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Decadal spatial trends in the feeding-type composition of Arctic deep-sea nematodes at LTER-HAUSGARTEN: A dual classification approach

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ABSTRACT

This study examined functional changes in free-living meiobenthic nematode communities across different water depths and sediment layers over a 20-year period along a bathymetric transect at LTER observatory HAUSGARTEN in the Fram Strait (1200 m, 2500 m, and 4000 m). The focus was on changes in feeding type composition and comparing the performance two different classification systems (Wieser's and Hodda's) to assess whether they yield consistent functional interpretations or highlight differences.

Published datasets were used to analyse nematode communities, with specimens identified morphologically to the lowest possible taxonomic level and assigned to feeding types. The study investigated how the trophic structure of nematode communities varied over time, with depth, and between sediment layers, aiming to reveal long-term spatio-temporal patterns at HAUSGARTEN.

Microbial feeding nematodes were consistently dominant across all stations and years. While feeding type composition changed significantly over time at each respective station and to a similar strength with water depth, sediment layer had a stronger influence than the temporal variation. Interannual variation of feeding types as well as within-group dissimilarity and dispersion were lowest at the shallowest station and increased with water depth. Similarly, feeding-type composition in the uppermost sediment layer remained most stable over the years and was gradually decreasing with sediment depth. Despite a decline in nematode abundances over time, the overall feeding type composition remained unchanged. Both classification systems produced comparable results, indicating that functional interpretations of nematode communities are robust across classification approaches.

1. Introduction

Nematodes are the most abundant metazoan animal on earth (Ptatscheck and Traunspurger, 2020), with an estimated number of 60 billion nematodes for every human (van den Hoogen et al., 2019). In marine sediments, free-living nematodes are a dominant component of the meiobenthos (minute benthic fauna retained by a 32 μm sieve), reaching densities of up to an estimated 12 million individuals per square metre (Giere, 2009; Heip et al., 1985; Soetaert and Heip, 1995). Their great abundance in virtually every habitat is accompanied by a great taxonomical diversity with currently about 6700 accepted marine species listed in the World Database of Nematodes (Nemys Eds., 2025). The high taxonomic diversity of nematodes translates into a wide range of functional roles. They occupy various trophic levels, exhibit different life strategies and are responsive to environmental variations, including organic enrichment and physical disturbances, making them useful indicators for environmental monitoring (Liao et al., 2020; Mohammad et al., 2024). This functional diversity allows nematodes to occupy a vast niche space and reduce competition for resources while providing important ecosystem services (De Meester et al., 2012, 2015; Guden et al., 2021; Schratzberger and Ingels, 2018). The high abundance, taxonomic diversity, and functional diversity of marine nematodes underscore their ecological importance in marine ecosystems, particularly in sedimentary habitats across various depths and environmental conditions.

In an ecological context, the categorisation of functional traits allows

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a broader perspective of biodiversity and interactions of communities, beyond a purely taxonomic classification. In addition to biomass, tail shape (presumably indicating nematode mobility), or life-history traits (colonising versus persistent), a common functional classification of nematode communities is the assignment of their feeding types (Bongers, 1990, 1999; Hodda, 2022; Riemann, 1974; Semprucci et al., 2022; Thistle et al., 1995; Thistle and Sherman, 1985; Wieser, 1953). Wieser (1953) proposed one of the earliest and also to this day widely applied nematode feeding type classifications. Based on the general morphology of the buccal cavity, Wieser categorizes four different feeding types for free-living nematodes: selective and non-selective deposit feeders, epistrate feeders and omnivores/predators.

Since Wieser's initial classification in 1953, several revisions and additions have been made to nematode feeding type classifications based on new observations. Boucher (1973) observed that some species could ingest food particles larger than their mouth size by widening their mouths during feeding. Jensen (1987) made modifications to Wieser's classification, incorporating additional morphological features like cephalic setation in the feeding mechanism. Yeates et al. (1993) classified nematodes into five functional groups and Moens and Vincx (1997) proposed a new scheme with six major nematode feeding guilds, particularly in estuarine environments. These revisions and new observations have expanded our understanding of free-living nematode feeding ecology beyond Wieser's initial classification, providing a more nuanced view of their functional roles in various ecosystems. The most recent and comprehensive feeding type classification has been published by Hodda (2022), which classifies nematode feeding types for all currently known nematode genera in a hierarchical way. This results in 25 unique feeding types across marine, limnic and terrestrial habitats (including parasites). In addition to its comprehensive coverage, Hodda's classification offers several further improvements compared to the older classifications. The hierarchical structure provides a more detailed understanding of nematode feeding ecology by classifying not only the diet of nematodes, but also how they obtain and process food. A further advantage of Hodda's classification is that it allows the backward annotation of Wieser's (1953) feeding types, enabling comparisons between studies using either of the two classifications. Hodda's classification also includes detailed morphological characteristics for each feeding type and provides a morphological key for identification which can also be applied to undescribed genera, if their affinities to existing genera can be determined. With these features, Hodda's 2022 classification has the potential to enhance ecological, environmental, and biodiversity studies, particularly in cases where morphological information is unavailable (e.g. metabarcoding studies).

Despite these advances, some challenges remain in the analysis of nematode feeding behaviour, particularly under natural field conditions where observations are extremely difficult to achieve. While indirect approaches – such as laboratory experiments – have provided valuable insights into nematode diets (e.g. Estifanos et al., 2013), and recent innovations like the Meioflume system now enable direct observation of meiofaunal behaviour in controlled laboratory environments that closely simulate *in situ* sediment conditions (Ballentine and Dorgan, 2024), such methods still are limited in their scalability and accessibility. Consequently, the assignment of feeding types is still predominantly based on the morphology of the buccal cavity rather than direct behavioural observations (Yeates et al., 1993). This reliance on morphological traits introduces a certain degree of arbitrariness in feeding type classification. Furthermore, the degree of redundancy within feeding groups remains uncertain and has proven difficult to predict in experimental setups (De Mesel et al., 2006; dos Santos et al., 2009; Gansfort et al., 2018; Guden et al., 2021). Nevertheless, morphological classifications currently represent the most suitable and cost-effective approximation for large-scale inference of nematode diets, and careful application of these classifications can still reveal the most probable trophic interactions within a community (Majdi et al., 2020 and references therein). Overall, Hodda's 2022 classification represents a significant step forward in understanding nematode feeding ecology, offering a more comprehensive and flexible system for researchers studying nematode communities and their ecological roles.

This framework is especially valuable when applied to extreme and understudied environments such as the deep sea, where unique ecological constraints shape community structure and function. With 65 % of the Earth's surface covered by a minimum 300 m of water, the deep seafloor is the largest habitat on the planet (Danovaro et al., 2008). The deep-sea ecosystem is characterised by food limitation, as the absence of sunlight below 300 m water depth prevents primary production. Hence the meiobenthic food web in the deep sea is directly dependent on production and organic matter export from the upper water column (Danovaro et al., 2000; but see Van Gaever et al., 2006). Due to consumption, degradation and remineralisation of the sinking organic-matter particles, only 0.5–2 % of the net primary production is available to the benthos upon its arrival on the seafloor in abyssal depths (Herndl and Reinthaler, 2013; Smith et al., 2008 and references therein). The organic matter content of sediments usually decreases with increasing water depth, which affects and drives the distribution and abundance of benthic populations (Grzelak et al., 2017; Wang et al., 2019). This results in fluctuation and patchiness in the basic food supply to benthic communities, accompanied by occasional pulses of large inputs of organic matter following seasonal algal blooms or deposition of carcasses (Billett et al., 1983; Romero-Romero et al., 2021; Smith Jr et al., 1994, 2008; Soltwedel et al., 2018). Another effect is the vertical stratification of food availability in the top layers of sediment. The availability and quality of fresh food decreases with increasing sediment depth, which is consistent across different water depths (Schnier et al., 2023). This profoundly influences nematode communities, which are usually found in the highest abundances in the uppermost sediment layer and gradually decreasing abundances towards a sediment depth of 5 cm leading to high similarities of community composition in the same sediment layers across different water depths (Heip et al., 1985; Jensen, 1988; Schnier et al., 2023, 2025a; Steyaert et al., 2003). Changes in food supply can therefore have direct consequences for nematode communities, as *in-situ* experiments at HAUSGARTEN deep-sea sites showed an increase in nematode abundance and differences in diversity in organically enriched, azoic sediment cores compared to natural communities (Gallucci et al., 2008; Hasemann et al. in prep.), but abundance increases were not always confirmed in such experiments (Guilini et al., 2011).

