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Nematodes as bioindicators of ecological status in midland Irish peatlands

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Abstract

Peatlands play a critical role in global carbon sequestration, yet widespread drainage and land-use change have disrupted their hydrology and soil biological integrity, accelerating peat decomposition and greenhouse gas emissions. Rewetting is increasingly promoted as a key restoration strategy, but its effectiveness in re-establishing belowground ecological structure remains insufficiently understood. This study assessed the response of nematode-based soil food webs across a broad range of peatland habitats, including intact bogs, degraded systems, rewetted and non-rewetted managed peatlands, fens, wasted peatlands, and semi-natural sites, using a combination of morphological identification and DNA-based molecular sequencing. Nematode community composition and functional structure were evaluated using Enrichment Index (EI) and Structure Index (SI) diagnostics. Intact bog habitats consistently exhibited higher SI and lower EI values, reflecting well-structured food webs dominated by fungal-associated and higher trophic nematode families, including Dorylaimidae and Qudsianematidae. In contrast, degraded and non-rewetted peatlands showed simplified food webs characterized by elevated EI and dominance of opportunistic bacterial-feeding families such as Rhabditidae and Cephalobidae. Rewetted sites generally exhibited reduced EI relative to non-rewetted counterparts, indicating dampened nutrient enrichment and microbial pulses following hydrological restoration; however, SI values remained low in the short term, suggesting limited recovery of higher trophic complexity. Comparisons between morphological and molecular datasets revealed strong concordance at the family level for dominant taxa, while molecular sequencing detected additional rare and cryptic nematode families not consistently recovered through morphology alone, underscoring the complementarity of both approaches. Fen peatlands displayed higher EI values consistent with naturally greater nutrient availability, whereas wasted peatlands supported persistently impoverished food webs regardless of management. Overall, the results demonstrate that rewetting effectively stabilizes nutrient dynamics and initiates early recovery of soil food web functioning, but full restoration of trophic complexity requires long-term ecological recovery. Integrating hydrological restoration with biological monitoring is therefore essential for maximizing peatland carbon storage and climate mitigation potential.

1. Introduction

Peatlands are among the planet's most efficient natural carbon sinks, accumulating partially decomposed organic matter under waterlogged and acidic conditions. Although they cover only about 3% of global land area, peatlands store approximately 550–650 gigatonnes of carbon, equivalent to over 40% of all soil carbon—more than is held in the world's forests combined (Gorham, 1991; Yu et al., 2010; Leifeld & Menichetti, 2018). Their significance for climate regulation is therefore profound: intact peatlands sequester atmospheric CO_2 over millennia, while degraded peatlands release it rapidly, becoming sustained sources of greenhouse gases (GHGs) such as CO_2, CH_4, and N_2O (IPCC, 2014; Evans et al., 2021).

Europe contains roughly 12% of global peatland area, but nearly 50% of these ecosystems are degraded, primarily due to drainage for agriculture, commercial peat extraction, afforestation, and infrastructural development (Tanneberger et al., 2017; Joosten et al., 2017). European drained peatlands are responsible for an estimated 5% of the continent's total GHG emissions, despite occupying less than 3% of land area, underscoring the disproportionate climate cost of their degradation (Leifeld & Menichetti, 2018; UNFCCC, 2021). Ireland possesses one of the most distinctive peatland landscapes in Europe. Historically, peatlands—principally raised bogs, blanket bogs, and fens—covered approximately 17–20% of the island, representing the highest percentage cover of peatland in the European Union (Renou-Wilson et al., 2011). Irish peatlands store over 1,000 million tonnes of carbon, accounting for more than 50% of national soil carbon reserves (Connolly & Holden, 2009; Renou-Wilson et al., 2019). However, centuries of turf-cutting, intensive mechanical peat extraction, drainage for agriculture, and commercial forestry have resulted in the degradation of over 80% of the country's peatland area (Cabot, 1999; Malone & O'Connell, 2009). As a result, peatlands in Ireland have shifted from being long-term carbon sinks to net carbon sources, emitting millions of tonnes of CO_2 annually (Renou-Wilson et al., 2018). The restoration of degraded peatlands—through rewetting, drain-blocking, reprofiling, and reintroduction of peat-forming vegetation such as Sphagnum spp.—is widely recognised as a cost-effective nature-based climate solution (Bonn et al., 2016). Rewetting slows decomposition, reduces CO_2 emissions almost immediately, promotes long-term peat accumulation, enhances biodiversity, improves water quality, and restores hydrological functions (Parish et al., 2008; Evans et al., 2021). In Ireland, national programmes such as the EU-supported LIFE projects, the Bord na Móna Peatlands Climate Action Scheme, and the National Peatlands Strategy have initiated large-scale restoration, targeting thousands of hectares of previously extracted bogs for rehabilitation (NPWS, 2015). Given the scale of historical loss and the urgency of the climate crisis, peatland restoration across Europe—and particularly in peatland-rich countries such as Ireland— is crucial. Protecting and rehabilitating peatlands represents one of the most effective, immediate, and scientifically validated strategies for enhancing carbon sequestration, reducing emissions, and strengthening ecological resilience.

The Green Restoration Ireland (GRI) cooperative, the industry partner for this project, is actively restoring peat grasslands and other peatland habitats through initiatives such as the Farm Carbon Project and the European Innovation Partnerships (EIP). GRI's efforts contribute simultaneously to climate-change mitigation and the rehabilitation of key ecosystem services, while also enabling farmers to diversify their income streams. To promote the restoration of agriculturally managed peatlands, GRI is developing innovative, sustainable farming systems that operate with elevated water tables, working closely with farmers, scientists, and technical specialists. Alongside conventional rewetting techniques, GRI has introduced paludiculture (wetland agriculture) in Ireland's first on-farm trials as an alternative land-use approach for degraded peat soils. Paludiculture utilises plant species that prosper in fully rewetted conditions and can support the production of fodder, fruit, horticultural crops, vegetables, timber, and raw materials such as Sphagnum moss and cattails. The Intergovernmental Panel on Climate Change (IPCC) recognises paludiculture as an effective method for reducing CO_2 and nitrous oxide emissions (Hiraishi et al., 2014). Consequently, the practice has gained substantial attention in recent years as a

promising strategy for managing agricultural peatlands, prompting numerous countries to initiate paludiculture trials aimed at restoring degraded bogs (Temmink et al., 2023; Sari et al., 2025).

