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Highlights

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- Identifies limitations in single-species HAB studies
- Advocates for multi-method frameworks for HABs

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Making Waves: Emphasizing Integrated Research on Harmful Algal Blooms Over Single-Species Laboratory Studies

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Abstract

This paper emphasizes the need for more integrated research approaches when studying harmful algal blooms (HABs). Single-species research on HAB-forming algae provides important insights but fails to account for the interactions between multiple species and their surrounding ecosystems, which is critical to understanding HAB dynamics, including HAB mitigation. To enhance our understanding of complex ecological phenomena and management of HABs, we emphasize approaches like multi-species field-based experiments, big data analysis and ecological modelling, and real-time monitoring, complemented by remote sensing that better represent actual natural environmental conditions, drivers, abiotic and biotic interactions.

Keywords: Harmful algal blooms; Ecosystem dynamics; Multispecies interactions; Community ecology; Mesocosms; Algal assemblage progression

Highlights

- Emphasizes the diversity, species dynamics and interactions in HABs
- Identifies limitations in single-species HAB studies
- Advocates for multi-method frameworks for HABs

1. Introduction

Harmful algal blooms (HABs) represent a significant ecological phenomenon with profound impacts on aquatic environments across the globe (Qin et al., 2019; Lim et al., 2023). These blooms, characterized by rapid growth and accumulation of bloom-forming algae, can produce toxins detrimental to wildlife, structurally and functionally disrupt aquatic ecosystems, and pose human health risks (Paerl, 2018; Zhou et al., 2021a; Plaas and Paerl, 2020). Traditionally, research into HABs has largely focused on the study of single species in laboratory settings, aiming to understand the conditions that promote their proliferation and the mechanisms behind their toxicity (Orr et al., 1998; Chang et al., 2022; Wang et al., 2022). This approach, however, often does not address the intricate interactions that occur in natural settings and fails to capture the ecological dynamics of HABs, a point emphasized by recent research showing the disparity between laboratory and field conditions in understanding cyanobacterial distributions (Xiao et al., 2020). Single-species research on HAB-forming algae often provide data that are difficult to extrapolate to natural environments because they are inherently unable to incorporate factors such as interspecies interactions under varying environmental conditions (Banerji and Benesh, 2022). The limitations of such approaches have been noted in earlier commentaries (e.g., Smayda, 1997; Anderson et al., 2012; Wells et al., 2015), particularly regarding their reduced ability to represent ecological complexity. Here we provide a systematic review and analysis of recent HAB research, identifying key patterns in experimental design over the past decade that have not been previously quantified, with an emphasis on moving beyond single-species studies. Next, we explore HABs within their broader ecological context, emphasizing how bloom-forming algae interact with biotic and environmental factors (Paerl and Barnard, 2020). We then critically discuss the limitations of single-species studies in replicating the complexity of natural environments. To address these challenges, we emphasize integrated approaches to better simulate the complexity of HAB dynamics through: (1) the use of big data analysis and advanced ecological modeling to identify drivers of HABs across ecosystems; (2) multi-species, field-based experiments such as mesocosm studies to capture the ecological interactions and environmental influences on HABs; and (3) real-time monitoring systems, complemented by remote sensing to provide actionable insights for

effective management. These three areas were selected because they correspond directly to the major gaps identified based on patterns revealed in our analysis—namely, the lack of multi-scalar analysis, ecological realism, and temporal responsiveness. The aim of adopting these approaches is to enhance the predictive power and ecological relevance of HAB research, ultimately contributing to the development of scientifically sound and practical strategies for HAB mitigation and management (Tullos et al., 2025).