This highlights the importance of studying nematode communities in regions subject to pronounced environmental shifts, such as the Arctic Ocean, which is one of the fastest changing regions on Earth (Previdi et al., 2021). The HAUSGARTEN observatory was established in Fram Strait, the only deep-sea connection to the central Arctic Ocean, to study these changes in a multidisciplinary approach using annual sampling and experimental set-ups (Soltwedel et al., 2005, 2016). Increased surface water temperatures by a total of almost 1 °C since 1997, as well as a series of warm (0.4 °C above mean water temperature) and cold (−0.5 °C below mean water temperature) anomalies caused significant changes in the plankton community composition of HAUSGARTEN (Bauerfeind et al., 2009; Beszczynska-Möller et al., 2012; Lalande et al., 2013; McPherson et al. in prep.; Nöthig et al., 2020). This is the probable cause of altered food supply to the deep seafloor of HAUSGARTEN which was found over the same time period: Bacterial counts and biomass, as well as the total amount of degraded phytodetrital matter in the sediments increased, potentially affecting the composition and diversity of the nematode community, which declined in abundance by up to 75 % from 2000 to 2019 (Hasemann and Soltwedel, 2024; Schnier et al., 2025a).

Previous HAUSGARTEN nematode studies (Grzelak et al., 2017; Hoste et al., 2007; Schnier et al., 2023) primarily focused on spatial diversity and used Wieser's (1953) feeding type classification. In contrast, the present study employs both Wieser's (1953) and Hodda's (2022) classifications to facilitate a more comprehensive analysis of the functional characteristics of nematode communities at the HAUSGARTEN observatory. By utilizing both classification systems, the study maintains continuity with previous HAUSGARTEN studies that used Wieser's system and gains new insights through the application of Hodda's more recent and detailed classification. In addition, the application of the same multivariate statistical tests on this dual-classification approach enables us to evaluate the differences in their respective performances.

This approach permits a more nuanced examination of functional diversity and trophic interactions within nematode communities across time and space (both water depth and sediment depth) at the HAUSGARTEN observatory. The aim of this study was to address the following research questions:

1. Did the decrease in total nematode abundance over time lead to significant changes in overall feeding-type composition?
2. Does the feeding type composition differ between different water depths and different sediment layers as food availability decreases with depth?
3. Does the dual-classification approach reveal differences in performance between the two feeding-type classifications?

2. Material & methods

2.1. Study site and sampling

This study was conducted at the LTER observatory HAUSGARTEN, which is situated at approximately 78°N-80°N to 05°W-11°E in Fram Strait between the east coast of Greenland and the west coast of Svalbard (Soltwedel et al., 2005, 2016). Sampling was carried out with R/V POLARSTERN (Knust, 2017) during thirteen expeditions that took place during each Arctic summer annually from 2000 to 2010 as well as in 2014 and 2019 (Budéus et al., 2008; Budéus and Lemke, 2007; Fahrbach, 2002; Kattner, 2009; Klages, 2010; Klages et al., 2004; Klages and Thiede, 2011; Krause and Schauer, 2001; Lemke, 2003; Lherminier et al., 2009; Metfies, 2020; Schewe, 2015; Soltwedel, 2010). Calculated from the respective cruise and station metadata, sampling occurred on average on July 28th ± 21 days. In this study, we examined sediment samples from three HAUSGARTEN stations located along a bathymetric transect off Svalbard: HG-I (1200 m depth), HG-IV (2500 m depth) and HG-VII (4000 m depth; Fig. 1). Sampling at HG-VII was unsuccessful in 2009 and 2014 due to the high inclination of the seabed.

Virtually undisturbed sediment cores (10 cm diameter, 78.54 cm^{-2} area) were obtained with one deployment of a multiple corer (MUC) at each station. From each MUC deployment, the top five sediment centimetres of three randomly selected cores were subsampled as (pseudo-) replicates for meiofauna analysis using cut-off syringes (2.2 cm diameter, 3.801 cm^{-2} area). Meiofaunal subsamples were sectioned in centimetre layers and fixed individually in borax-buffered 4 % formalin/filtered seawater solution (v/v) for later analysis in the home laboratory.

Details for each sampling point with exact coordinates and dates can be found in the datasets archived at PANGAEA (see Supplementary Material section).

2.2. Sample processing and nematode preparation

Meiofauna samples were rinsed in freshwater over a 32 μm sieve. Separation of fauna and sediment was achieved by density gradient centrifugation carried out two times in a colloidal silica solution (LUDOX® TM-50, Sigma-Aldrich 420778; specific gravity of 1.18 g/cm^{-3}) for 15 min at 900 rpm (for method see Heip et al., 1985). The meiofauna was transferred into a Petri dish, stained with Rose Bengal

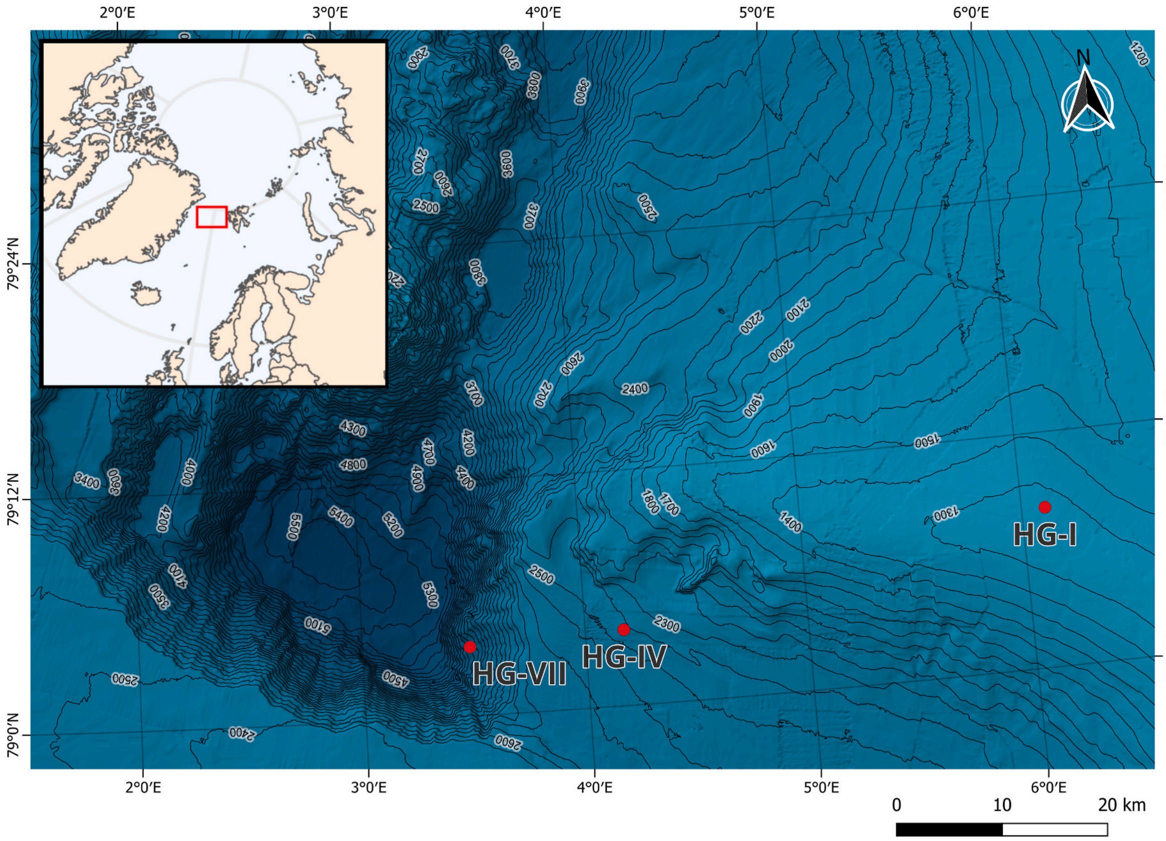

Fig. 1. General location of LTER HAUSGARTEN observatory in Fram Strait (red square in small map) and the location of the three sampled stations in the large map. HG-I is at approximately 1200 m depth, HG-IV is at approximately 2500 m depth and HG-VII is at approximately 4000 m depth (Basemap: GEBCO Bathymetric Compilation Group, 2023). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

and examined under a stereomicroscope. All found nematodes were hand-picked and transferred to anhydrous glycerine. They were then mounted as permanent slides for morphological determination (see Pfannkuche and Thiel, 1988).

