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Tracking aquatic non-native macroinvertebrate species in Germany using long-term data

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Abstract

Biological invasions pose a global challenge, threatening both biodiversity and human well-being. Projections suggest that as invasions increase, the financial costs associated with management and the ecological harm they cause will also escalate. Here, we examined whether long-term biomonitoring strategies were adequate to identify and track benthic aquatic non-native macroinvertebrate species by using the German subset (151 time series; 129 of which reported non-native species) of the currently most comprehensive European long-term dataset of 1816 macroinvertebrate community time series from 22 European countries. The detection of aquatic non-native species was directly linked to the availability of long-term sites and thus, monitoring effort, having identified the spatio-temporal occurrence of 32 non-native species. The available long-term monitoring site data were mostly concentrated in the western part of Germany, predominantly covering the Rhine River and its tributaries. The spatially biased network of long-term monitoring sites, therefore, naturally skews the detection and reporting of aquatic non-native species toward this area and underestimates Eastern and Southern regions, impeding the comprehension of invasion dynamics. However, based on the available data, we found that the absolute number of non-native species increased and the proportion of non-native species relative to native species decreased over time. This indicates complex ecological interactions between native and non-native species and underlines the value of long-term data for investigating invasion dynamics. Considering the value of comprehensive monitoring networks, a spatially biased network delays the application of management and mitigation plans, possibly worsening the ecological and economic effects of biological invasions in Germany. The results provided here indicate the disadvantages of biased datasets, but simultaneously underline the enormous potential of a dense network of long-term monitoring. Our results also highlight the urgent need to increase and diversify long-term biomonitoring efforts throughout Germany to cover the main freshwater resources and their connections where the introduction risk of non-native species is the highest. Centrally collating such data would provide a profound basis for the monitoring of spreading aquatic non-native species and could serve the implementation of national biosecurity efforts.

Keywords Freshwater, Non-native species, Biodiversity, Species conservation, Species introduction

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Introduction

The phenomenon of biological invasions, caused by direct human actions and propelled by anthropogenic disruptions within natural habitats, presents a global challenge that affects both biodiversity and human wellbeing [23, 66]. The introduction of non-native species ranks among the principal causes of biodiversity diminution, accounting for the majority of species extinctions [5], numerous ecological disturbances [58], and monetary losses [15]. Mirroring the upward trajectory of invasion rates [24, 62], increasing financial costs and growing ecological threats are expected in the future [3, 24].

Freshwater ecosystems are particularly threatened by non-native species introductions due to their covering nature (i.e. hiding non-native species from detection; [29, 49, 60] as well as substantial human alterations and uses facilitating non-native species introductions [31, 74]. Management strategies in Europe currently aim to tackle biological invasions through a blend of policy initiatives and practical measures. At the national level, individual European countries have increasingly relied on 'black-' or 'deny-lists'—although these lists face valid criticisms [13, 67]—as essential tools for prioritising non-native species for management efforts [6, 17, 19, 55]. Recognizing the benefits from e.g. canalisation for global trade [9, 51], the interconnected nature of river systems extending beyond national borders [18] continues to play a crucial role in the continental (i.e. European) dispersal of non-native species [4, 41]. Both international and regional cooperation are therefore pivotal [38], with significant legislation such as the EU Regulation on Invasive Alien Species (1143/2014) being crucial for safeguarding Europe's biodiversity and reducing economic losses. However, especially for the management or biosecurity measures for aquatic invasions, the basis remains congruent data, stemming from continuously surveying aquatic ecosystems. Despite being a demanding and costly endeavour [73], established long-term monitoring sites remain an indispensable tool for the understanding and mitigation of biological invasions at regional [25] or national levels [33, 34] which are vital not only for preserving biodiversity but also for safeguarding economic interests and public health in the face of ongoing socio-economic challenges [43].

