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Nematode diversity in rice fields of Java, Indonesia

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Abstract. *Kurniawati F, Supramana, Kusumah RYM, Quamilla DS, Sobikhin. 2025. Nematode diversity in rice fields of Java, Indonesia. Biodiversitas 26: 6273-6284.* Rice (*Oryza sativa*) is a staple crop in Indonesia; however, its productivity is constrained by plant-parasitic nematodes that cause substantial yield losses. This study investigates the diversity and abundance of nematodes in soil and rice roots across Java Island. Soil and root samples were purposively selected based on symptoms of nematode infection, and nematodes were extracted and identified morphologically. Ecological indicators, including Maturity Index family and diversity metrics (H', E, D), were quantified to evaluate food web structure and soil ecosystem conditions using Microsoft Excel and the NINJA platform. Plant-parasitic nematodes were widely distributed, with *Hirschmanniella* and *Meloidogyne* dominating the assemblage, reflecting strong herbivory pressure in flooded rice systems. Free-living nematodes were predominantly bacterivores, indicating a bacterial-driven decomposition pathway typical of anaerobic paddy soils. Maturity Index (MI) values (2.65-3.07) suggested moderate and relatively uniform disturbance across regions, although ΣMI varied significantly, with higher values in Bogor and Malang indicating more mature soil food webs. Diversity indices showed that Malang and Sukabumi exhibited the highest ecological stability, whereas Banten and Bojonegoro displayed low diversity and high dominance, characteristic of stressed environments. The consistently high Enrichment Index (EI) and Structure Index (SI) values indicated active nutrient cycling and resilient trophic structures. Overall, Java's rice ecosystems experience moderate disturbance yet maintain functionally robust nematode communities, underscoring the need for region-specific management, particularly in high-Plant Parasitic Index (PPI) areas, to improve soil health and mitigate nematode-associated yield losses.

Keywords: Bioindicator, Maturity Index, nematode community, *Oryza staiva,* soil food web

INTRODUCTION

Rice (*Oryza sativa*) is one of the world's most important food crops, serving as the primary staple for the majority of the global population, especially in Asia, which accounts for more than 90% of global rice consumption (Fukagawa and Ziska 2019). Indonesia ranks as the fourth-largest rice producer globally, after India, China, and Bangladesh, and approximately 95% of Indonesians rely on rice as their main staple (USDA 2025). Domestic demand continues to increase in parallel with population growth. Although rice is cultivated throughout the archipelago, Java Island remains the dominant production hub, contributing 54.18% of national rice output across an estimated 5.04 million hectares in 2024 (BPS 2025). This dominance underscores the necessity of understanding biotic factors that threaten rice productivity on the island.

Among biotic constraints, Plant-Parasitic Nematodes (PPNs) are increasingly recognized as a serious but often underestimated threat. Their symptoms (stunting, chlorosis, poor tillering, and reduced vigor) are commonly misdiagnosed as nutrient deficiencies or drought stress, leading to a neglect of their actual impact. Yield losses due to PPN infestations vary widely, from 10% to 80%, depending on species, environmental conditions, and nematode population density (Kyndt et al. 2014; Mantelin et al. 2017). Previous studies in Java have identified a diverse assemblage of nematodes associated with rice cultivation, including *Aphelenchoides besseyi*, *Hirschmanniella mucronata*, *H. oryzae*, *Meloidogyne graminicola*, *Helicotylenchus*, *Radopholus*, *Pratylenchus*, *Longidorus*, *Plectus*, *Eudorylaimus*, *Dorylaimus*, *Diplogaster*, *Cephalobus*, and *Rhabditis* (Diana et al. 2018; Indarti et al. 2020; Amir et al. 2023; Tarno et al. 2024; Mutala'liah et al. 2025). Because PPNs feed primarily on below-ground tissues, infections are difficult to detect during early stages. Initial symptoms may include slow growth and yellowing leaves, which can progress to stunting, reduced panicle formation, and plant death (Bernard et al. 2017). Key species such as *M. graminicola* induce root galls, *Hirschmanniella* spp. cause root lesions, and *A. besseyi* results in the white-tip disease in rice leaves (Kurniawati and Supramana 2016; Rusinque et al. 2021; Amir et al. 2023). These nematodes are favored by continuous monocropping, high soil moisture, and poorly drained soils, conditions typical of lowland paddy systems in Java.