Nematode examination was carried out under a light microscope equipped with a digital camera and associated software. Specimens were determined to genus level using the keys of Platt and Warwick (1983, 1988), Warwick et al. (1998) and Schmidt-Rhaesa (2014) and current taxa names with AphiaIDs were acquired from the World Database of Nematodes (Nemys Eds., 2025).

2.3. *Nematode feeding type classification*

The diversity of feeding types was assessed in two different ways which are described in the following two sections. Both feeding type classifications are based on the morphology of the nematodes mouth opening (i.e. buccal cavity).

2.3.1. *Classification after Wieser (1953)*

Initially, the nematodes were classified into the four feeding types according to Wieser (1953), namely selective deposit feeders (1A), non-selective deposit feeders (1B), epistrate feeders (2A) and predators/omnivores (2B). Selective deposit feeders (1A) are characterised by a minute, unarmed buccal cavity, which only allows feeding upon specific small-sized microbes, whereas non-selective deposit feeders (1B) also have an unarmed, but larger buccal cavity, allowing feeding upon larger microbes or organic deposits. Epistrate feeders (2A) tend to have a larger buccal cavity and specialised 'tooth'-like structures that allow them to scrape off biofilm and process food. Predatory nematodes and omnivores (2B) have very large, armed buccal cavities, which allows these nematodes to hunt and hold prey.

2.3.2. *Classification after Hodda (2022)*

Recently, a revised nematode feeding type classification has been proposed by Hodda (2022). This classification provides a total of 24 different sub-divided hierarchical trophic categories to better reflect the true diversity of nematode feeding habits. Hodda's (2022) classification is based on a list of all at the point of publication described nematode genera and further provides a universal key which also allows backward annotation of feeding types after Wieser (1953). Therefore, we were able to apply both classifications to our dataset and to directly compare their respective performance in the present study. The hierarchical classification of Hodda (2022) differentiates on the highest level between microbial feeders (mic), predators (pred) and parasites. As we are focussing on free-living nematodes in the present study, we excluded the parasites from further analyses, which leaves nine trophic sub-categories. The sub-categories are defined on the specific feeding method and the type of food: Microbial feeding nematodes could for instance feed on suspended (susp) or particulate material (part), either by sucking (mic-suck-susp; mic-suck-part), by processing (mic-proc-susp; mic-proc-part), by crushing (mic-crush), by scraping (mic-scrap) or by piercing (mic-pierce) the food items. Predatory nematodes are differentiated whether they ingest (pred-ingest) or pierce (pred-pierce) their prey. Hodda (2022) lists some genera with multiple feeding types, as nematodes may have multiple food sources, or the feeding type of certain nematodes may be changing during their development. For the statistical analysis we therefore grouped these genera into two additional feeding types: mic-multi and pred-multi. The mic-multi group includes all nematode genera listed in Hodda (2022), which have multiple, but exclusively microbial feeding modes during their development. The pred-multi group includes all nematode genera that are listed in Hodda (2022), which have multiple feeding modes, of which at least one is predatory. This means, that pred-multi includes nematodes, which can be microbial feeders at one stage of their development, but can switch to a predatory lifestyle at a later stage.

2.4. *Data analysis*

For the analysis, nematode abundances were standardised to an area representing 10 cm^{-2} of seafloor. Absolute abundances of feeding types were used for performing the statistical tests. Relative abundances were visualised as stacked barplots.

To estimate the relative distribution of feeding types, we calculated the index of trophic diversity (ITD, Θ) based on the formula provided by Heip et al. (1985, 1998):

$$\Theta = \sum_{i=1}^{n} q_i^2$$

where q_i is the proportion of feeding type i in the assemblage and n is the number of feeding types. In essence, the ITD measures the evenness of feeding-type distribution and with an increasing number of unique feeding-types, it becomes less likely to find an even distribution. The ITD thus is a proxy for imbalanced communities and a larger number of feeding types increases the chance to detect compositional changes. Since the feeding type classifications of Wieser (1953) and Hodda (2022) contain different numbers of feeding types, the calculated ITDs may not be directly comparable between the two classifications. To test for potential significant differences of ITD values over the years, Kruskal and Wallis (1952) tests and subsequent post-hoc tests after Dunn (1961) were performed for both classifications respectively.

Multivariate statistics were performed for both feeding type classifications using non-metric multidimensional scaling (nMDS) on a Bray-Curtis similarity matrix of square-root transformed nematode feeding type abundance data. The nMDS was calculated in two iterations: the first with water depth as a factor, and the second with sediment layers as a factor. For the water depth analysis, the individual sediment layers were aggregated to 0–5 cm per replicate. The nMDS plots for the individual sediment layers were kept separated and a dummy variable was included in the similarity matrix.

We performed a permutational multivariate analysis of variance (PERMANOVA) with a three-factor nested design (9999 permutations, alpha = 0.05) on the aforementioned Bray-Curtis similarity matrix to assess the effect of each factor on the feeding type composition. This analysis was carried out for both classifications respectively. Year and station were used as fixed main factors, sediment layer was used as random factor nested in station. A subsequent permutational analysis of multivariate dispersions (PERMDISP) was carried out on the same design to assess the homogeneity of dispersions around the respective group centroids. The PERMDISP enhances the interpretability of the PERMANOVA by testing whether group differences in the multivariate space occurred because of the location of their group centroid, the relative dispersions around their group centroid, or both.

The similarity percentage SIMPER (Clarke, 1993) was investigated for both feeding type classifications to test which feeding types contribute the most to the relative difference between samples in the Bray-Curtis similarity matrix. The SIMPER was carried out for water depth and for individual sediment layers respectively.

The nMDS, PERMANOVA, PERMDISP and SIMPER calculations were performed using PRIMER 7 (version 7.0.24) with the PERMANOVA + add-on (Clarke and Gorley, 2006; Anderson et al., 2008).

The overview map, the stacked barplots, the Kruskal-Wallis tests and Dunn tests were created using R (version 4.4.1; R Core Team, 2024) in the RStudio environment (version 2024.9.0.375; Posit team, 2024) and the packages 'tidyverse' (Wickham et al., 2019), 'ggplot2' (Wickham, 2016), 'ggpmisc' (Aphalo, 2022), 'ggpubr' (Kassambara, 2023a), 'ggtext' (Wilke and Wiernik, 2022), 'rstatix' (Kassambara, 2023b), 'forcats' (Wickham, 2023), 'ggOceanMaps' (Vihtakari, 2023) and 'paletteer' (Hvitfeldt, 2021). The station map was created with QGIS v.3.30.1 (QGIS Development Team, 2009).

3. Results

3.1. Feeding-composition with water depth and time

The relative abundance of feeding types over time at the three different water depths are plotted in Fig. 2 for the Wieser (1953) classification, and in Fig. 3 for the Hodda (2022) classification. Over time, the feeding type composition varies at all three depths, with biggest interannual variation at HG-VII. Deposit/Microbial feeders (1A, 1B, mic-suck, mic-proc, mic-multi, mic-crush) were generally the most dominant feeding groups at all stations with a combined dominance between 50 and 70 %. Epistrate feeders (2A, mic-scrap) were the second most abundant, with an average dominance of 26 % over all years and stations. Predators (2B, pred-ingest, pred-multi) were the least abundant feeding type with an average dominance of 7 % over all years and stations.