The Molecular Ecology and Nematode Research Group within enviroCORE at SETU has been invited to collaborate with GRI to assess the outcomes of the cooperative's peatland productivity and restoration programme. This assessment focuses on analysing nematode community structure and diversity in peatland habitats before and after restoration. Nematodes serve as highly effective environmental bioindicators due to their abundance, ecological diversity, sensitivity to environmental change, and strong representation of soil food-web processes.

In the current study, the nematodes biodiversity in 22 peatland habitats across 2 counties in Irish midlands have been investigated using both morphological and molecular tools. All of the nematodes information has been fed into the NINJA platform to evaluate the ecological status of the studied peatlands. Attempts have been made to investigate the status of the rewetted peatland sites compared to that of their non-rewetted counterparts using different nematode based indices.

2. Materials and methods

2.1. Peat soil sampling and description of the sampling sites

Sampling from 22 peatland habitats was carried out. The details of the peatland sampling sites along with their location are provided in Table 1. Samples were collected using a W-shaped sampling pattern, with five sub-samples taken per replicate from the top 10–20 cm of the soil/benthos layer using an auger, while carefully avoiding roots and stones. To obtain three composite replicates, this sampling procedure was repeated twice more following the same W pattern. Each sample was placed in an individually labelled, sealable plastic bag indicating the specific peat habitat, and stored on ice packs in an insulated portable bag. The samples were then transported to the enviroCORE laboratory. In the laboratory, the soil samples were sieved and homogenised to produce three composite replicates (500 g each) for every peatland habitat. Each composite replicate was then split into two equal portions: one half was used for morphological analysis, and the other half for molecular analysis

Table 1. Details of the investigated peatland habitats.

Site	Peatland habitat	Location	Rewetted/Non-rewetted
1	Healthy bog hummock (HBH)	53.01142 "N and 7.57155 "W	Rewetted
2	Healthy bog lawn (HBL)	53.01142 "N and 7.57155 "W	Rewetted
3	Degraded bog hummock (DBH)	53.01142 "N and 7.57155 "W	Non-rewetted
4	Degraded bog lawn (DBL)	53.01142 "N and 7.57155 "W	Non-rewetted
5	Wasted peat 1 (WP-1)	53.01142 "N and 7.57155 "W	Non-rewetted
6	Rough grazing (RG-1)	53.01142 "N and 7.57155 "W	Non-rewetted
7	Cutover scrub rewetted (C-RW)	53.01142 "N and 7.57155 "W	Rewetted
8	Cutover scrub non-rewetted (C-NRW)	53.01142 "N and 7.57155 "W	Non-rewetted
9	Woodlands rewetted (W-RW)	53.01142 "N and 7.57155 "W	Rewetted
10	Woodlands non-rewettted (W-NRW)	53.01142 "N and 7.57155 "W	Non-rewetted
11	Fenpeat	53.051401 "N and 7.876996 ' 'W	Undisturbed
12	Improved fen peat grassland rewetted (IFPG1- RW)	53.051401 "N and 7.876996 ' 'W	Rewetted
13	Improved fen peat grassland non-rewetted (IFPG1- NRW)	53.051401 "N and 7.876996 ' 'W	Non-rewetted
14	Rich fenpeat	53.06084 "N and 7.80084 "W	Undisturbed
15	Rough grazing 2 rewetted (RG2-RW)	53.166584830 ' 'N and 7.622959280 "W	Rewetted
16	Rough grazing 2 non-rewetted (RG2-NRW)	53.166584830 "N and 7.622959280 "W	Non-rewettted
17	Semi-natural peatland 1 (SNP-1)	53.041352300 "N and 7.999256190 "W	Rewetted
18	Improved fen peat grassland 2 (IFPG-2)	53.041355650 ' 'N and 7.999255840 " W	Rewetted
19	Semi-natural peatland 2 (SNP-2)	53.041356570 "N and 7.999255070 "W	Rewetted
20	Wasted peat 2 (WP-2)	53.041349840 "N and 7.999253240 "W	Non-rewetted
21	Semi-natural peatland 3 (SNP-3)	53.05455291 "N and 8.07305370 "W	Rewetted
22	Wasted peat 3 (WP-3)	53.04135474 "N and 7.99925402 "W	Non-rewetted

2.2. Nematode extraction for morphological and molecular identification

The initial portion of each composite replicate was utilized for the extraction of nematodes, adhering to the methodology outlined by Pulavarty et al., (2024). For the purpose of morphological analysis, nematodes were permanently fixed and mounted onto glass slides employing a mixture of 8.5% formaldehyde, glycerine, and ethanol-based solutions as described by Seinhorst (1962). The morphological identification was done based on various nematode features (for example, mouth cavity, bulbs, gender, tail shape, presence/absence of special features like amphids, caudal and cephalic setae), using a high-power light microscope (Euromex Delphi-X Observer, trinocular microscope DX.2153-PLPHi). Subsequently, identification was commenced using the keys, nematode images, and illustrations from manuals, books, and research articles authored by Gharahkhani et al., (2022), Mirbabaei Karani et al., (2015), Smythe, (2015), Schmidt Rhaesa, (2013), Mekete et al., (2012), Holovachov et al., (2009), and Bongers, (1988). Yeates et al., (1993) were referred to categorize feeders for the identified nematode families. For each peatland habitat, approximately 50–80 nematodes were fixed and identified to the family level, and to genus or species level where possible. Relative abundance of each nematode family was calculated for each habitat using the following formula:

Relative abundance (family, habitat) = (Number of individual nematodes in a given family / Total number of nematodes identified in that habitat)

The second half of each composite replicate was processed for DNA extraction. Approximately 20-25 g of soil from each replicate, along with 5-10 ml of dH_2O, was placed onto a 1000 µm sieve. The filtrate was gathered in a sterile mortar, ensuring it was free from roots and other soil debris. The collected filtrate in the mortar was allowed to sit at room temperature overnight to enable water evaporation. The soil was then uniformly mixed using a sterile pestle, and subsequently, 100 mg of soil per replicate was utilized for total soil DNA extraction employing the Qiagen DNeasy® PowerSoil® Pro kit, in accordance with the manufacturer's guidelines. The total soil DNA was quantified using both the Invitrogen™ Qubit 4 Fluorometer and NanoDrop™, and its quality and integrity were verified through agarose gel electrophoresis. Three technical DNA replicates for each peatland habitat were sent out to a sequencing company (Novogene Private ltd.). The 18S V4 rRNA region of nematodes was sequenced using the MN18F (5'CGCGAATRGCTCATTACAACAGC 3') and 22R (5'GCCTGCTGCCTTCCTTGGA 3') primer pairs (Karpinska et al., 2021; Bhadury et al., 2006) on an Illumina paired-end platform. This sequencing was conducted by Novogene (UK) Ltd. (Cambridge, UK), and the data obtained were analyzed to assess nematode biodiversity in the peatland soil samples. The results, including operational taxonomic units (OTUs), relative abundance, heat maps, bar plots, and alpha and beta diversity, were examined as outlined in Pulavarty et al. 2022.