2. The Prevalent Approach to HAB Research has relied on Single-Species Studies

HABs arise from different algal groups in freshwater and marine environments. In freshwater, cyanobacterial bloom genera such as Microcystis, Dolichospermum, Aphanizomenon, Oscillatoria, Raphidiopsis, Nodularia and Planktothrix dominate as HAB-formers (Paerl et al., 2001; Wiedner et al., 2007; Sukenik et al., 2012). In marine systems, dinoflagellate genera Alexandrium, Karenia, and Prorocentrum, as well as diatoms such as Pseudo-nitzschia, are frequent bloom formers (Anderson et al., 2012; Bates et al., 2018). To assess the proportion of single-species versus multi-species studies in HAB research and analyze the balance between laboratory and field-based studies, a systematic review was conducted, the process and results from which are illustrated in Fig. 1. A total of 1,688 records were identified through the Web of Science (WoS) core collection database over the past decade (from August 6, 2014, to August 6, 2024) on the topics of HABs and environmental studies.¹ Of these, 879 records were excluded after screening titles and abstracts, as they did not involve experimental studies. The remaining 809 records were subjected to full-text screening, with an additional 180 records excluded after in-depth review for not involving experimental studies. Of the remaining 629 full-text articles, 267 were excluded for focusing on surveys or observational studies that, while typically sampling natural water bodies during HABs and measuring various physico-chemical parameters, did not include controlled experiments. Ultimately, 362 studies were included in the final systematic analysis.

Although the limitations of single-species approaches were already recognized by Smayda as early as 1997 (Smayda, 1997), our results show that nearly 30 years later, single-species studies still dominate

¹ Search terms were ((((((TS=(environmental)) AND TS=(harmful algal blooms)) AND DT=(Article)) NOT DT=(Data Paper)) NOT DT=(Book)) NOT DT=(Book Chapter)) NOT DT=(Review)

experimental HAB research. Among the 362 studies, 64 % utilized a single species of algae in their experimental research, and we further examined the yearly proportions of single-species studies from 2014 to 2024. The results confirm that in every year during this period, single-species studies consistently accounted for over 50% of experimental HAB publications. Of these single-species studies, in freshwater environments 68 % focused on Microcystis spp., while 5 % used Chlorella spp.², 4 % used Planktothrix spp. as their primary research subjects, the remaining 23 % divided among other species representing 4 % or less of freshwater studies. In marine environments, the top three algal species studied were Alexandrium spp. (25 %), Karenia spp. (9 %), and Prorocentrum spp. (9 %), with the remaining 57 % divided among other species representing 6 % or less of marine studies. These thresholds (≥ 4 % in freshwater and ≥ 6 % in marine) reflect the cutoff values corresponding to the three most frequently studied species in each environment, and were not meant to imply different selection criteria. Most of these species represent primary HABs-forming algae, however, Chlorella spp. is not acknowledged as a HAB. Of the algal experiments in these 362 studies, only 10 % were conducted in the field, while the remaining 90% were carried out under controlled laboratory conditions. It is important to note that while many studies collected algae from field environments, single species were often isolated from natural assemblages and subsequently studied under laboratory conditions, often under axenic conditions. Axenic algal cultures have often been used in biotechnological applications, but they represent a strong departure from natural environmental conditions because they lack essential algal-microbial interactions that are critical for nutrient cycling, metabolic exchange, and ecological stability (Paerl and Millie 1996; Ramanan et al., 2016; Dextro et al., 2024).

² Although *Chlorella* spp. is not typically classified as a HAB species, some studies included in our literature review used *Chlorella* to simulate bloom-like conditions or to explore HAB-related control strategies and explicitly framed their work within the HAB research context.



Fig. 1. Flow chart showing the process used to characterize the current state of HAB research, which has a strong emphasis on single-species studies in controlled laboratory environments. Only experiments where controlled experimentation on algae was conducted directly in the field were categorized as field studies.

3. Why Do Single-Species Studies Miss HAB Complexity?

HABs originate in ecosystems composed of a myriad of algae and other species that interact such that bloom-forming algae are able to gain ascendancy and become the predominant population, with growth and biomass far outstripping that of all other algae (e.g., the work of Kim et al, 2021a on *Microcystis*). Cyanobacterial bloom-formers such as *Microcystis*, *Dolichospermum*, *Aphanizomenon*, *Raphidiopsis*, *Nodularia* and *Oscillatoria*, are known for their production of highly hazardous toxins and, for some, highly noxious taste and odor problems (He et al., 2016; Huisman et al., 2018). Although single algal species of genera such as *Microcystis* can often dominate in HABs, the bloom-forming species' growth and dominance are influenced by metabolic and trophic interactions with other organisms in the ecosystem, as illustrated in Fig. 2, hence the ecosystem context cannot constructively be disregarded (Paerl and Kellar 1978; Paerl, 1982; Fulton and Paerl, 1988; Paerl and Millie 1996).