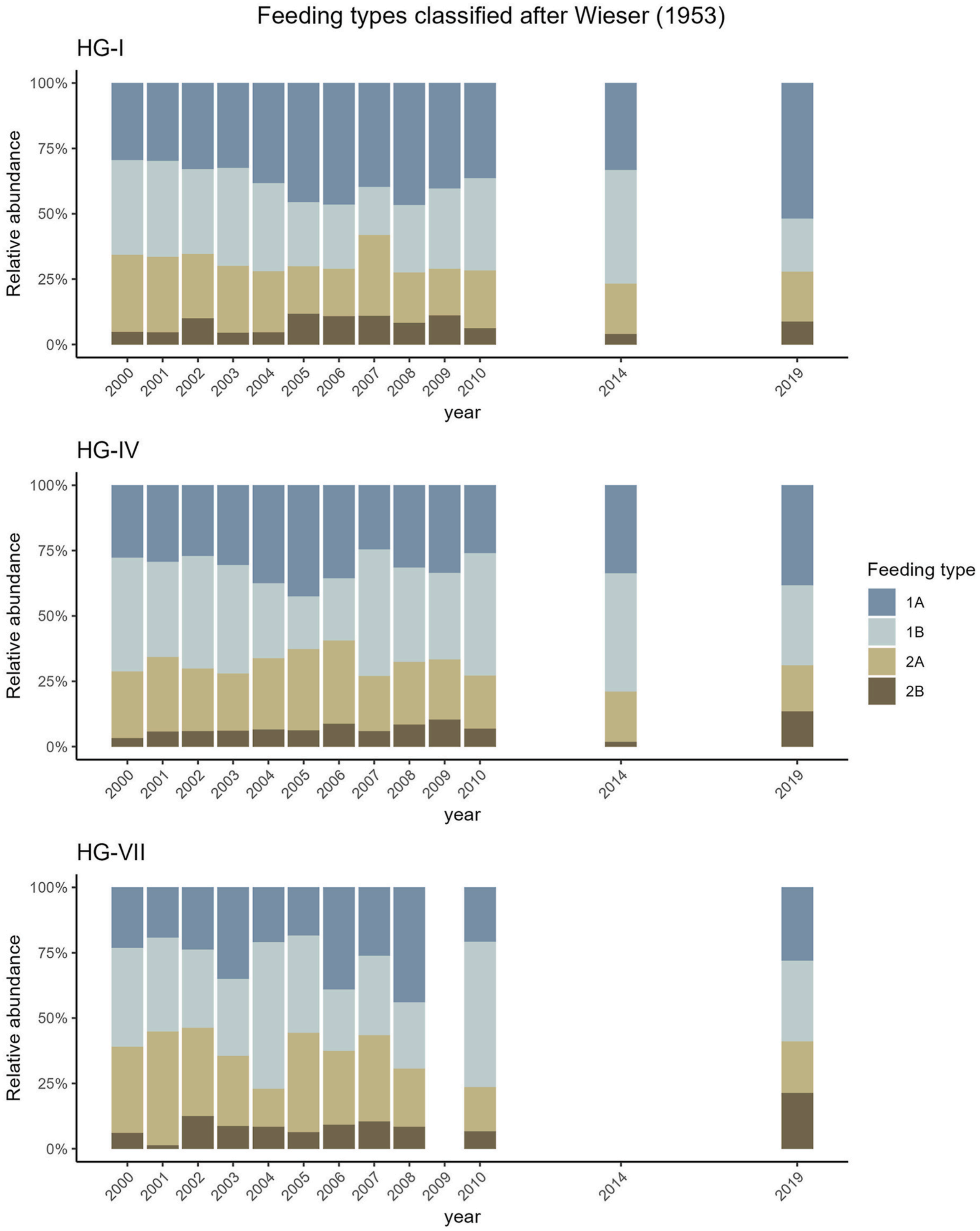

Fig. 2. Relative abundance of nematode feeding types classified after Wieser (1953) at HG-I (1200m), HG-IV (2500m) and HG-VII (4000m) over the entire HAUSGARTEN nematode time series. 1A Selective microbial feeders; 1B Unselective microbial feeders; 2A Epistrate feeders; 2B Omnivores/predators.

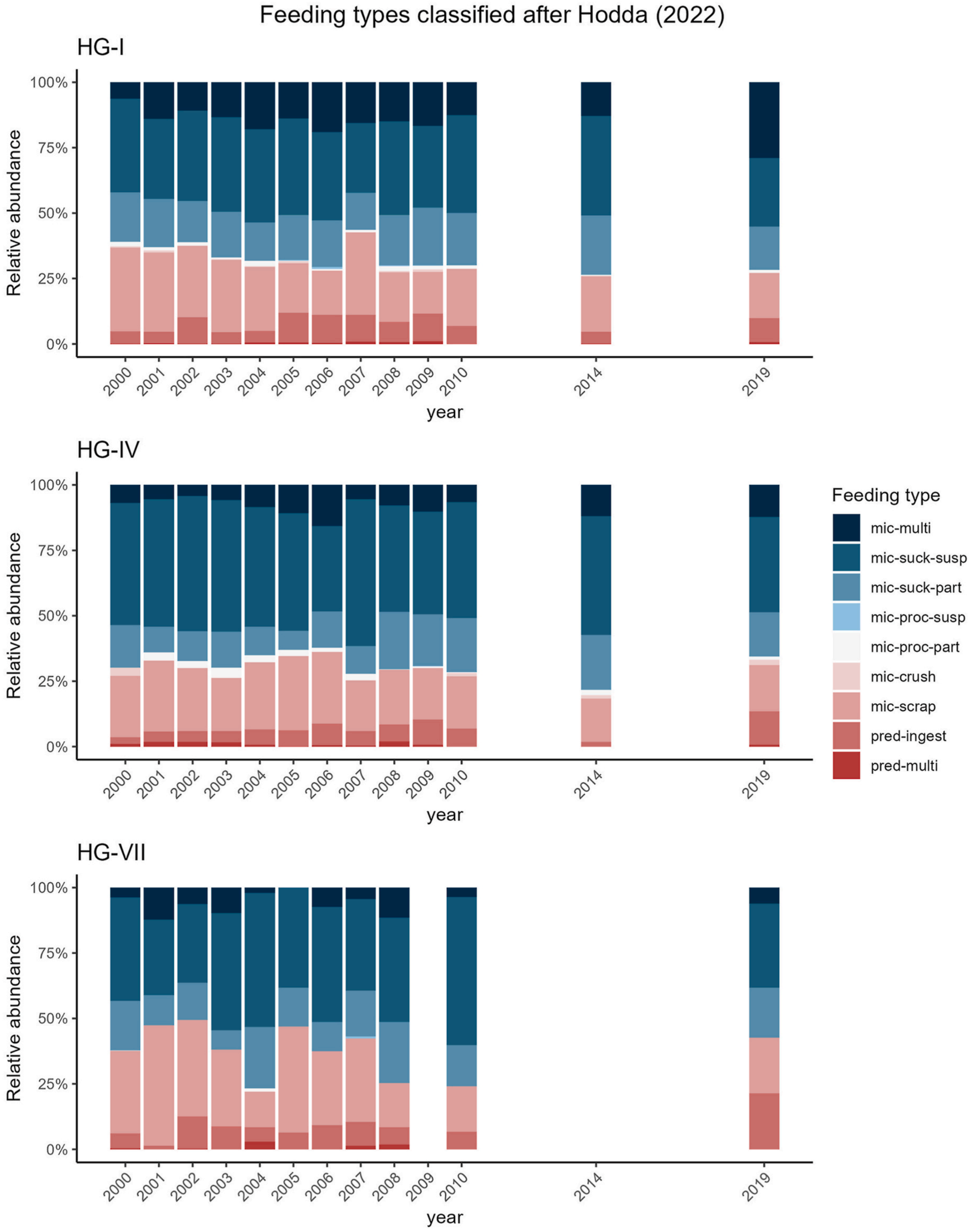

Fig. 3. Relative abundance of nematode feeding types classified after Hodda (2022) at HG-I (1200m), HG-IV (2500m) and HG-VII (4000m) over the entire HAUSGARTEN nematode time series.