2.3. Analysis of ecological status of peatland habitats: Nematode Indicator Joint Analysis (NINJA)

The molecular data obtained from the sequencing company was used to calculate the absolute and relative abundance of the nematode families in the each peatland habitat. The relative abundance data

was organised as described on the online NINJA platform (https://subsites.wur.nl/en/show-10/ninja-nematode-indicator-joint-analysis.htm). The NINJA online tool provides a user-friendly platform for analyzing nematode communities, integrating various ecological indicators to support soil health assessment and biomonitoring.

The organized data excel sheet was uploaded onto the online NINJA platform. The online NINJA tool helped to analyse nematode communities using several indices: the Maturity Index (MI) and Plant Parasitic Index (PPI) based on Bongers (1990), and food web indicators including the Enrichment Index (EI), Channel Index (CI), and Structure Index (SI) following Ferris et al. (2001). The MI and PPI were determined by summing the weighted relative abundance of families categorized by the cp scale for free-living and plant-parasitic nematodes (Bongers, 1990). The EI was calculated by weighting the relative abundance of functional guilds sensitive to nutrient enrichment within cp groups 1 and 2, while the SI was based on the weighted relative abundance of guilds responsive to physical disturbance in cp groups 3, 4, and 5. The CI was calculated as the weighted ratio of fungal-feeding to bacterial-feeding nematodes in cp groups 1 and 2. The metabolic footprint results generated by NINJA were used to assess and distinguish the ecological status of the rewetted site compared to its non-rewetted counterpart.

3. Results

3.1. Identification of nematodes based on morphology

A total of 40 nematode families were recorded across the 22 peatland habitats. Relative abundance of nematode families in various peatland habitats based on morphological identification is shown in Table 2.

Members of the family Dorylaimidae were the most abundant across all habitats. Within this family, the genera *Mesodorylaimus*, *Dorylaimus*, and *Labronema* were predominant. Dorylaimids showed the lowest abundance in bog (HBH, HBL, DBH, DBL) and fen peat (FP, R-FP) habitats compared with other peatland types. Habitats located in close proximity to bogs (C-RW, C-NRW, W-RW, W-NRW) also exhibited reduced abundances of Dorylaimidae. In contrast, the highest abundances were observed in improved fen peat grasslands (IFPG1-RW, IFPG2). Rewetted IFPG-1 exhibited a three-fold increase in Dorylaimidae abundance compared with its non-rewetted counterpart. Similarly, rewetted seminatural peatland habitats (SNP1, SNP2) showed increased numbers of Dorylaimidae individuals.

Tylenchidae nematodes were recorded in 16 peatland habitats out of the 22 studied. Their abundance was noticed to be higher in the bog (HBH, HBL, DBH, DBL) and fen peat (FP, R-FP) habitats compared to others. The rewetted rough grazing (RG2-RW), cutover bog (C-RW) and woodlands (W-RW) had slightly higher abundance of nematodes belonging to this family compared to that of their non-rewetted counterparts (RG2-NRW, C-NRW, W-NRW). Nematodes belonging to Tylenchidae were completely absent in case of seminatural peatland habitats (SNP-1, SNP-2, SNP-3).

Members of the family **Hoplolaimidae** were recorded in 14 of the 22 peatland habitats. Their abundance was slightly higher in rewetted rough grazing (RG2-RW), cutover bog (C-RW), and woodland (W-RW) habitats compared with their non-rewetted counterparts (RG2-NRW, C-NRW, W-NRW). Hoplolaimidae were absent from bog (HBH, HBL, DBH, DBL) and fen peat (FP, R-FP) habitats. Although their presence was detected in wasted peat and seminatural peatland habitats, abundances in these habitats were minimal.

Members of the family **Plectidae** were recorded in 13 of the 22 peatland habitats examined. Their abundance was higher in bog (HBH, HBL, DBH, DBL) and fen peat (FP, R-FP) habitats compared with other peatland types. Nematodes belonging to family Plectidae were completely absent in case of seminatural peatland habitats (SNP-1, SNP-2, SNP-3).

Members of the family **Cephalobidae** were recorded in 12 of the peatland habitats studied. Their highest abundance was observed in the wasted peat-1 (WP-1) habitat at site 1. Nematodes belonging to this family were also present in bog and fen peat habitats, as well as in woodland and cutover bog habitats, where abundances were comparable across these habitat types.

Members of family Aphlenchoididae, Achromodoridae and Mononchidae, were recorded in 12, 12 and 11 of the peatland habitats out of the 22 studied. Nematodes belonging to Achromodoridae were present in all the bog (HBH, HBL, DBH, DBL) and fen peat (FP, R-FP) habitats. The abundance in HBL, FP, R-FP was significantly similar. The distribution of nematodes belonging to Aphlenchoididae was very random without any specific pattern. Their prescence was noted in both fen peat habitats, whereas, in the bog they were noted in HBH and DBL and absent in case of HBL and DBH. Similarly, they were detected in two of the three WP, SNP, and IFPG habitats. Mononchidae were found in all three SNP habitats and in the woodlands (W-RW, W-NRW).

Members of family Teratocephalidae were recorded only in the bog and fen peat habitats. Their abundance was 5 folds higher in healthy bog (HBH, HBL) and R-FP compared to degraded bog habitats (DBH, DBL).

Members of families Dolichodoridae, Pratylenchidae, Heteroderidae, Criconematidae, Hemicycliophoridae, Aphelenchidae, Rhabditidae, Panagrolaimidae, Myolaimidae, Neodiplogastridae, Diplopeltidae, Prismatolaimidae, Tobrilidae, Tripylidae, Thornenematidae, Belondiridae, Leptonchidae, Qudsianematidae, Nordiidae, Aporcelaimidae, Anatonchidae, Bathyodontidae, Alaimidae, Aulolaimoidea, Amphidelidae, Mylonchulidae, Rhabdolaimidae, Chromadoridae, Tylencholaimoidea, Mydonomidae, Nygolaimidae were recorded in 2, 4, 1, 4, 2, 2, 9, 7, 1, 1, 5, 6, 3, 3, 6, 3, 5, 6, 6, 6, 2, 5, 3, 6, 2, 2, 2, 2, 2, 1, 1 peatland habitats respectively. Details of the same have been provide in Table 2.