Fig. 2. Conceptual diagram illustrating the role of HABs within ecosystems. Note – HGT is an abbreviation for horizontal gene transfer, and numbers refer to relevant references for processes shown: 1 Anand et al., 2023, 2 Taylor et al., 1999, 3 Barbara and Mitchell, 2003, 4 Paerl and Kellar, 1978, 5 Paerl, 1982, 6 Paerl and Pinckney, 1996, 7 Paerl and Millie 1996, 8 Li et al., 2024, 9 Zhaxybayeva and Doolittle, 2011, 10 Kim et al., 2021a, 11 Sweat et al., 2021, 12 Vanni, 1987. 13 Ger et al., 2016, 14 Fulton and Paerl, 1988, 15 Shen et al., 2022, 16 Grasso et al., 2022, 17 Lin et al., 2024, 18 Kirsten and Karl, 2003, 19 Koonin and Yuri, 2012. 20 Nagasaki, 2008. 21 Monier et al., 2016.

Examples of recent research demonstrating this point are found in the work of Pound et al. (2021), Grasso et al. (2022), and Zhang et al. (2023). Building on the early insights of Paerl and Millie (1996), Pound et al. (2021) further investigated the cyanobacterial microbiome and showed how its role in metabolic exchanges can either stabilize or increase the toxicity of blooms. Specifically, their study showed that microbial interactions modify nutrient availability (nitrogen and phosphate) and alter environmental conditions (light), thereby affecting bloom toxicity, persistence, and the broader metabolic profile of the cyanobacterial community. Early work by Paerl and Kellar (1978) demonstrated a similar role of

microbial interactions, showing how bacteria associated with Anabaena stimulated N₂ fixation by the host cyanobacterium, further highlighting the importance of microbial-cyanobacterial associations in bloom development. Grasso et al. (2022) focused on cyanophages, viruses that regulate cyanobacterial populations, and revealed how these viral interactions can control bloom cycles by influencing the mortality and turnover rates of cyanobacterial populations. Cyanophages can initiate bloom decline by lysing host cells, reducing population density, and redistributing nutrients into the surrounding water, which may subsequently affect the onset, duration, and collapse of blooms, depending on the timing and extent of viral infections. Zhang et al. (2023) further explored how external stressors, including the limitation of key nutrients like nitrogen and silica, as well as competition with diatoms and dinoflagellates, shape bloom characteristics and outcomes. Their study confirmed that nitrogen scarcity notably suppresses cyanobacterial growth, while silica limitation disadvantages diatoms. Under these conditions, dinoflagellates, including toxin-producing species such as those capable of synthesizing saxitoxins, gain a competitive advantage due to their adaptation to low-nutrient environments. This shift not only reduces cyanotoxin production but also increases the prevalence of other harmful species, potentially exacerbating ecological and health risks (Zhang et al., 2023). The presence of zooplankton in natural ecosystems adds further complexity to these interactions, as illustrated in Fig. 2. Zooplankton, such as Daphnia, are grazers, feeding on various algae and reducing their populations, or, alternately, indirectly augmenting algal populations in the case of species such as *Microcystis* that produce toxins deterring zooplankton predation. (Fulton and Paerl, 1987; Fulton and Paerl, 1988; Ger et al., 2016; Shen et al., 2022). Other phenomena, like aerotaxis/chemotaxis—the movement of bacteria towards algal-produced compounds—result in the redistribution of nutrients within blooms by facilitating bacterial migration towards areas of high algal productivity (where these bacteria help decompose organic matter and release nutrients, such as ammonium and phosphate, that are readily accessible to algae), and also guide blooms towards more favourable growth locations (Gallucci and Paerl 1983; Paerl and Gallucci 1985; Taylor et al., 1999; Barbara and Mitchell, 2003). Nagasaki (2008) demonstrated that a wide range of algal viruses, particularly those infecting dinoflagellates and diatoms, can significantly modulate bloom trajectories by inducing host

cell lysis. The findings from these studies underscore the complex ecological mechanisms that influence HAB formation, persistence, and composition. Such findings illustrate how physical conditions, nutrient availability, microbial interactions, and competition among species determine not only which organisms become dominant but also the potential toxicity and ecological impact of a bloom.