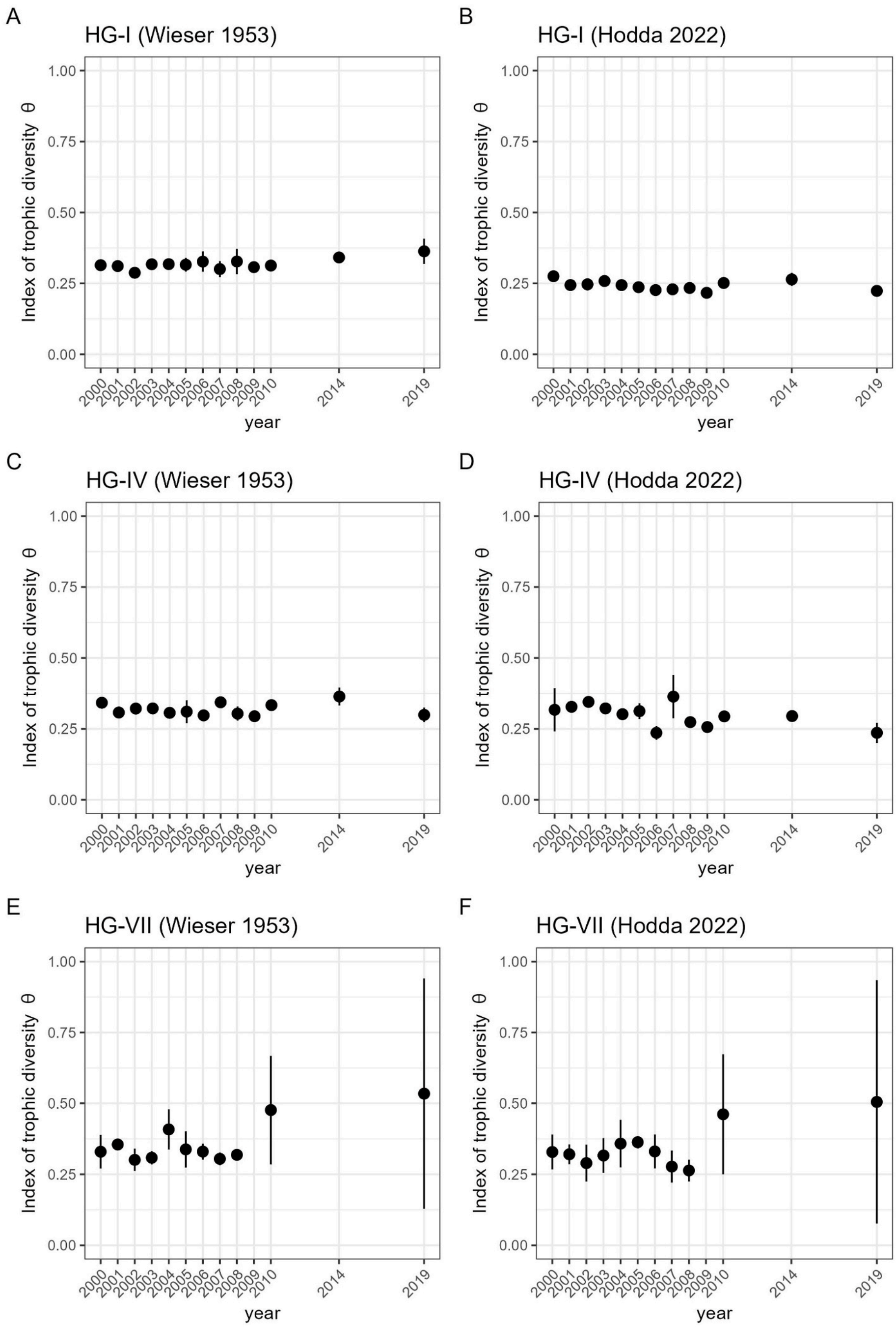

Fig. 4. Development of the index of trophic diversity (ITD, Θ) over time at the three stations, calculated separately for the feeding type classification after Wieser (1953) and Hodda (2022). Values are shown as the mean of three replicates per station. Error bars represent the standard deviation. In some years the standard deviation was very low, which led to the obstruction of the error bars by the data points in the plot.

Individually over time, the relative abundance of feeding type 1A increased from 2000 to 2005 at HG-I and HG-IV, while the relative abundance of 1B decreased during the same period at HG-I and with higher interannual fluctuations also at HG-IV. This pattern was reversed again from 2005 to 2010, when relative abundances of 1A and 1B were about the same as in 2000. In 2014, 1B increased slightly but was overall similar in composition compared to 2010. In 2019, 1A increased again and the composition pattern is comparable to 2005.

For HG-I, the index of trophic diversity (ITD, Θ) is constant in the range of 0.29–0.36 for Wieser's (1953) classification and in the range of 0.22–0.28 for Hodda's (2022) classification over all years (Fig. 4A and B). At HG-IV, the ITD is again constant in the range of 0.29–0.36 for Wieser's (1953) classification, but varies slightly more for Hodda's (2022) classification, ranging from 0.24 to 0.35 (Fig. 4C and D). At HG-VII the interannual fluctuations of the ITD are greatest, with a range of 0.30–0.51 for Wieser's (1953) classification and a range of 0.28 and 0.51 for Hodda's (2022) classification (Fig. 4E and F). Kruskal-Wallis and Dunn tests did not reveal significant differences in ITD values between any year or station, except for years 2000 and 2009 at HG-I using the Hodda (2022) classification (Bonferroni adjusted $p_{adj} = 0.04$). All