Germany stands out among European countries due to its robust economy, high levels of economic activity, and strategic position at the centre of European trade and travel networks [70]. Particularly in research-intensive Germany [45, 78], the effective identification and management of aquatic non-native species could be facilitated using existing biodiversity long-term monitoring sites [47]. Using data from just the Rhine River, Haubrock and Soto [25] emphasised the value of sustained monitoring efforts in detecting aquatic non-native species over space and time, highlighting the link between increasing nonnative and decreasing native biodiversity. Yet, despite the evident threat biological invasions pose to Germany's economy [23], there remains a notable deficiency in the availability of comprehensive data on the presence and ecological as well as economic impacts of non-native species. This knowledge gap is particularly surprising considering (1) the rich scientific history of Germany [40] and (2) the presence of approximately 1080 non-native species in this country, with only about 10.7% being recognised as invasive [26]. Furthermore, the most thorough recent compilations, such as the Established Alien Species in the European Union [30] and the Global Invasive Species Database (GISD; [56]), indicate that only 8.1% of the non-native species in Germany are considered invasive based on observed impacts as defining criterium [26, 69]. Given these circumstances, it is crucial to evaluate the effectiveness of long-term biodiversity monitoring for the identification and tracking of freshwater invasions in Germany. This evaluation is essential, because it would help to systematically bridge existing data gaps, provide a clearer understanding of the ecological and economic impacts of non-native species, and improve the management and mitigation strategies for these invasions.

Considering how the vast European river networking has facilitated the spread of numerous non-native species [27, 68], the presence of aquatic non-native species is unlikely contained. This, paired with the pervasive knowledge gaps outlined above, hinders the effective management of biological invasion and the implementation of biosecurity measures (including deny-lists [17, 33, 34, 55]). To generate an overview of the efficacy of long-term monitoring sites in Germany for the detection and tracking of aquatic non-native species, we use a recently collated database of European long-term benthic macroinvertebrate time series [22]. We aimed to identify whether available data (1) covers all major German river networks and (2) if available long-term biomonitoring data can comprehensively identify and track the introduction of aquatic non-native species in Germany over space and time. While we acknowledge the probable existence of several shortcomings in every database, including the database collated by Haase et al. [22] (i.e. inadequate sampling information [28]), we hypothesised that while (i) the network of available long-term biomonitoring sites in Germany may not cover the extensive river network exhaustively, opening the door for nonnative species spreading undetected, (ii) long-term data can effectively identify non-native species in freshwater ecosystems and track freshwater invasion in German rivers, even those dating back decades. This research will contribute to the growing body of studies investigating

the temporal dynamics of freshwater invasions and the relationship between invasion dynamics and long-term biodiversity monitoring.

Methods

Data compilation

We investigated the adequacy of long-term biomonitoring approaches for detecting non-native species in Germany (Supplementary Table 1) using the recently collated and to date most comprehensive European long-term database by Haase et al. [22]. This database contains 1816 macroinvertebrate community time series from rivers and streams in 22 European countries. The data were collected for purposes such as research projects or regulatory biomonitoring that meet the following criteria: (i) each time series contained the abundance of macroinvertebrate taxa, (ii) sampled in a minimum of 8 (not necessarily consecutive) years, and (iii) had consistent sampling effort per site (see [22] for further details). Although macroinvertebrate community sampling protocols varied among time series, they were kept consistent over time within each time series. The nativeness of species in Haase et al. [22] was assessed at the country level by consulting two open databases: the Global Alien Species First Record Database [62] and the Invasive Species Compendium (CABI; www.cabi.org). In case of a mismatch in the species' non-nativeness among country assessments, we followed the Global Alien Species First *Record Database* [62] classification as the most reliable and updated database to date. For a comprehensive explanation of the data used, see Haase et al. [22]. Although data from the Water Framework Directive-compliant freshwater ecosystem monitoring has previously been used to investigate invasion dynamics in Germany [26], the majority of sites were sampled only once based on the available data. Furthermore, the duration and number of samples per site in those that were sampled multiple times are sporadic and highly variable. Consequently, this data would only allow a space-for-time analytical approach and would not be compatible with the data from Haase et al. [22].

Statistical analyses

To evaluate if long-term biodiversity monitoring of aquatic ecosystems covered all major rivers in Germany and could effectively be used for the detection of benthic non-native macroinvertebrate species (henceforth referred to as 'non-native species'), we first investigated the spatio-temporal distribution of long-term sites in Germany and compared these with those that reported non-native species (hypothesis *i*).