Table 2: Relative abundance of nematode families in various peatland habitats based on morphological identification.

3.2. Identification of nematodes based on molecular data

Molecular sequencing data recorded a total of 30 nematode families across the 22 peatland habitats investigated. Relative abundance of nematode families in various peatland habitats based on molecular identification is shown in Table 3.

Molecular analyses revealed that nematodes belonging to the families **Tylenchidae, Plectidae, Rhabdolaimidae, Monhysteridae,** and **Cyatholaimidae** were present across all peatland habitats studied. Within the family **Plectidae**, the genera **Plectus** and **Anaplectus** were identified. The family **Rhabdolaimidae** was represented by the genus **Rhabdolaimus**, while **Monhysteridae** included the genus **Eumonhystera**. In the family **Cyatholaimidae**, the genera **Achromadora** and **Ethmolaimus** were recorded.

Members of the family **Cephalobidae**, represented by the genera **Acrobeloides** and **Eucephalobus**, were detected in 21 of the 22 peatland habitats. Other nematode families recorded across the study sites included **Hoplolaimidae** (*Rotylenchus*, *Helicotylenchus*), **Tylenchulidae** (*Paratylenchus*), **Tripylidae** (*Tripyla*), **Aphelenchoididae** (*Aphelenchoides*), **Criconematidae** (*Mesocriconema*), **Pratylenchidae** (*Pratylenchus*), **Merliniidae**, **Meloidogynidae** (*Meloidogyne*), **Aporcelaimidae, Steinernematidae** (*Steinernema*), and **Anguinidae** (*Ditylenchus*), occurring in 15, 12, 11, 10, 10, 9, 9, 9, 7, 7, and 7 habitats, respectively.

In contrast, **Panagrolaimidae** (*Panagrolaimus*), **Aphelenchidae** (*Aphelenchus*), **Heteroderidae** (*Heterodera*), **Mononchidae** (*Clarkus*), **Mylonchulidae** (*Mylonchulus*), and **Telotylenchidae** were infrequently observed, being recorded in only 4, 3, 3, 3, 2, and 2 habitats, respectively. Additionally, single representatives of **Neodiplogasteridae** (*Pristionchus*), **Alaimidae** (*Alaimus*), **Mermithidae**, **Trischistomatidae, Trichodoridae, Neotylenchidae**, and **Diplogasteridae** were detected exclusively in IFPG-2, C-NRW, FP, SNP-2, RG2-NRW, SNP-1, and SNP-1, respectively.

In the cutover bog (Figure 1a), comparison between rewetted and non-rewetted areas showed that **Tylenchidae** and **Criconematidae** exhibited higher relative abundances in the rewetted site, with increases of approximately 4.0-fold and 1.3-fold, respectively, compared to the non-rewetted counterpart. In contrast, other nematode families, such as Hoplolaimidae, Plectidae, Monhesteridae and Cyatholaimidae displayed greater relative abundances in the non-rewetted cutover bog (C-NRW), with values that were approximately 1.5-, 4.9-, 7.0-, and 1.4-fold higher respectively than those observed in the rewetted site (C-RW). Notably, members of the family **Cephalobidae** showed a pronounced reduction in relative abundance in the rewetted area compared with the non-rewetted counterpart.

In the Improved fen peat grasslands (Figure 1b), members of family Tylenchidae, Tripylidae, Rhabdolaimidae, Tylenchulidae and Meloidogynidae exhibited 5.4, 1.7, 3.4, 7.1 and 22.4-fold higher relative abundance in the rewetted areas compared to their non-rewetted counterpart. However, members of families Pratylenchidae, Cephalodidae, Plectidae and Cyatholaimidae were noted to be less abundant in rewetted area compared to the non-rewetted counterpart.

In the woodlands (Figure 1c), only members of Plectidae were recorded to be 3.4-fold higher in rewetted area compared to its non-rewetted counterpart. Whereas, members of families Tylenchidae,

Criconematidae, Cephalobidae, Rhabdolaimidae and Monhysteridae were noted to less abundant in the rewetted areas compared to their non-rewetted counterparts.

Finally, in case of Rough grazing peatland habitat (Figure 1d), Tryplidae and Rhabdolaimidae were the nematode families noted to be highly abundant in rewetted areas compared to non-rewetted counterparts. In contrast, abundance of Tylenchidae, Hoplolaimidae, Pratylenchidae, Aphelenchoididae, Panagrolaimidae, Steinernematidae and Cyatholaimidae were noted to be 1.8, 1.5, 31.1, 6.9, 7.4, 3.9 and 19.8 -folds higher in the non-rewetted areas compared to that of rewetted counterparts.

Members of the family **Tylenchidae** showed increased relative abundance in rewetted areas of both cutover bog and improved fen peat grassland habitats. Similarly, **Tripylidae** exhibited higher abundances following rewetting in improved fen peat grassland and rough grazing habitats. In contrast, **Cephalobidae** were consistently reduced in rewetted cutover bogs, improved fen peat grasslands, and rough grazing areas. With the exception of woodland habitats, **Cyatholaimidae** generally exhibited decreased abundance following rewetting across all habitat types.

3.3. Analysis of ecological status of peatland habitats: Nematode Indicator Joint Analysis (NINJA)

The ecological status of the peatland habitats was assessed using molecular data. Where taxonomic resolution permitted, analyses were conducted at both the family and genus levels. Figure 2 presents the nematode community structure and food web analysis of the different peatland habitats generated using the NINJA tool.