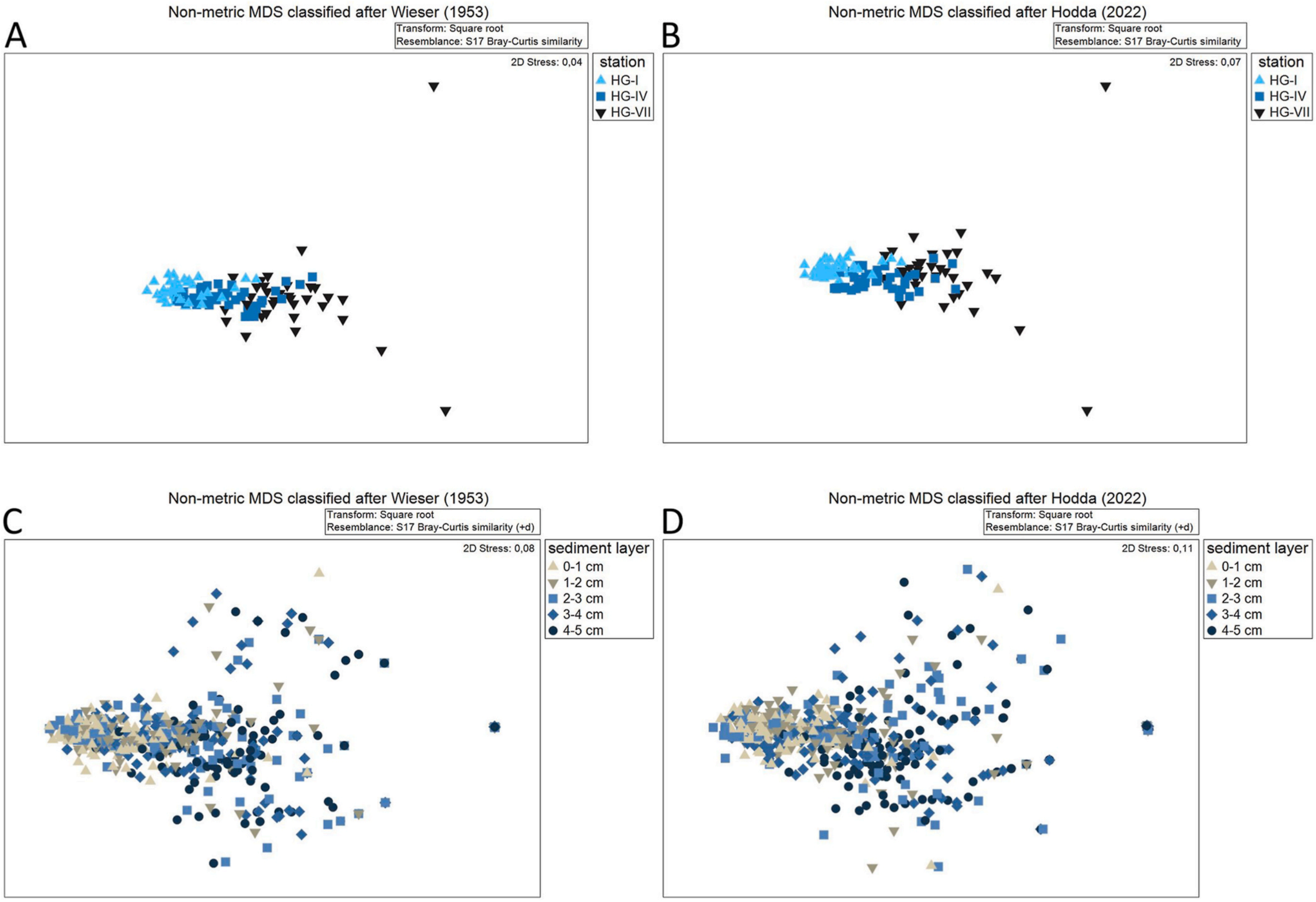

Fig. 5. nMDS plots of feeding type abundances over the entire HAUSGARTEN nematode time series. Plots A and C were created using Wieser's (1953) classification, plots B and D using Hodda's (2022) classification. To increase readability of plots A and B, the feeding type abundances of the individual sediment layers for each replicate were aggregated and a mean abundance was calculated for the three replicates per station. The mean abundances were used for calculation of the nMDS.

ITD-values can be found in Supplementary Table 1.

The nMDS plots resolved to water depth displays the bathymetric transect for both feeding type classifications with a tight grouping of HG-I samples, which transition to the also comparatively tightly grouped HG-IV samples (Fig. 5A and B, Fig. 6). The HG-IV samples overlap with the HG-VII samples to a certain extent; however, the within-group similarity at HG-VII is lower, indicated by the bigger spread in the nMDS plot.

Global PERMANOVA results show that the factor sediment layer nested in station had the highest effect on the feeding type composition, followed by year and station (Table 1). The combination of year and station resulted in a significant effect as well, whereas the combination of year and sediment layer within station did not show a significant effect.

The PERMDISP analysis revealed significantly different multivariate dispersions between the groups (Table 2). Wieser's classification resulted in a slightly higher mean dispersion (27.5) compared to Hodda's classification (24.3).

The SIMPER analysis revealed that the average group similarity decreases with increasing water depth for both classifications (Supplementary Table 2). With the Wieser (1953) classification, the average similarity was 85.71 % at HG-I, 80.23 % at HG-IV and 70.62 % at HG-VII. For the Hodda (2022) classification, the average similarity was 83.14 % at HG-I, 76.46 % at HG-IV and 66.94 % at HG-VII. The biggest differences were found between HG-I and HG-VII, with an average dissimilarity of 46.3 % (after Wieser's classification) respectively 50.1 % (after Hodda's classification). Average dissimilarity is smallest between HG-I and HG-IV with 24.2 % (after Wieser's classification), respectively 28.7 % (after Hodda's classification).

At HG-I, highest contributing feeding types to within-group similarity were 1A (33,1 %), 1B (28.7 %) and 2A (24.7 %), respectively mic-suck-susp (26.2 %), mic-scrap (20.8 %), mic-suck-part (19.1 %) and mic-multi (16.8 %). At HG-IV, biggest contributors to similarity were 1B (31.5 %), 1A (30.2 %) and 2A (25.4 %), respectively mic-suck-susp (31.3 %), mic-scrap (21.9 %) and mic-suck-part (18.0 %). At HG-VII, biggest contributors to similarity were 1B (31.5 %), 2A (27.9 %) and 1A (26.8 %), respectively mic-suck-susp (32.0 %), mic-scrap (25.5 %) and mic-suck-part (21.6 %).

Relative abundances of the top five dominant taxa contributing to each feeding type in each year and station are presented in Supplementary Table 3 (Wieser's classification) and Supplementary Table 4 (Hoddas classification). Over the years, the composition of taxa within each feeding group at each station was characterised by the dominance of few taxa per feeding group. Interannual variation in relative abundances mostly were small.

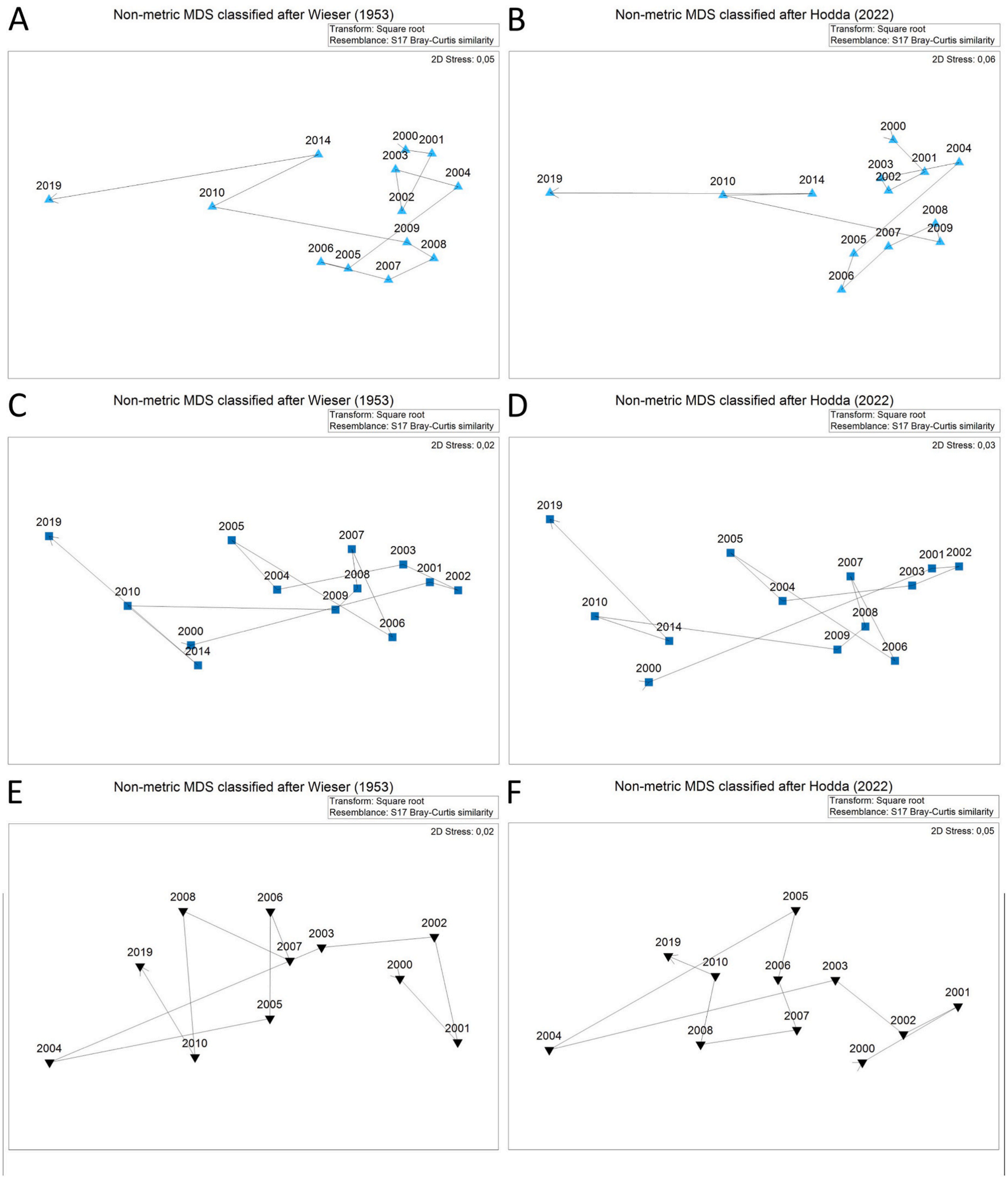

Fig. 6. nMDS plots with trajectory lines of feeding type abundance showing the group centroids for each year. Plots are were created for both classifications respectively, with Wieser's classification in the left column (A, C, E) and Hodda's classification in the right column (B, D, F) and were separated by station (HG-I: A, B; HG-IV: C, D; HG-VII: E, F).