While the primary goal for many researchers in single-species studies is to gain a deeper understanding of the target/bloom-forming species, some studies explicitly aim to extrapolate single-species laboratory experiments to predict the effects of practical interventions in managing blooms in natural settings (Greenfield et al., 2014; Cai et al., 2016; Wu et al., 2022). A mismatch between laboratory studies and reality, however, is not unusual. As one example, for *Microcystis aeruginosa* and *Raphidiopsis raciborskii*, Xiao et al. (2020) found a stark difference between biomass accumulation measured in the field versus that predicted from growth rate measured in the laboratory.

The fundamental limitation of single-species studies in laboratories is their inability to accurately replicate the multiplicity of both abiotic and biotic factors operating in concert to influence ecosystems in natural environments (Guy-Haim et al., 2017; Xu et al., 2022). For instance, Zhou et al. (2021b) showed that algae exposed to fluctuating light intensities in the field had significantly different photosynthetic rates compared to those grown under laboratory conditions. A study by Ras et al. (2013) highlights how outdoor microalgal cultures are subject to significant temperature fluctuations, both seasonally and daily, which drastically affect growth conditions and metabolic rates. These temperature variations, which may lead to energy re-balancing and cell shrinking, which in turn influence algal community structure and production efficiency, are not reliably captured in laboratory settings. As another example, in stratified water columns, diatoms thrive in deeper, nutrient-rich layers where light is limited but silicate is abundant, while cyanobacteria such as *Microcystis* dominate the well-lit surface waters, especially in nutrient-rich environments (Paerl et al., 2001). This vertical distribution creates distinct niches, allowing multiple species to coexist while competing for resources (Hutchinson, 1961). Unlike laboratory settings, in natural environments, nutrient fluctuations, seasonal changes, and mixing events can shift the balance of these

interactions, altering which species dominate in different layers and how. For example, long-term work on *Alexandrium fundyense* in the Gulf of Maine has shown that bloom initiation and transport are closely linked to the combined action of nutrient inputs, water column stratification, and current patterns (Anderson et al., 2005). These interacting factors are difficult to replicate in simplified laboratory settings. Similarly, the 2014–2016 *Pseudo-nitzschia* bloom in the northeast Pacific occurred during a marine heatwave and was associated with multiple stressors acting in concert, including warming, reduced upwelling, and altered nutrient conditions (Trainer et al., 2020). This event exceeded predictions from prior single-species lab studies.

4. Making Waves in Future HAB Research

To better simulate the complexity of HABs and improve research outcomes, several approaches are of interest and relevance: multi-species field-based experiments, big data analysis and ecological modeling, and real-time monitoring. Multi-species experiments are important to compensate for limitations of singlespecies research, and perhaps one of the more accessible and well-known approaches to effect multispecies research is the use of mesocosms. Introduced by Odum in 1984, mesocosms are small to moderately-sized, controlled environments that mirror natural ecosystems, enabling researchers to study individual species within their broader ecological contexts (Odum, 1984). This methodology integrates the precise control of laboratory settings with the realism of natural environments (e.g., in situ light and temperature conditions, as well as biotic interactions). Meta-analyses by Elser et al. (2007) on 1069 studies and Spivak et al. (2011) on 359 freshwater mesocosm experiments, ranging widely in size and duration, concluded that findings from mesocosm research are applicable to larger-scale, ecosystem-level processes. Studies such as those by Lewandowska and Sommer (2010), Ma et al. (2015) and Li et al. (2021) serve as examples of the utility of mesocosms in multi-species research and/or research involving actual environmental conditions. Lewandowska and Sommer (2010) conducted a mesocosm study to explore how varying temperature and light conditions affect competition between phytoplankton groups, specifically diatoms and cyanobacteria, under simulated climate change conditions. By using 1400-liter