We then analysed trends in the reporting of non-native species over space and time with regard to the availability of long-term monitoring sites to evaluate whether longterm data reported in Haase et al. [22] can track nonnative species in Germany (hypothesis ii). This was achieved using a series of Generalised Additive Models (GAMs) using the mgcv library in R [77]. Every model contained the respective response variable (i.e. the raw and the relative non-native species abundance) and the explanatory variables: 'year' to infer temporal trends, 'longitude and latitude' using a spherical spline to correct for spatial autocorrelation, 'site_id' to correct for site-specific effects, and the number of sites sampled per year to account for differences in the intensity or scale of sampling across different locations and times. To assess correlations among predictors [16], we employed the variance inflation factor (VIF) analysis using the vif function from the R package car [20]). We retained all predictors as none expressed any collinearity (threshold = 7). Moreover, we analysed the relationship between occurring non-native species over time and monitoring sites as well as the cumulative occurrence of different macroinvertebrate groups over time using a series of Pearson's product-moment correlations using the *cor.test* function of base R. In addition, we investigated the occurrences of four prominent Ponto-Caspian non-native species (i.e. the two most frequently reported species Dreissena polymorpha and Corophium curvispinum, and the two nonnative species not as frequently reported over space and time, Eriocheir sinensis and Iaera istri). Note that one occurrence does not reflect the number of sites, but the number of individual years a species was reported. All analyses were performed in R version 4.2.3 [61].

Results

In total, the database from Haase et al. [22] contained 151 German long-term monitoring sites reporting long-term macroinvertebrate data from 1968 to 2021 (Fig. 1a). From these, 129 sites (81.13%) reported non-native species, covering the period 1971–2019. These sites were predominantly situated along the Rhine River catchment and to some degree the Ems. Several sites were placed in the Weser River catchment, but not in the Weser River itself. Only one site was on the river Elbe (Fig. 1b).

German long-term data reported in Haase et al. [22] contained occurrence information for 32 non-native species (Supplementary Table 1). The most often reported non-native was *Dreissena polymorpha* (n=1157 occurrences), followed by *Corophium curvispinum* (n=610 occurrences), *Dugesia tigrina* (n=515; synonymous to *Girardia tigrina*), *Dikerogammarus villosus* (n=439), *Gammarus tigrinus* (n=393), *Potamopyrgus antipodarum* (n=263), *Jaera istri* (n=221), *Corbicula fluminea* (n=217) and *Echinogammarus ischnus* (n=165). All other species occurred less than one hundred times



Fig. 1 Distribution of German long-term biodiversity monitoring sites collated in Haase et al. [22] (a) and the subset reporting non-native species (b). The colour gradient indicates the year a non-native species was first recorded in the respective site

(Supplementary Table 1). Whereas the yearly raw abundance of non-native species reported in German longterm biodiversity monitoring sites increased from on average~30 individuals in 1971 to~305 individuals in 2019 by+917% (Fig. 2a; Supplementary Table 2), their relative abundance as a fraction of the invaded communities decreased over time by $\sim 5\%$ (from $\sim 16\%$ in 1971 to ~11% in 2019), reflecting a decline of ~31% (Fig. 2b; Supplementary Table 3). Both trends over time were found to be significant (p < 0.05). Moreover, site ID and coordinates were found to be significant as well (p < 0.05), suggesting site-specific and spatial factors affecting the raw and, respectively, the relative abundance over time. The number of unique sites sampled per year, however, only significantly affected the relative abundance of nonnative species. It suggests that the increase in the number of unique sites sampled per year is associated specifically with changes in the relative, but not the raw abundance of non-native species (Supplementary Table 2, 3). It should be acknowledged that the adjusted R-squared and the deviance explained of both models was very low (< 0.01; 0.2%), indicating that the predictors were not effective in explaining the variability in the data.

The applied Generalised Additive Model identified a bell-shaped progression in the reporting of non-native

species per year over time (despite being corrected for sampling effort), driven by the number of unique sites sampled per year and reaching the highest value in 2002 with 16 reported non-native species (Fig. 3a; Supplementary Table 4). Concomitantly, the number of sites monitoring biodiversity per year increased in a comparably bell-shaped progression (Fig. 3b). The increase in unique sites was significantly correlated with the number of unique non-native species reported per year (p < 0.001; t=5.09; df=46; $R^2=0.60$) as well as the cumulative total number of non-native species reported over time (p < 0.951; t=-0.06; df=15; $R^2=-0.02$).