3.2. *Feeding type composition with sediment layer and time*

The results of the SIMPER analysis are presented in Supplementary Table 2. SIMPER and the nMDS plot (Fig. 5C and D) revealed highest average group similarity in the 0–1 cm layer (72.5 % after Wieser; 68.0 % after Hodda) and a continuous decrease in similarities towards the 4–5 cm layer (41.7 % after Wieser; 36.7 % after Hodda). Highest dissimilarity was found between the 0–1 and the 4–5 cm layer (61.2 % after Wieser; 64.1 % after Hodda). Lowest dissimilarity was found between the 0–1 and the 1–2 cm layer (34.7 % after Wieser; 39.1 % after Hodda).

Highest contributing feeding types within the 0–1 cm sediment layer were 1A (32.7 %), 1B (29.4 %) and 2A (26.6 %), respectively mic-suck-susp (32.5 %), mic-scrap (23.7 %) and mic-suck-part (18.4 %). In the 1–2 cm layer, a change of the highest contributor to similarity occurred after Wieser's classification with 1B (33.2 %), 1A (27.1 %) and 2A (25.3 %). After Hodda's classification, only the relative abundances changed in the 1–2 cm layer, while identities remained: mic-suck-susp (37.6 %), mic-scrap (24.8 %) and mic-suck-part (19.7 %). In the 2–3 cm layer again a change in feeding-type similarity after Wieser occurred with 1B (36.1 %), 2A (26.5 %) and 1A (25.3 %), while after Hodda's classification only a change in relative abundances occurred: mic-suck-susp (35.2 %), mic-scrap (23.9 %) and mic-suck-part (17.4 %). In the 3–4 cm layer, feeding types 1B (35.6 %), 1A (27.6 %) and 2A (26.6 %), respectively

Table 1

Results of the PERMANOVA analysis after 9999 permutations in a reduced mixed model. Factors years (ye) and stations (st) were fixed, while the factor sediment layer was random and nested in station (se(st)). df degrees of freedom, SS sum of squares, MS mean of squares, $p_{(Perm)}$ p-value for permutation, $p_{(MC)}$ p-value after Monte Carlo resampling.

Source	df	SS	MS	Pseudo-F	$p_{(perm)}$	Unique perms	$p_{(MC)}$
Wieser's classification							
ye	12	42173	3514.4	4.590	0.0001	9871	0.0001
st	2	1.00E+00	50204	4.149	0.0330	9955	0.0074
se(st)	12	1.56E+00	12990	15.862	0.0001	9897	0.0001
ye x st[a]	22	63294	2877	3.763	0.0001	9837	0.0001
ye x se(st)[a]	133	1.01E+00	761.39	0.930	0.7883	9694	0.7987
Res	369	3.02E+00	818.94				
Total	550	7.90E+00					
Hodda's classification							
ye	12	46005	3833.7	4.406	0.0001	9851	0.0001
st	2	1.11E+00	55691	4.254	0.0295	9937	0.0043
se(st)	12	1.69E+00	14050	15.006	0.0001	9882	0.0001
ye x st[a]	22	74117	3368.9	3.878	0.0001	9822	0.0001
ye x se(st)[a]	133	1.15E+00	864.94	0.924	0.8348	9667	0.8421
Res	369	3.45E+00	936.28				
Total	550	8.86E+00					

[a] Term has one or more empty cells.

Table 2

Results of the PERMDISP test, performed after Wieser's and Hodda's classification using 9999 permutations respectively. df degrees of freedom, F F-statistic, $p_{(Perm)}$ p-value for permutation, SE standard error.

Wieser's classification	F	df1	df2	$p_{(Perm)}$
Deviations from centroid (year)	5.2323	12	538	0.0007
Deviations from centroid (station)	27.501	2	548	0.0001
Means and standard errors:	**Group**	**Size**	**Average**	**SE**
	2000	45	31.00	1.84
	2001	45	41.31	2.31
	2002	45	31.74	2.44
	2003	45	30.71	2.61
	2004	41	30.64	1.93
	2005	44	33.49	2.08
	2006	45	37.25	2.59
	2007	45	33.13	2.44
	2008	45	35.94	2.31
	2009	30	21.34	1.45
	2010	46	36.28	2.42
	2014	30	21.51	1.83
	2019	45	35.79	2.26
	HG-I	220	31.41	1.31
	HG-IV	198	25.72	1.04
	HG-VII	133	39.16	1.03
Hodda's classification	**F**	**df1**	**df2**	**$p_{(Perm)}$**
Deviations from centroid (year)	4.9936	12	538	0.0008
Deviations from centroid (station)	24.258	2	548	0.0001
Means and standard errors:	**Group**	**Size**	**Average**	**SE**
	2000	45	34.92	1.86
	2001	45	42.52	2.24
	2002	45	33.96	2.34
	2003	45	34.12	2.49
	2004	41	34.29	1.69
	2005	44	36.24	1.95
	2006	45	39.62	2.44
	2007	45	35.56	2.34
	2008	45	39.53	2.22
	2009	30	25.57	1.40
	2010	46	38.22	2.30
	2014	30	23.47	1.79
	2019	45	38.45	2.05
	HG-I	220	33.34	1.27
	HG-IV	198	29.51	1.01
	HG-VII	133	41.61	0.96

mic-suck-susp (37.6 %), mic-scrap (24.8 %) and mic-suck-part (17.4 %) were biggest contributors to similarity. In the 4–5 cm layer, the biggest contributors to similarity were 1B (44.7 %) and 2A (26.3 %), respectively mic-suck-susp (43.0 %), mic-scrap (25.0 %) and mic-suck-part (21.0 %).

4. Discussion

4.1. *Differences in feeding type composition with water depth over the years*

Our study showed that nematode feeding types at HAUSGARTEN, regardless of the classification used, changed significantly over time and that the effect of time is slightly larger than the effect of water depth (however both are less pronounced than sediment layer). The increasing dissimilarity of feeding type composition between stations could further indicate a higher functional feeding type redundancy in the nematode communities at bathyal depths and conversely, lower functional redundancy at abyssal depths. However, the variations in feeding type composition were not large enough to induce significant changes in the index of trophic diversity (ITD) over the years. It should be noted that the decreasing group similarity with water depth may be at least partly attributed to increased dispersion around the respective group centroids we found with increasing depth. The dispersion could be indicative for increased variation in the environment, i.e. a less predictable environment with increasing depth. This is likely influencing the nematode communities and indeed the bathymetric zonation we found for the feeding-type composition in the present study was also described for the taxonomic diversity of HAUSGARTEN nematode communities (Grzelak et al., 2017; Hoste et al., 2007; Schnier et al., 2023, 2025a) and other deep-sea regions (e.g. Mokievsky et al., 2007). Grzelak et al. (2017) and Schnier et al. (2023) previously explained 50–66 % of the variation in taxonomic nematode diversity of HAUSGARTEN communities with the variation in environmental parameters in the sediments by the use of distance-based linear models. It should be mentioned that inferences of resource dependence from feeding type composition alone must be made with caution, as hundreds of individuals with similar feeding types may exist in small patches (Majdi et al., 2020). Nevertheless, the increased dominance of deposit/microbial feeders (1A, mic-multi) at HG-I in 2019 is likely caused or influenced by the increasing trend in bacterial abundance and biomass that was observed from 2016 to 2019 (Schnier et al., 2025a). An experimental study concluded, that Arctic deep-sea nematodes prefer bacteria over phytodetritus with reduced uptake rates of freshly deposited material (Ingels et al., 2010), which may explain the general dominance of microbial feeders over scrapers we found. The cause for the massive increase in sediment-bound bacteria abundance and biomass is likely related to increased surface water temperatures and changed plankton composition of HAUSGARTENs euphotic zone (Bauerfeind et al., 2009; Beszczynska-Möller et al., 2012; Lalande et al., 2013; McPherson et al., in prep.; Nöthig et al., 2020; Ramondenc et al., 2024). Settling detritus can either be a direct food source for nematodes or acts as a vector for bacteria that decompose the detritus (Cho and Azam, 1988; Fadeev et al., 2021; Herndl and Reinthaler, 2013).