According to the food web diagnostics of the NINJA tool, higher values of the **Channel Index (CI)** indicate a greater proportion of energy flow through the slow, fungal-based decomposition pathway. The **Enrichment Index (EI)** reflects the level of nutrient enrichment, while the **Structure Index (SI)** is indicative of ecosystem maturity and structural complexity. The food web analysis derived from the NINJA tool illustrates variation in ecosystem condition across the peatland habitats based on the **EI** and **SI.**

At the **genus level**, HBH and HBL samples (Figure 2a) were generally positioned at **higher Structure Index (SI)** values compared to DBH and DBL, indicating a more complex and structured soil food web in healthy bog habitats. These sites also exhibited **low to moderate Enrichment Index (EI)** values, suggesting limited nutrient enrichment and a dominance of slower energy pathways. In contrast, DBH and DBL samples clustered at **lower SI values,** reflecting simplified food web structure and reduced trophic complexity. Several degraded bog samples exhibited relatively **higher EI values,** indicating greater nutrient enrichment and dominance of opportunistic nematode guilds. Family-level analysis showed a broadly similar pattern; however, the separation between habitat types was less pronounced. While HBH and HBL still tended toward higher SI values relative to degraded sites, overlap among habitats increased, and EI–SI gradients appeared compressed. This suggests that family-level resolution captures general trends in food web condition but may underestimate subtle differences among habitat types that are evident at finer taxonomic resolution.

Food web analysis using the NINJA tool revealed differences between the rewetted (C-RW) and non-rewetted (C-NRW) cut-over bog habitats (Figure 2b). In both genus- and family-level analyses, C-RW samples were generally associated with lower Structure Index (SI) values, indicating reduced soil food web complexity following rewetting. Enrichment Index (EI) values in the rewetted site were low to moderate, suggesting limited nutrient enrichment and dominance of opportunistic functional guilds. In contrast, C-NRW samples exhibited relatively higher SI values, reflecting a comparatively more developed trophic structure. Overall, these patterns suggest that rewetting has not yet resulted in increased food web structural maturity in the cut-over bog.

Food web analysis using the NINJA tool showed distinct patterns between the fen peat (FP) and rich-fen peatland (R-FP) habitats (Figure 2c). Both genus- and family-level analyses indicated that **R-FP samples tended to exhibit higher EI values** than FP, reflecting greater nutrient availability characteristic of rich-fen systems. However, **SI values in both FP and R-FP remained generally low to moderate**, indicating limited trophic complexity and relatively simplified soil food webs. Compared with healthy bog habitats, which displayed higher SI and lower EI values, both fen peat habitats showed a shift toward **nutrient-enriched but less structurally developed food webs.** These results suggest that while rich-fen peatlands support increased nutrient-driven activity, they do not attain the structural maturity observed in healthy bog ecosystems.

Food web analysis using the NINJA tool revealed relatively similar patterns between rewetted (W-RW) and non-rewetted (W-NRW) woodland habitats (Figure 2d). In both genus- and family-level analyses, samples from the two woodland conditions clustered within low to moderate SI values, indicating limited trophic complexity and a moderately simplified soil food web. EI values were generally low to intermediate in both habitats, suggesting an absence of strong nutrient enrichment effects following rewetting. Compared with other peatland habitats, woodland sites exhibited more stable EI–SI distributions, with only subtle differences between rewetted and non-rewetted conditions. Overall, these results indicate that rewetting had a limited influence on nematode-based food web structure in woodland habitats, with ecosystem condition appearing largely resilient to hydrological change.

Food web analysis using the NINJA tool revealed comparable patterns among the rough grazing peatland sites RG-1, RG2-RW, and RG2-NRW (Figure 2e). In both genus- and family-level analyses, samples from all three sites were predominantly associated with **low to moderate SI values**, indicating simplified soil food web structure typical of managed or disturbed peatlands. The **EI** values showed limited variation among sites, although the rewetted rough grazing site (RG2-RW) tended to exhibit slightly lower EI values compared to the non-rewetted site (RG2-NRW), suggesting reduced nutrient enrichment following rewetting. The reference rough grazing site (RG-1) displayed intermediate EI and SI values, falling between the two RG2 conditions. Overall, these results suggest that rewetting in rough grazing peatlands has led to only modest changes in nematode-based food web structure, with no clear shift toward increased ecosystem maturity.

Food web analysis using the NINJA tool revealed similar patterns across the wasted peatland sites WP-1, WP-2, and WP-3 (Figure 2f), where peat depth was less than 40 cm. In both genus- and family-level analyses, samples from all three sites were predominantly associated with **low SI values**, indicating simplified soil food web structure and reduced trophic complexity. **EI** values were generally low to moderate across the sites, suggesting limited nutrient enrichment and dominance of opportunistic nematode functional guilds. Minor variation among the three wasted peatland sites was observed; however, no consistent trend toward increased food web maturity was evident. Overall, these results indicate that wasted peatlands support poorly developed nematode-based soil food webs, likely reflecting shallow peat depth, historical disturbance, and constrained ecosystem functioning.

Food web analysis using the NINJA tool revealed broadly similar patterns among the improved fen peat grassland sites IFPG-1, IFPG2-RW, and IFPG2-NRW (Figure 2g). In both genus- and family-level analyses, samples from all IFPG sites were primarily associated with **low to moderate SI values**, indicating simplified soil food web structure typical of managed grassland systems. The **EI** values showed modest variation among sites, with the rewetted site (IFPG2-RW) tending toward slightly lower EI values compared to the non-rewetted site (IFPG2-NRW), suggesting reduced nutrient enrichment following rewetting. The reference site (IFPG-1) exhibited intermediate EI and SI values. Overall, these results indicate that rewetting in improved fen peat grasslands has resulted in only minor changes in nematode-based food web structure, with no clear evidence of increased ecosystem maturity.

Food web analysis using the NINJA tool revealed comparable patterns among the semi-natural peatland sites SNP-1, SNP-2, and SNP-3 (Figure 2h). In both genus- and family-level analyses, samples from all SNP sites were primarily associated with **low to moderate SI values**, indicating moderately simplified soil food webs with limited trophic complexity. **EI** values were generally low to intermediate across the sites, suggesting minimal nutrient enrichment and a dominance of basal and opportunistic nematode functional guilds. Although minor variation among the three semi-natural sites was observed, no consistent gradient in food web structure or enrichment was evident. Overall, these results indicate that semi-natural peatlands support moderately developed but not fully mature nematode-based soil food webs.

4. Discussion

This study provides an integrated assessment of nematode community composition across a range of peatland habitats using both morphological identification and molecular sequencing approaches. By combining these complementary methods, we were able to evaluate the ecological effects of rewetting, identify potential nematode indicators of peatland condition, and assess the level of agreement between traditional and molecular techniques.