The cumulative number of reported non-native species (i.e. their first occurrence in long-term biodiversity monitoring over time) increased steadily. The first reported non-native species, *Physella acuta*, occurred in 1971. By 1980, the number of reported non-native species had increased to five, increasing to 12 in 1983 and 17 in 1986. In 2000, the number of non-native species reached 25, totalling 32 reported non-native species in 2012 (Fig. 4).

Using the two most often reported non-native species *D. polymorpha* (Fig. 5a) and *C. curvispinum* (Fig. 5b), we identified their first occurrences in the lower Rhine River close to the Germany–Netherlands border, followed by their spread along the entire Rhine River in the early



Fig. 2 Trends in the reporting of the raw (a) and relative abundances (b) of non-native species over time according to the applied Generalised Additive Model. Please see Supplementary Fig. 1 for the distribution of individual data points



Fig. 3 The trend in the total number of non-native species reported over time but corrected for sampling effort according to the applied Generalised Additive Model (a) and the number of unique sites (b; red) and unique non-native species reported per year (b; blue)

1990s. Following the simultaneous emergence of additional reports along the Rhine River in the 2000s, more appeared westwards towards the Weser River and isolated occurrences in the Elbe River in the 2010s. While *E. sinensis* appeared less frequently, its oldest occurrence in the lower Weser catchment indicates spread going back to the 1990s, with one report in the Elbe and three in the Rhine River, whereas the latest observation was indicated close to the lower Weser catchment in the period 2006–2010 (Fig. 5c). *Jaera istri* was identified predominantly in the Rhine River (aside from one report in the Elbe). Contrasting *D. polymorpha* and *C. curvispinum*, occurrences



Fig. 4 Cumulative number of non-native species first reporting over time, indicating exemplary key species over time and the composition of non-native species classes over time

of *J. istri* indicated spread outgoing from the upper Rhine River in the period 1991–1995 downwards, with the latest report in the lower Rhine River as early as 2006–2010.

Discussion

This study, leveraging the database collated by Haase et al. [22], provides crucial insights into the efficacy of existing long-term monitoring sites from German rivers and streams for detecting non-native species [25, 39]. We found that while the long-term data successfully captured several introductions of non-native macroinvertebrate species dating back decades, the network of monitoring sites did not comprehensively cover Germany's extensive river network, particularly missing significant rivers such as the Danube. Moreover, the analysis indicated a strong correlation between research efforts and the detection of non-native species (thereby also the detection of native species), highlighting the critical role of continuous and expanded biomonitoring to detect non-native species introductions and understand invasion dynamics in Germany and subsequently manage biological invasions effectively.

We also identified opposing trends in the absolute (raw) and relative abundances of aquatic non-native macroinvertebrates since the 1970s. While the absolute number of non-native specimens increased over time, the relative abundance of these species decreased, suggesting that native specimens proliferated even more. This could be explained by higher productivity of aquatic ecosystems driven by increased temperatures and eutrophication [8], but could also indicate a possible resilience of native species or adaptive responses to changing environmental conditions [48, 50]. Raw and relative abundances are a critical metric for the assessment non-native species and their temporal dynamics (as discussed previously [26, 68], but can also highlight an increase in raw numbers of non-native species, thus reflecting a stable or even thriving native biodiversity [63]. Our findings therefore also indicate that ecosystems may have the capacity to support higher overall biomass and diversity, where native species are not necessarily outcompeted by non-native



Fig. 5 Spatio-temporal occurrences of *Dreissena polymorpha* (a), *Corophium curvispinum* (b), *Eriocheir sinensis* (c), and *Jaera istri* (d) based on their respective occurrences in German long-term biodiversity monitoring data reported in Haase et al. [22]

ones but coexist, possibly due to niche differentiation or other ecological mechanisms [12]. Finally, the inverse nature of the trends in raw and relative abundance identified here also suggests that management strategies focusing solely on the presence of non-native species without considering the overall community structure and function may overlook important aspects of ecosystem health and resilience [7].