mesocosms to manipulate temperature and light conditions, they demonstrated that higher temperatures triggered earlier phytoplankton blooms and led to a shift towards smaller phytoplankton species due to increased zooplankton grazing pressure. The mesocosm study by Ma et al. (2015) at Lake Tai, China investigated how nitrogen and phosphorus enrichment affect competition between cyanobacteria and green algae. This study found that, under conditions of both high nitrogen and phosphorus, green algae could outcompete cyanobacteria, challenging the typical assumption that cyanobacteria consistently dominate in highly eutrophic conditions. Li et al. (2021) used mesocosms to investigate the effects of copper and iron micronutrients on Microcystis and mixed algal communities in natural lake water. The authors found strongly modulated chalkophore and siderophore production that was a function of the biological assemblage present, the amount of copper/iron amended, as well as finding chalkophore to be a predictor of microcystin synthesis. While mesocosms offer an effective approach for studying multi-species interactions, using them is often limited by the need for suitable equipment and deployment sites locations used must remain undisturbed throughout the experimental period while being readily accessible to researchers. The larger physical scale of mesocosms, relative to conventional laboratory setups, necessitates scaling up all aspects of the experiment, thereby increasing labour demands and associated costs. The circumstance of increased demands imposed by mesocosm work may explain the persistent popularity of single-species laboratory studies, however, this entrenches HAB research in the approaches of the past rather than the needs of the future.

Integrating big data analysis and ecological modeling is a cogent way to identify key drivers of HABs across diverse ecosystems. With the ability to reveal how multiple environmental variables interact across different temporal and spatial and geographic scales, they offer information that complements findings from controlled laboratory studies, which usually isolate specific variables. Importantly, this framework encompasses a range of computational tools—including machine learning and artificial intelligence—that are increasingly applied to develop predictive models trained on large, multi-source datasets (Kim et al., 2021b). For example, Jeong et al. (2022) demonstrated that using a machine learning technique referred to

as extreme gradient boosting improved HAB prediction accuracy by approximately 15 %, while Hill et al. (2020) achieved a detection accuracy of 91% and an 8-day prediction accuracy of 86% by integrating Convolutional Neural Networks (CNNs) with Long Short-Term Memory (LSTM) networks. These results significantly outperformed traditional approaches such as chlorophyll-a anomaly threshold methods and other spatiotemporal classification methods based on small datasets. Qian et al. (2024) developed an intelligent early warning system for HABs in Lake Tai, China, by applying the Bloomformer-2 model to depth-specific water parcels, parcels that were identified based on a clustering algorithm ("DeepDPM-Spectral Clustering.") that used water quality determinants including chlorophyll-a concentration, turbidity, dissolved oxygen, and temperature. This approach achieves prediction accuracies superior to a conventional model (namely Long Short-Term Memory (LSTM) networks), with the mean absolute percentage error (MAPE) for single-step predictions reduced by up to 73 %. Similarly, for multistep predictions—forecasting multiple future time steps sequentially or simultaneously—the errors decreased by 79 %. These improvements allow timely identification of blooms, including an understanding of triggers such as wind-driven nutrient redistribution and the role of colored dissolved organic matter. Recent advances in molecular and optical technologies, such as eDNA metabarcoding and hyperspectral buoy networks, provide valuable tools for real-time HAB monitoring and remote sensing, and their integration with ecological modeling further enhances adaptive and predictive management within an integrated research framework.,

Implementing real-time monitoring systems with automated sensors and telemetry offers immediate insights into nutrient levels, water temperature, and algal biomass variations. This approach, distinct from predictive modeling, enables rapid response measures such as nutrient load reduction or algal removal. Using this approach, Yuan et al. (2023) developed an advanced real-time monitoring system utilizing the Imaging FlowCytobot. This device hybridizes flow cytometry and video technology to generate detailed images; the laser-induced fluorescence and light scattering from algae trigger a camera to take pictures. Deploying the device in Tolo Harbour, Hong Kong, the Device was able to achieve *in situ*, high-resolution imaging and automated classification of algal species with 99.87% accuracy. Leading into a red tide event