In contrast, Free-Living Nematodes (FLNs) play crucial ecological roles such as bacterivores, fungivores, predators, and omnivores within soil food webs. FLNs contribute to nutrient mineralization, organic matter decomposition, and microbial regulation. Due to their sensitivity to land-use changes, organic inputs, and soil disturbance, they serve as effective bioindicators of soil health (Bongers 1990; Neher 2001). Ecological indices such as the Maturity Index (MI), Enrichment Index (EI), and Structure Index (SI) provide quantitative insights into soil disturbance levels, trophic interactions, and food-web complexity. High FLN diversity and high MI/SI values generally indicate mature and stable ecosystems, whereas PPN dominance signals ecological imbalance.

Despite the ecological significance of nematodes, integrated assessments of PPN and FLN communities in Indonesian rice agroecosystems remain limited. Most existing studies focus on pathogenic species or are restricted to localized surveys, leaving broader ecological patterns underexplored. Although FLNs have been reported from several regions in Java (Amir et al. 2023; Mutala'liah et al. 2025), information remains fragmented, and comprehensive island-wide evaluations are lacking. Consequently, the variability of nematode diversity, trophic composition, and soil food-web maturity across Java's major rice-growing regions has not been fully characterized. Given Java's central role in Indonesia's rice production and the potential of nematodes as sensitive ecological indicators, a comprehensive assessment of nematode community structure is critical. Such baseline information essential for understanding of soil ecosystem functioning and support sustainable nematode management strategies. Therefore, this study aimed to (i) characterize plant-parasitic and free-living nematode communities in rice soil and roots across major rice-producing regions of Java; (ii) quantify nematode-based indices (MI, EI, SI, etc.) to assess soil food-web structure; and (iii) identify regions with relatively stable vs stressed nematode assemblages.

MATERIALS AND METHODS

Study area

This research was conducted in eight central rice-producing districts across the island of Java, Indonesia: Banten, Sukabumi, Bogor, Subang, Klaten, Sukoharjo, Bojonegoro, and Malang (Figure 1). Two representative sites were purposively selected in each district, totaling 16 sites. Sampling was carried out during the dry season planting period from July to August 2025, and all fields were sampled within the same season and year. All fields were continuously irrigated lowland paddies managed under rice monoculture for the previous 3-5 years. Pesticide use targeted insects and fungi, and no nematicides were applied. Sites were selected based on symptoms associated with nematode infestation (stunting, uneven growth, chlorosis, white-tip symptoms, reduced tillering). Therefore, findings represent symptomatic flooded rice monocultures, not all rice fields across Java. The study sites were purposively selected based on observations from an initial field survey, which identified locations where plants exhibited symptoms consistent with nematode infection. These sites were prioritized because, although such symptoms were present, no prior reports had confirmed nematode-associated disease in these districts. Additional site information is provided in Table 1.

At each field, individual soil and root samples were collected from plants showing variable symptom expression. Each soil and root sample pair represented one sampling point. The number of sampling points per field varied (8-14 sampling points) depending on field size and symptom distribution. Across all surveyed fields, a total of 178 samples were collected, comprising 89 soil samples and 89 root samples. The soil was taken using a single core at a depth of 10-15 cm with a soil sampler with random sampling. The number of samples obtained per district was not uniform, reflecting the purposive nature of the survey and field heterogeneity. Soil and root samples were processed within 1-3 days of collection and stored at 4°C until extraction.