Several nematode families identified in this study show strong potential as indicators of peatland condition. Rewetted and semi-natural peatlands were consistently associated with higher proportions of *Rhabdolaimidae*, *Plectidae*, *Monhysteridae*, and *Aporcelaimidae*, families commonly linked to stable,

water-saturated soils and slow nutrient turnover (Ferris et al., 2001; Kardol et al., 2011). The frequent occurrence of *Tylenchulidae* and *Steinernematidae* in rewetted woodlands and fen peat grasslands further suggests increasing trophic complexity following rewetting. In contrast, degraded and non-rewetted sites showed higher abundances of *Tylenchidae*, *Hoplolaimidae*, *Pratylenchidae*, and *Criconematidae*, particularly in wasted peat and rough grazing habitats. These families are widely recognised as indicators of disturbance, drainage, and vegetation change, often responding rapidly to increased aeration and nutrient availability (Bongers & Ferris, 1999). Their dominance in non-rewetted sites supports their use as bioindicators of peatland degradation.

Rewetting had a pronounced influence on nematode community composition across the investigated peatlands. Rewetted habitats, including healthy bog hummocks and lawns (HBH, HBL), rewetted cutover scrub (C-RW), rewetted woodlands (W-RW), semi-natural peatlands (SNP-1 to SNP-3), and rewetted fen peat grasslands (IFPG1-RW, IFPG-2), were characterised by higher representation of families typically associated with moist, organic-rich, and structurally complex soils. In both molecular and morphological datasets, these sites showed consistently high relative abundances of *Rhabdolaimidae*, *Plectidae*, and *Monhysteridae*, alongside moderate contributions from *Cephalobidae* and *Tylenchidae*. In contrast, non-rewetted and degraded habitats such as degraded bog hummocks and lawns (DBH, DBL), wasted peat sites (WP-1 to WP-3), and non-rewetted rough grazing areas (RG-1, RG2-NRW) displayed communities dominated by disturbance-tolerant and enrichment-associated families. These sites showed elevated proportions of *Tylenchidae*, *Hoplolaimidae*, *Pratylenchidae*, and *Criconematidae*, particularly in the molecular dataset, indicating increased plant-associated and stress-tolerant taxa. Such patterns are consistent with previous findings that drainage and degradation favour opportunistic nematode groups adapted to fluctuating resources and aerated soils (Bongers, 1990; Briones et al., 2014). The relative similarity between rewetted sites and undisturbed fen peat (FP, R-FP) suggests that rewetting promotes partial recovery of below-ground biological structure, although full convergence with reference conditions was not observed across all habitats.

At the level of major ecological patterns, morphology-based and molecular datasets showed strong agreement. Both approaches consistently distinguished rewetted from non-rewetted habitats and identified similar dominant families within each habitat type. Families such as *Rhabdolaimidae*, *Plectidae*, *Cephalobidae*, and *Tylenchidae* were detected across most sites using both methods, confirming their widespread distribution in peatland soils. However, molecular sequencing revealed higher taxonomic richness and detected additional families that were rare or absent in the morphological dataset. For example, *Anguinidae*, *Mermithidae*, *Trischistomatidae*, *Neotylenchidae*, *Telotylenchidae*, and *Diplogasteridae* were primarily detected through sequencing, particularly in semi-natural and rewetted peatlands (e.g. SNP-1, SNP-2, IFPG-2). This reflects the known limitations of morphological identification in detecting cryptic, juvenile, or low-abundance taxa (Porazinska et al., 2009; Creer et al., 2016). Conversely, dominant families such as *Rhabdolaimidae* and *Plectidae* showed comparable relative patterns across both datasets, supporting the reliability of morphological identification for ecologically abundant taxa. The observed mismatches therefore reflect methodological complementarity rather than inconsistency and highlight the value of combining approaches for peatland biodiversity assessment.

Recovery of nematode-based soil food web structure is closely linked to peatland carbon sequestration and their role in climate mitigation. Well-structured food webs, characterized by higher Structure Index (SI) values, promote slow, fungal-dominated decomposition pathways that enhance carbon stabilization and long-term peat accumulation. In intact and rewetted peatlands, reduced dominance of opportunistic, bacterial-feeding nematodes and gradual re-establishment of higher trophic groups can limit rapid organic matter mineralization and associated greenhouse gas emissions. Rewetting restores anoxic conditions that suppress peat oxidation, while the concurrent recovery of soil food web complexity further regulates carbon turnover by constraining microbial activity and nutrient release. Although short-term responses to rewetting may not immediately increase food web maturity, the stabilization of energy flow and reduction of nutrient-driven decomposition represent critical early steps toward rebuilding carbon-rich peat soils. Consequently, long-term restoration strategies that facilitate both hydrological recovery and biological food web development are essential for maximizing peatland carbon storage and strengthening their function as natural climate mitigation systems.

The nematode-based food web analyses across a wide range of peatland habitats revealed consistent patterns in ecosystem condition, disturbance, and recovery potential, highlighting the ecological significance of rewetting as a restoration strategy. Across all habitat types examined—ranging from healthy bog microforms (HBH, HBL) to degraded, managed, and rewetted systems—the Enrichment Index (EI) and Structure Index (SI) provided valuable insights into nutrient dynamics, trophic complexity, and ecosystem maturity.

Healthy bog habitats (HBH and HBL) consistently exhibited higher SI values and comparatively lower EI values, indicating well-structured soil food webs dominated by slow, fungal-mediated decomposition pathways. This pattern is characteristic of intact peatland ecosystems where carbon sequestration and nutrient cycling are tightly regulated (Bongers & Ferris, 1999; Ferris et al., 2001). In contrast, degraded bog habitats (DBH and DBL) showed reduced SI values and, in some cases, elevated EI values, reflecting simplified food webs dominated by opportunistic nematode guilds and a shift toward bacterial-driven energy channels. These changes are indicative of ecosystem disturbance and loss of trophic stability.