in February 2020, this system identified a sharp increase in algal counts, particularly for key HAB-forming species like *Scrippsiella* and *Mesodinium*, several days before the official onset of the event as reported by the Agriculture, Fisheries and Conservation Department of the Hong Kong Special Administrative Region Government. This early detection resulted in timely communication with fish farmers and the consequent pre-emptive measures of adjusting feeding schedules and deploying aeration systems, measures taken to mitigate the impact of oxygen depletion from the HAB. The FlowCytobot's ability to classify algae within 0.01 seconds demonstrates its capability to provide both accurate and actionable information for HAB management. The FlowCytobot system represents a fluorimetry-based approach to real-time HAB monitoring; however, a wide range of alternative spectrometric (e.g., Raman spectroscopy, light scattering), imaging (microscopy), and acoustic sensing techniques offer expanded scope for diverse applications in real-time monitoring (Orenstein et al., 2020; Ostrovsky et al., 2020; Oliva-Teles et al., 2021; Yang et al., 2023; Zhao et al., 2023). While field sampling and subsequent laboratory analysis remain invaluable for controlled experimentation and detailed mechanistic studies, such sampling and analysis is subject to delay and as such limited in addressing rapidly fluctuating conditions. Remote sensing techniques have been increasingly employed to detect HABs and assess environmental conditions across diverse aquatic systems (Liu et al., 2022; Alharbi, 2023). For example, recent studies have demonstrated the effectiveness of satellite imagery and machine learning models in mapping HAB dynamics (Kislik et al., 2022), quantifying bloom extent across large geographic regions (Schaeffer et al., 2022), and supporting real-time health advisories in recreational water bodies (Lopez Barreto et al., 2024). While satellite platforms offer broad spatial coverage, they are often limited by cloud cover, revisit time, and moderate spectral resolution. To address such limitations, hyperspectral buoy networks have been developed. These systems consist of fixed or floating platforms equipped with hyperspectral radiometric sensors that operate continuously under variable environmental conditions. They provide higher spectral and temporal resolution, allowing more accurate differentiation of phytoplankton groups based on their optical signatures and improved detection of rapid, fine-scale bloom dynamics in situ (Babin et al., 2005; Sawtell et al., 2019). The integration of remote sensing with *in situ* monitoring and ecological modeling

will be crucial in improving HAB prediction and management strategies.

While our discussion here has focused on mesocosms, big data analysis/ecological modeling, and realtime monitoring because these three areas address major structural gaps identified in recent HAB research—namely, the lack of ecological realism, multi-scalar integration, and temporal responsiveness, this merely illustrates representative shifts toward more integrated and scalable approaches. Many other innovative strategies are also emerging, such as environmental DNA analysis for community-level bloom detection and trait-based modeling for predicting species-specific responses under dynamic environmental conditions (Jacobs-Palmer et al., 2021; Zhang et al., 2024) and the application of machine learning and artificial intelligence to improve HAB prediction and early warning capabilities.

5. Conclusions

This paper synthesizes recent evidence and case studies to support a shift in HAB research design moving from traditional single-species laboratory experiments toward more integrated, ecologically grounded approaches. This shift addresses long-standing methodological limitations and provides practical pathways to improve the scientific validity and real-world applicability of HAB studies. This paper adduces the rational basis for more integrated research approaches in the study of HABs, moving beyond the traditional single-species laboratory focus. The key conclusions are as follows:

• Single-species studies accounting for 64 % of the HAB research from the last decade, provide valuable data, but fail to replicate the ecological complexity of HABs in natural environmental settings.

• Mesocosm studies have been demonstrated to be an effective method to bridge the gap between laboratory and field studies, offering controlled environments that mimic natural conditions more accurately and allowing for a deeper understanding of multispecies interactions and environmental influences on HABs.

• Beyond mesocosms, expanding research to include more focus on big data analysis/ecological modelling, and real-time monitoring complemented by remote sensing will support a deeper understanding of HABs needed for developing management strategies that are both scientifically sound and ecologically relevant. By synthesizing patterns across recent literature, this paper identifies persistent structural gaps—

specifically, the lack of ecological realism, multi-scalar integration, and temporal responsiveness—and demonstrates how current methodological shifts are able to address them. These insights have direct implications for future HAB research design and for the development of evidence-based, proactive management strategies. Increased nutrient runoff from intensive agricultural and urbanization, climate change, increased coastal development, increasing amounts of ballast water discharge from the ever-expanding fleet of global shipping, these are among a few examples of why the occurrence of HABs has been escalating exponentially over the last few decades, an escalation that represents a very modern problem. To really make waves in addressing this modern problem requires modern tools and modern approaches.

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Declaration of interests

 \square The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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