Trends in the raw abundance of non-native species differed from those in their richness, with the latter showing a bell-shaped distribution peaking around 2006. This peak could be attributed to the opening of the Rhine-Main-Danube Canal in 1992 [4], which facilitated an influx of non-native species from the Ponto-Caspian region, leading to a temporary surge in non-native species richness as new species were introduced and established. Additionally, other factors such as changes in monitoring intensity, improvements in detection methods, and shifts in regulatory policies might have contributed to this pattern. The subsequent decline in richness after the peak could, however, also indicate a saturation point where the ecosystems reached their carrying capacity for non-native species, thus leading to a 'boombust' sigmoidal dynamic [68], while it is unlikely that this bell-shaped distribution reflects successful management and mitigation efforts reducing the establishment of nonnative species (see e.g. [2]). Our findings, however, also underscore the dynamic nature of biological invasions and highlight the importance of long-term time series in understanding and managing these events. The early detection and subsequent spread of D. polymorpha and C. curvispinum along the Rhine River demonstrate the rapid and extensive dispersal capabilities of certain nonnative species once they establish in a new environment. The less frequent but notable occurrences of *E. sinensis* (being among the oldest captured in the data from [22]) and J. istri further emphasize the variability in invasion success and spread among different species. The historical monitoring data from Germany's freshwater ecosystems, therefore, do provide invaluable insights into the temporal and spatial patterns of these invasions, revealing critical periods and locations of introduction and expansion, despite being limited.

The dataset from Haase et al. [22] provides a comprehensive overview of the long-term macroinvertebrate data from 151 riverine long-term biodiversity monitoring sites, yet primarily focuses on the Rhine River catchment and, to a lesser extent, the Ems and Weser catchments. Notably, major river systems like the Elbe are under-represented or even absent as in the case of the Danube. This is a considerable shortcoming considering that monitoring data from e.g. the River Elbe revealed a poor ecological quality due to high pollution [59, 75, 76]. Ecological disturbances are of critical importance for biological invasions, as they increase the potential for non-native species introductions and their respective outgoing spread through these river systems [21]. However, despite data being scarce before the German reunification, this lack of data [64] could have been exacerbated by the strict criteria for data to be included in Haase et al. [22], e.g. a minimum of 8 sampling years within a period of 15 years. This criterium might have resulted in numerous sites not being included (i.e. from the Integrated European Long-Term Ecosystem, critical zone and socioecological Research; eLTER; [46]) or others such as data obtained in the light of the Water Framework Directiverelated monitoring activities [52].

The potential for non-native species to spread across the German river network is significantly heightened by the interconnected nature of these waterways, particularly with artificial links such as the Rhine-Main-Danube Canal opened in 1992, facilitating the spread of Ponto-Caspian species into European, and particularly German waters, a phenomenon termed "Ponto-Caspianization" [68]. This man-made canal especially serves as a direct link between several major basins, potentially accelerating the dispersal of non-native species across ecological barriers [4, 68]. The geographical concentration of monitoring sites in West Germany is due to several factors, including the responsibility of the Bundesanstalt für Gewässerkunde (BfG), which has focused on the Rhine for decades due to its location in Koblenz and the Rhine's status as the main navigable river in Germany due to its connection to the Rhine-Main-Danube canal. This suggests a regional bias that could lead to an underestimation of non-native species richness in the national context. This spatial bias implies that the reported increase in non-native species, from the initial detection of Physella acuta in 1971 to a total of 32 species by 2012, might not fully capture the scope of biological invasions across Germany's riverine ecosystems [53]. Indeed, the Global Alien Species First Record Database [62] lists 243 non-native macroinvertebrate species in Germany's freshwater ecosystems, indicating that long-term data (originating from purely riverine ecosystems) used in this work identified only 13.2% of this non-native group. Despite data from Haase et al. [22] encompassing only data from rivers and streams, this percentage is low, but could indeed reflect the lack of lentic ecosystems, regional differences, or sites not coinciding with invasion hotspots [14]. Moreover, the significant trends observed in the raw and relative abundance of non-native species, alongside the bell-shaped progression of reporting and monitoring efforts, indicate a dynamic interplay between human activity, monitoring intensity, and non-native species proliferation [10, 35, 44]. Therefore, while the study sheds light on important trends and patterns, it also emphasizes the need for more comprehensive monitoring efforts [37, 71] that include all major German river systems and account for anthropogenic influences like canal constructions, to better understand and manage the impacts of non-native species on Germany's biodiversity.