Across rewetted and non-rewetted comparisons—including cut-over bogs (C-RW vs. C-NRW), improved fen peat grasslands (IFPG2-RW vs. IFPG2-NRW), rough grazing peatlands (RG2-RW vs. RG2-NRW), and woodland habitats (W-RW vs. W-NRW)—rewetting generally resulted in **modest reductions in EI** and **limited short-term increases in SI**. This suggests that rewetting effectively reduces nutrient enrichment and resource pulses associated with drainage and management but does not immediately restore higher trophic complexity. Similar lag effects between hydrological restoration and biological recovery have been reported in peatlands and other wetland ecosystems (Verhoeven & Toth, 1995; Ritzema et al., 2014). Fen peat (FP) and rich-fen peatland (R-FP) habitats showed higher EI values than bog systems, reflecting their naturally greater nutrient availability. However, SI values in both fen types remained lower than those observed in healthy bogs, emphasizing that nutrient-rich conditions alone do not confer food web maturity. Wasted peatlands (WP-1, WP-2, WP-3), characterized by shallow peat depth (<40 cm), consistently supported poorly structured food webs with low SI values, underscoring the importance of

peat depth and long-term organic matter accumulation for sustaining complex soil communities. Semi-natural peatlands (SNP-1, SNP-2, SNP-3) and reference rough grazing sites (RG-1) occupied intermediate positions along the EI–SI gradients, indicating partially developed food webs. These systems appear more resilient than heavily degraded or wasted peatlands but still fall short of the structural complexity observed in intact bogs.

The combined morphological and molecular analyses (Tables 2 and 3) together with nematode-based soil food web indices (Figure 2) demonstrate that peatland rewetting initiates biologically meaningful recovery, although full restoration of soil food web structure remains a long-term process. Across rewetted habitats, shifts in nematode assemblages were consistently observed away from enrichment-tolerant families such as *Tylenchidae* and *Hoplolaimidae*, which dominated degraded and non-rewetted sites including wasted peat and rough grazing systems (e.g. WP-1 to WP-3, RG-1; Tables 2,3). These sites also exhibited elevated EI values and low SI values (Figure 2), indicating simplified, bacterial-driven food webs and rapid organic matter turnover. In contrast, intact bog habitats (HBH, HBL) and semi-natural peatlands (SNP-1 to SNP-3) showed high relative abundances of *Rhabdolaimidae* (up to ~54%), *Plectidae* (up to ~21%), and *Monhysteridae*, taxa associated with stable, waterlogged conditions and fungal-dominated energy channels (Tables 2,3). These assemblages corresponded with higher SI values and lower EI values, reflecting well-structured soil food webs that promote slow decomposition and carbon stabilization (Bongers & Ferris, 1999; Ferris et al., 2001). Rewetted systems such as C-RW, IFPG-RW, and W-RW displayed intermediate patterns, with reduced dominance of enrichment-associated families and increasing contributions from structure-associated taxa, yet SI values remained lower than those of intact bogs (Figure 2). This lag highlights persistent legacy effects of drainage, peat loss, and limited recolonization of higher trophic groups (Verhoeven & Toth, 1995; Ritzema et al., 2014).

The Nematode Indicator Joint Analysis (NINJA) tool is widely used to interpret soil food web structure; however, it was primarily developed using data from mineral and agricultural soils. Therefore, this study also highlights the need to adapt the NINJA tool for use in peatland ecosystems. Given the unique hydrological and biogeochemical characteristics of peat soils, nematode indicator responses may deviate from those assumed in existing NINJA frameworks. Developing peatland-specific guild classifications and index thresholds would enhance the reliability of nematode-based assessments of peatland restoration and ecosystem functioning.

Overall, the findings demonstrate that **rewetting is a critical first step in peatland restoration,** effectively dampening nutrient enrichment and stabilizing soil food web dynamics. However, the persistence of low SI values across many rewetted sites highlights that **full recovery of soil food web structure is a slow process**, likely constrained by legacy effects of drainage, vegetation change, peat loss, and limited recolonization of higher trophic groups. Long-term monitoring and complementary restoration measures, such as vegetation re-establishment and reduced land-use intensity, are therefore essential to facilitate the gradual rebuilding of mature, resilient peatland ecosystems, maximize peat carbon sequestration, and strengthen peatlands as effective natural climate mitigation systems.

Declarations

Funding Declaration

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Data Availability Declaration

The data has been stored in the OneDrive folder of A.P., T.K.D., D.M. and library repository of SETU, Carlow campus, Ireland.

Competing Interest declaration

There are no Competing Interests

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Author Contribution declaration

Conceptualization, A.P.; methodology, A.P., T.K., L.R., E.C. and P.M.M.; software, A.P. and T.K.; validation, A.P., D.M. and T.K.D.; formal analysis, A.P., L.R. and T.K.; investigation, A.P.; resources, D.M. and T.K.D.; data curation, A.P., P.M.M. and T.K.; writing—original draft preparation, A.P.; writing—review and editing, A.P., D.M. and T.K.D.; visualization, A.P.; supervision, D.M. and T.K.D.; project administration, A.P. and T.K.D.; funding acquisition, D.M. and T.K.D. All authors have read and agreed to the published version of the manuscript

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Table

Table 2 is available in the Supplementary Files section.