Average deposition rates of organic matter in HAUSGARTEN are quite short, as the abundance of benthic bacteria at 3000 m depth peaks around 100 days after a phytoplankton bloom (Ramondenc et al., 2024). It is plausible that the nematode communities responded quickly to exploit the available food (Guilini et al., 2011; Hasemann et al. in prep.; Vanaverbeke et al., 2004) and that the interannual variation in feeding type composition reflects different timing of the phytoplankton bloom each year. Furthermore, despite the 20-year time span, we only have one point-sample taken during a period from late June to early September (average July 28th ± 21 days) each year. This limits temporal resolution and could be a factor for the greater effect of bathymetry than the effect of time on nematode feeding type composition. As sedimentation time and organic matter consumption increase with depth, food quantity and quality for the benthos decreases, which could explain the greater interannual feeding type variability found at HG-VII. Furthermore, HG-VII is located in an area with a much steeper seafloor slope compared to HG-I and HG-IV. Therefore, the variation in feeding type composition could also be induced by habitat structure, as turbidity currents have a strong effect on nematode communities and it can take several years for a community to return to its pre-disturbed state after a catastrophic disturbance (Bigham et al., 2024).

Interestingly, the overall relative abundance of feeding types does not appear to be affected by a decline in taxonomic diversity and absolute abundance in the nematode communities. A previous long-term study of the same bathymetric transect showed that nematode abundance decreased significantly with 75 % at HG-I, 53 % at HG-IV and 66 % at HG-VII between 2000 and 2019, accompanied by high genus exchange ratios between years (Schnier et al., 2025a). This shows a high degree of resilience in the feeding type composition over time. However, generalisations of the relationship between taxonomic and functional diversity are difficult to make and should be carried out precisely, as this information originate at different organisational levels (Mlambo, 2014). Danovaro et al. (2008) described an exponential relationship between taxonomic nematode diversity and function i.e. limited functional redundancy, as the addition of new species would lead to an increase in function. In contrast, the results of Baldrighi and Manini (2015) show, that higher nematode species number did not increase the functional diversity and that the relationship between taxonomic and functional diversity depend on the type of the investigated functional trait.

4.2. Differences in feeding type composition with sediment layer over the years

Our results indicate that feeding type composition is most influenced by sediment layer nested in station (water depth), although time and water depth also had a significant, but smaller effect on the feeding type composition. The biggest dissimilarities were observed between the uppermost and deepest sediment layer, regardless of the feeding type classification used or water depth. Additionally, at all stations the nematode communities in the 0–1 cm layer exhibited the highest within-group similarity and the highest total nematode abundance over time, whereas the communities in the 4–5 cm sediment layer showed the lowest within-group similarity and abundance. A previous study of the same transect from Górska et al. (2014), who investigated meiofauna in the timeframe from 2005 to 2009, described the same pattern.

Nevertheless, vertical sediment profile data for nematodes, particularly regarding feeding type composition, remain scarce, especially over the long-time scale considered in this study. The observed decline in nematode abundance with increasing sediment depth aligns with findings of other deep-sea studies (Horacek III et al., 2022; Itoh et al., 2011; Shimabukuro et al., 2022; Tietjen, 1989; Vanhove et al., 2004).

Free-living marine nematodes generally do not exhibit seasonal vertical migration in response to organic matter input following algae blooms, including in deep-sea environments. Studies have shown that nematodes display a consistent vertical distribution pattern influenced more by sediment chemical and physical properties, such as oxygen availability and hydrogen sulfide concentration, rather than food availability (Guilini et al., 2011; Schratzberger et al., 2019; Schratzberger and Warwick, 1998; Shimabukuro et al., 2022; Soetaert et al., 2002). Górska et al. (2014) argue, that the importance of oxygen in controlling the vertical meiofauna distribution in the sediments of HAUSGARTEN may be limited, as the sediments in the top 5 cm are well oxygenated. It is thus probable that other factors than oxygen supply are a bigger factor in explaining nematode (feeding type) diversity in the upper sediment layers of HAUSGARTEN. Interannual variation induced by different sampling time each year (discussed in section 4.1.) is probably only a minor factor in vertical distribution of nematodes in the sediments. While seasonal vertical migration has been documented in some meiobenthic taxa, such as kinorhynchs or copepods, similar behaviour has not been observed for nematodes, whose general distribution pattern was not influenced by input of organic matter following algae blooms (Shimanaga et al., 2000).

4.3. Impact of classification scheme choice on the trophic interpretation of nematode communities

Wieser's (1953) classification is widely used due to its simplicity and practicality, making it a standard approach in studies of free-living nematodes for more than 70 years. In contrast, Hodda's (2022) classification offers scalable resolution and an updated list of genera, allowing for a more detailed analysis of patterns in feeding type composition. Our study demonstrated that, regardless of the classification system used, statistical analyses of nematode feeding type composition (nMDS, PERMANOVA/PERMDISP and SIMPER) yielded comparable results. The mid-level hierarchy of Hodda's classification (mic-suck, mic-proc, mic-crush, mic-scrap, pred-ingest) closely aligns with Wieser's classification system, particularly when applied to free-living marine nematodes.

For specific research questions, the choice of classification system becomes crucial. Hodda's classification offers finer resolution for examining within-group variation in dominant genera, as it includes more feeding type categories. This allows for a clearer distinction of genera that may be dominant in a given context. For example, *Vasostoma*, classified as a mic-crush feeder under Hodda's system, was absent in the early years at HG-I but became dominant in 2014 (67 %) and 2019 (100 %). However, under Wieser's classification, *Vasostoma* is placed in feeding group 1B, which includes a broader range of genera with higher overall dominance. As a result, *Vasostoma* does not rank among the top five dominant genera in any year. The key difference is that in Wieser's system, feeding type 1B represents a larger number of genera, diluting the dominance of any individual genus, while Hodda's mic-crush category is smaller, making it easier for a genus like *Vasostoma* to emerge as dominant within that specific group.

While Hodda's classification provides greater functional accuracy at its lowest hierarchy level, the increased number of categories also complicates data analysis and interpretation. To manage this complexity, we introduced the mic-multi and pred-multi groups as arbitrary groups to account for genera with multiple feeding types. An alternative approach would have been to account these genera twice, once for each feeding type, which could artificially alter relative abundances of feeding types. Another possible method, used by de Jesús-Navarrete et al. (2022), assigns feeding types based on developmental stage. However, this information is unavailable for the 2000–2009 dataset, though it is likely the most accurate approach. Given its detailed classification key feeding type for newly discovered genera, Hodda's (2022) system is likely more future-proof.

The choice of feeding-type classification should therefore be guided by the intended level of detail and the specific context of the study. For broad-scale assessments and improved comparability with existing literature, Wieser's (1953) classification remains a valid and widely accepted approach. However, when a more detailed trophic resolution is required, such as for genus-level assignments in taxonomic or functional analyses, Hodda's (2022) more nuanced classification may offer a more appropriate framework.

CRediT authorship contribution statement

Jannik Schnier: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Christiane Hasemann:** Writing – review & editing, Supervision, Conceptualization.

Data availability statement

Cruise metadata, nematode abundance on genus level for the years 2000–2009, as well as nematode counts and annotated feeding types for the years 2010, 2014 and 2019 are archived in two different datasets at PANGAEA (Schnier et al., 2025b, 2025c). A harmonised, curated version of the datasets is also available for download in the CRITTERBASE data warehouse (Teschke et al., 2022).

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Declaration of competing interest

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Appendix A. Supplementary data

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