Higher research effort generally translates into higher species detection rates, suggesting that the intensity and scope of investigation directly influence the likelihood of identifying non-native species [36, 54]. Despite potential shortcomings in detecting non-native species with the currently employed long-term biomonitoring efforts [28], there exists a clear connection between the number of unique sites reporting non-native species and the total number of reported non-native species. The current distribution of long-term monitoring sites, which predominantly focuses on the western part of Germany, inherently skews the detection and reporting of nonnative species towards this region, leaving the Eastern and Southern parts of the country under-monitored. It can, therefore, be assumed that the observed decline in total non-native species richness in recent years may not accurately reflect real trends but rather indicate a monitoring effort-linked lag time in the reporting of nonnative species and the nature of our dataset, underscoring (a) the critical need for continuous and expanded surveillance to capture a more accurate picture of species introductions and dynamics over time (b) the value of increasing the number of monitoring sites in the future to monitor their population growth and spread.

Biosecurity and management efforts [1, 42] are needed to mitigate the threat posed by biological invasions, in particular in the face of staggering introduction rates [3, 65] and implemented regulations like EU Regulation No. 1143/2014 "on the prevention and management of the introduction and spread of invasive alien species" or of the EU Biodiversity Strategy for 2030, which contains the commitment to manage established invasive alien species. Highlighting the critical role of sustained research efforts in shedding light on the presence and spread of non-native species within aquatic ecosystems, the findings demonstrate that increased research activity, as evidenced by the number of unique sites and the volume of data collected over time, is fundamentally linked to the enhanced detection and understanding of non-native species richness. Such correlations highlight the importance of comprehensive and continuous biomonitoring programs to accurately assess and mitigate the impacts of non-native species on local biodiversity and ecosystem health [11, 32, 72]. Having identified spatio-temporal patterns in the occurrence of non-native species, this lack of spatially more coherent and comprehensive coverage across the entire German river network risks allowing

non-native species to establish and spread largely undetected. Such a scenario not only hinders our understanding of invasion dynamics and ecosystem health across Germany, but also delays the implementation of effective management and mitigation strategies tailored to these underrepresented regions, potentially exacerbating the ecological and economic impacts of biological invasions, thus minimizing the effectiveness and reliability of denylist approaches [17, 55]. Thus, only with a coherent network of sites monitored consistently over time, changes in biodiversity and drivers of its deterioration (including non-native species), can be adequately assessed. Considering the large research and development expenditure (reaching 112.6 billion € in 2021, 3.13% of the national GDP; www.destatis.de) and the high scientific productivity in Germany [57], it is likely that the observed spatial coverage of long-term sites, and thus the detection rate of non-native species, might be even lower in other countries, underlining the importance of the so-far collected data concomitant to the need to extend the existing longterm monitoring network.

Conclusion

The findings presented here underline the critical need for expanding and diversifying long-term biomonitoring efforts across Germany, especially at the intersections of major rivers and canals where the risk of non-native species introduction and spread is particularly high. Such an expansion is not only crucial for achieving a more comprehensive and representative understanding of the current state and trends of aquatic ecosystems, but also indispensable for the early detection of newly arriving non-native species. Moreover, long-term trend analysis, afforded by extensive monitoring efforts, holds invaluable potential for describing temporal trends in non-native species abundance and distribution, facilitating prompt and well-informed management strategies. Consequently, to safeguard biodiversity and maintain the ecological integrity of Germany's aquatic ecosystems, it is essential to invest in and commit to more geographically extensive and strategically placed long-term biomonitoring sites.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12302-024-00986-7.

Supplementary material 1.

Acknowledgements

We thank TÜBİTAK BİDEB (2219 Program), which supported Irmak Kurtul with a one-year scholarship during her post-doc research in the United Kingdom.

The research was conducted in accordance with the objectives of the European consortium DANUBIUS RI.

Authors contributions

P. J. H. conceived the idea. I. K and P. J. H. visualised the results. All authors contributed equally to the writing of the manuscript.

Funding

Open Access funding enabled and organized by Projekt DEAL.

Availability of data and materials

No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication

All authors agreed to the submission of this work.

Competing interests

The authors have no conflict of interest (financial or non-financial) to declare.

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Received: 26 June 2024 Accepted: 26 August 2024 Published online: 10 September 2024

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