Figures

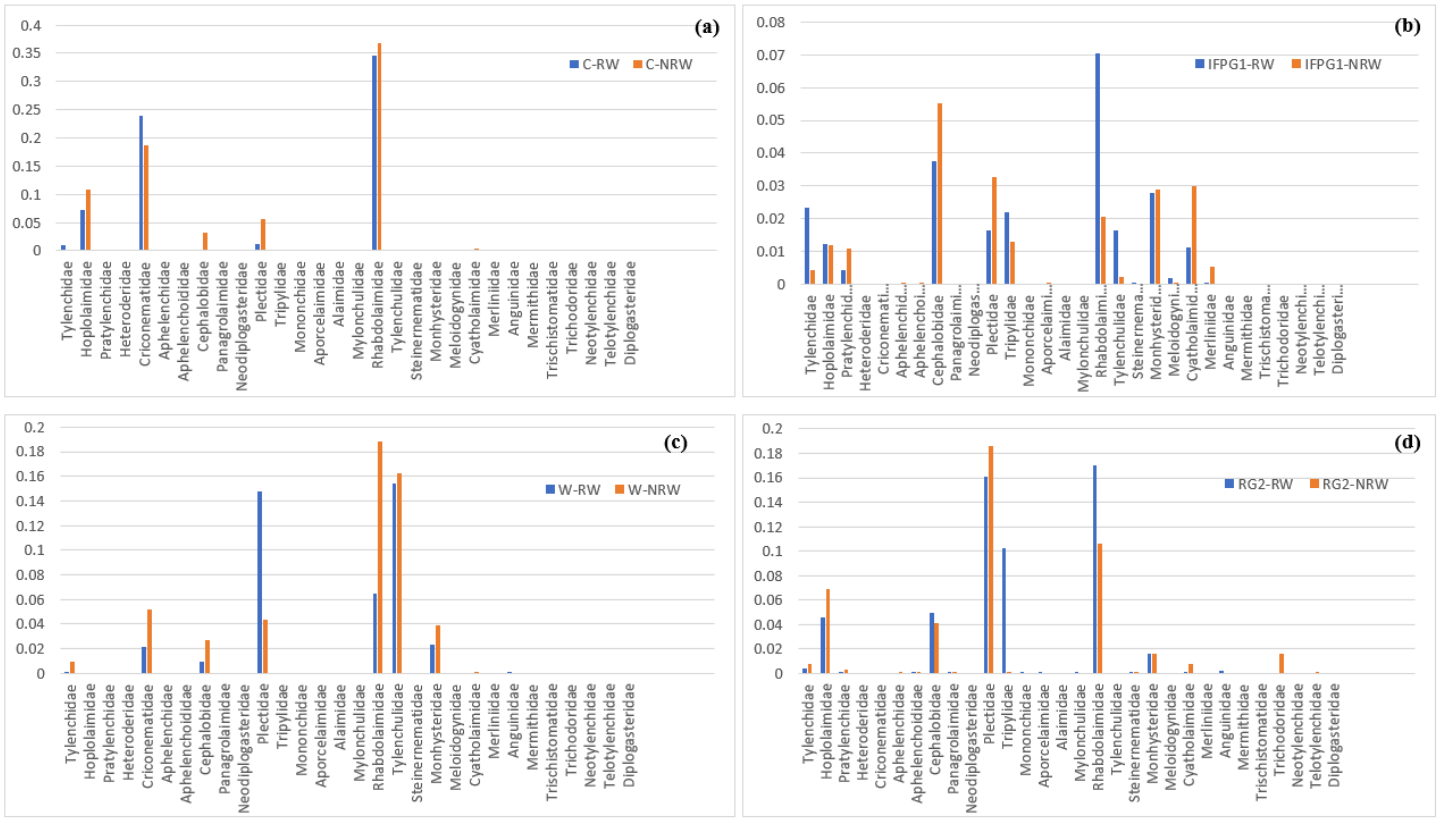


Figure 1

Comparison of relative abundance of nematode families in (a) C-RW Vs C-NRW (b) IFPG1- RW Vs IFPG1-NRW (c) W-RW Vs W-NRW (d) RG2-RW Vs RG2-NRW

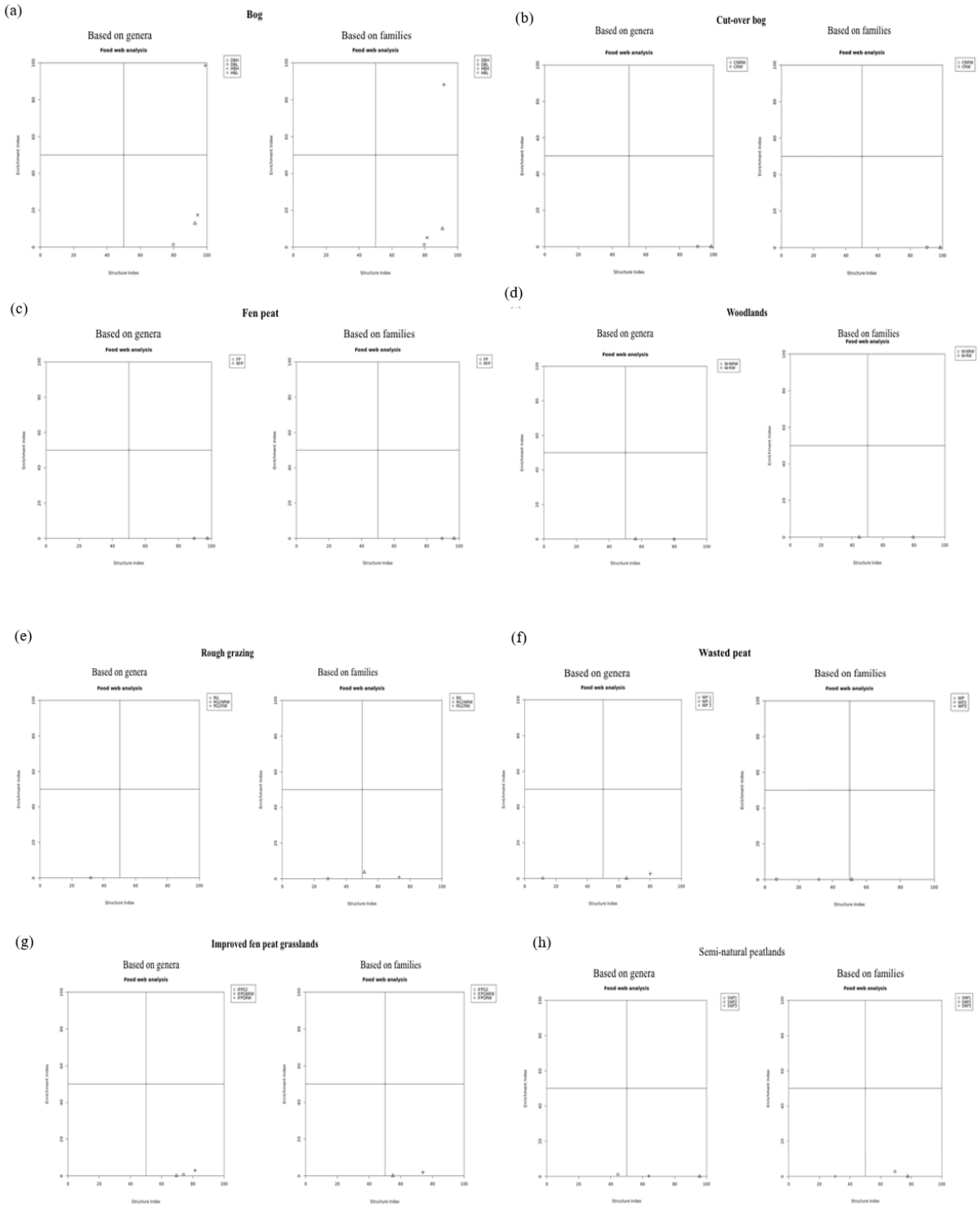


Figure 2

Interpretation of nematode community structure and Food web diagnosis of the following peatland habitats: (a) Bog (b) Cut-over bog (c) Fen peat ((d) Woodlands (e) Rough grazing (f) Wasted peat (g)

Improved fen peat grasslands (h) Semi-natural peatlands

Supplementary Files

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- Table2.docx