recalcitrant (Paredes et al., 2021), limiting their tractability as models. Attempts at cryopreservation have been successful for some Symbiodiniaceae strains (Di Genio et al., 2021; Kihika et al., 2022), but generalizability to other dinoflagellate taxa remains to be investigated.

The common phylogenetic marker genes, such as the nuclear ribosomal operon (e.g., the small and large subunits of the ribosomal RNA and internal transcribed spacers) or organellar genes remain inadequate for delineating the complex phylogenetic diversity of dinoflagellates plagued with cryptic diversity. The rRNA markers occur in multiple copies (up to  $10^6$ – $10^8$ ) that vary within genomes (Ruvindy et al., 2023; Thornhill et al., 2007), and remarkably for the Gonyaulacales, HAB taxa such as *Gambierdiscus* and *Alexandrium* species show individual strains within a population that can exhibit varying genome copies of the rRNA array (Ruvindy et al., 2023). Therefore, phylogenetic identification of dinoflagellates would benefit from careful

consideration of single-copy orthologous genes, which may include conserved genes for which functions are yet to be determined (Stephens et al., 2018). As more genome-scale data become available, a curated reference set of dinoflagellate orthologs—e.g., BUSCO genes (Manni et al., 2021) for Dinophyceae—will benefit comparative sequence analysis, e.g., in assessing the completeness of omics data and in characterizing dinoflagellate diversity from metagenomic data, as has been done for bacteria and archaea (Parks et al., 2022). Recent studies have demonstrated the use of whole-genome sequences to inform taxonomic classification and the complex evolutionary histories of genes (Chen et al., 2022; Dogan, González-Pech, et al., 2022). These data also enable the investigation of phylogenetic relatedness based on short, conserved sequence motifs (Lo et al., 2022; Van Etten et al., 2023); the data expand beyond the boundaries of genes or specific genomic elements and the delineation of phylogenetic diversity that are obscured in morphological, ecological, and/or paleontological data.

Existing genomic resources of dinoflagellates (Figure 1) provide a good reference point for designing analytic workflows tailored to their idiosyncratic gene and genome features. Genome assemblies of Symbiodiniaceae taxa based on chromosome conformation capture (Li et al., 2020; Marinov et al., 2021; Nand et al., 2021) provide insights into spatial genomic and chromosomal structure, including topologically associated domains and their potential role in gene regulation (Lin et al., 2021). With the bulk of technical challenges in data analysis resolved and the falling costs of genome sequencing, the large genomes of HAB species are now within reach. Understandably, genome size and cell ploidy are key deciding factors, favoring smaller-sized haploid genomes. This is particularly relevant to species that exhibit genome-copy variation among strains, e.g., *Alexandrium pacificum* (Ruvindy et al., 2023).

Central to microbial functional genomics is a stable genetic transformation system. Although several dinoflagellates have been genetically transformed (Faktorová et al., 2020; Gornik et al., 2022), the generalizability of these methods is poorly understood. A stable and reproducible transformation system for dinoflagellates enables functional validation of key genes and genomic elements inferred from sequence data. Many of these genes are likely important for niche specialization, local adaptation, and stress response, but they lack sequence similarity to known genes from public data repositories (Stephens et al., 2018). Experimental molecular tools, such as the CRISPR-Cas9 system developed for diatoms (e.g., Belshaw et al., 2023; Hopes et al., 2016), are extremely useful for validating gene functions and manipulating target genes to enhance desirable traits. These tools still need to be developed for dinoflagellates, particularly since targeted gene

knockout is challenging due to the expansive gene families in these taxa.

In parallel to the development of these genetic tools, an omics approach integrating genome, transcriptome, proteome, and/or metabolome data remains powerful for elucidating molecular response, cellular regulations, and putative gene functions of dinoflagellates (Beedessee et al., 2020; Dougan, Deng, et al., 2022; Murray et al., 2016). Proteins and metabolites are key to the validation of gene and pathway functions predicted using transcriptome analysis, and their differential rates of synthesis and turnover would reflect regulatory constraints (Tarazona et al., 2021). These data also complement investigations of molecular regulation in dinoflagellates, which thus far is known to implicate microRNAs, RNA editing, and differential exon usage (Baumgarten et al., 2013; Dougan, Deng, et al., 2022; Liew et al., 2017), presenting the emerging research avenue of epitranscriptomics. For functional genomic studies of Symbiodiniaceae, the relevant host and other interacting biotic partners need to be considered, because these organisms function as a holobiont to sustain symbiosis. Hologenomic or other holo-omic approaches (Robbins et al., 2019; Williams et al., 2021) will elucidate holobiont functions without the need for separate analyses of the interacting partners. For host-specific symbionts that are difficult to maintain in culture, accessibility of genome data of these taxa could leverage innovative sequencing approaches, e.g., single-cell sequencing (Delmont et al., 2022) or depletion of host sequence data via adaptive sampling sequencing (Martin et al., 2022); adaptation of these techniques for dinoflagellates would help improve tractability of Symbiodiniaceae taxa as a model.

## CONCLUDING REMARKS

Research in the post-genomic era is greatly enhancing our understanding of how dinoflagellate genomes have evolved and diversified, and it enriches the urgently needed genomic resources for the research community. In the search for *the* model species, it is clear that no one model is adequate to encapsulate the vast phylogenetic and ecological diversity of dinoflagellates, and importantly, the transferability of knowledge between different lineages may be limited. Therefore, we argue in favor of context-specific models, at least one each for the Symbiodiniaceae, the deep-branching lineages, and HAB species, because each is useful for addressing different hypotheses about the biology, ecology, and evolution of dinoflagellates. Such a multi-pronged approach to developing dinoflagellate models is desirable, and the selection of target species could be guided by the set of criteria discussed herein. Building on

existing resources and continuing development of technologies, the time is ripe for the community to expand genomic investigations to other lineages of dinoflagellates, and importantly of HAB species. Due to the substantial research funding and support that may be required, multi-institutional, inter-disciplinary collaborations (McKenna et al., 2021) and diversified funding support will be key to undertaking such endeavors.

## AUTHOR CONTRIBUTIONS

**Hisatake Ishida:** Conceptualization (equal); visualization (lead); writing – original draft (lead); writing – review and editing (supporting). **Uwe John:** Writing – review and editing (supporting). **Shauna Murray:** Writing – review and editing (supporting). **Debashish Bhattacharya:** Funding acquisition (supporting); writing – review and editing (supporting). **Cheong Xin Chan:** Conceptualization (equal); funding acquisition (lead); supervision (lead); visualization (supporting); writing – review and editing (lead).

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