Table 1. Localities of the rice fields of different sites in Java Island, Indonesia

Site	Location	Cultivar	Age (DAT)	Coordinate
1	Subang 1	Inpari 32	30	-6.433807, 107.883761
2	Subang 2	Ciherang	52	-6.4609915,107.8303135
3	Sukabumi 1	Mawar	30	-6.9282172, 106.9068478
4	Sukabumi 2	Tri Sultan 05	90	-6.94395, 106.9440133
5	Bogor 1	Inpari 32	40-50	-6.6046306, 106.7268469
6	Bogor 2	Inpari 32	30-40	-6.5504613, 106.7395132
7	Bojonegoro 1	M49, Ciherang	36	-7.1227297, 112.0827531
8	Bojonegoro 2	M49, Ciherang	36	-7.1767176, 111.932835
9	Malang 1	Cimelati, Mustajab, Ciherang	50	-7.907259, 112.611670615
10	Malang 2	Lampung, IR 64	45	-7.8964, 112.6313
11	Sukoharjo 1	Inpari 32	36	-7.7367629, 110.7882734
12	Sukoharjo 2	Inpari 32	36	-7.7687286, 110.736443
13	Klaten 1	Inpari 32, Logawa	60	-7.758939, 110.698185
14	Klaten 2	Inpari 32	45	-7.667327,110.7507509
15	Banten 1	Inpari 88 dan 32	45	-6.1054633, 106.2401367
16	Banten 2	Inpari 32	45	-6.2369844, 106.3767816

Note: DAT: Days after transplanting

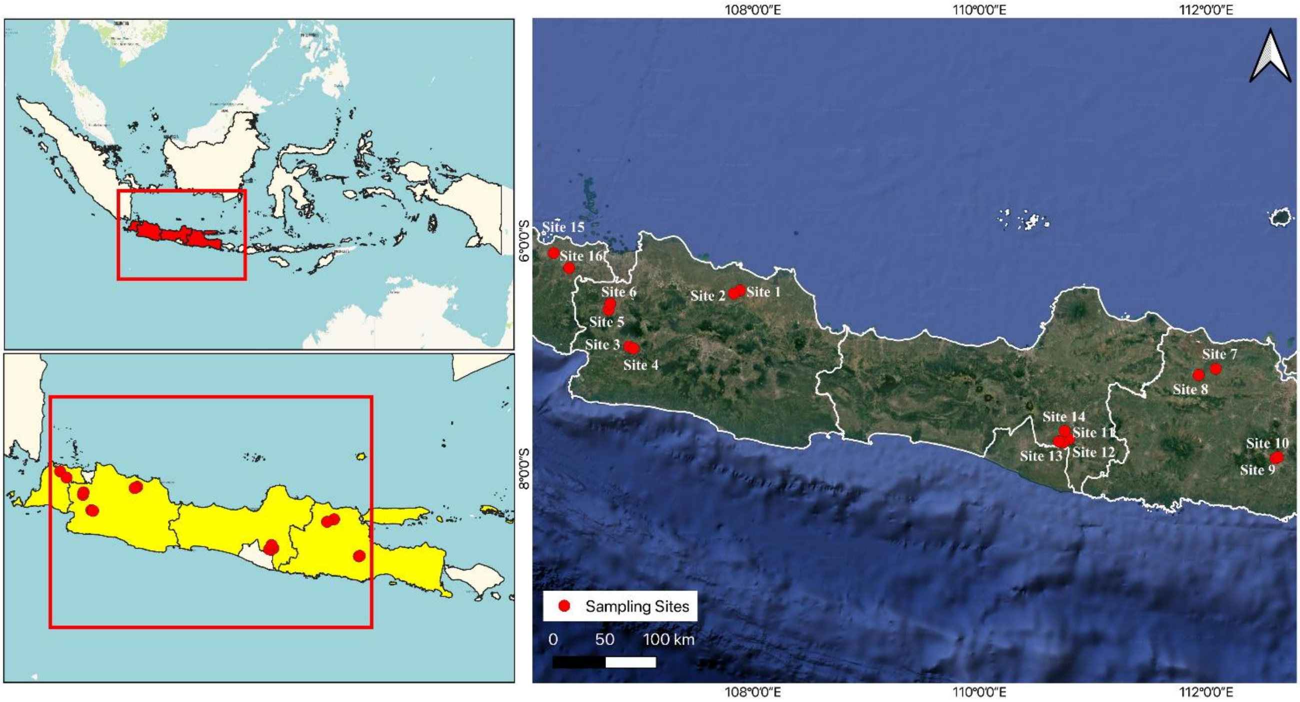

Figure 1. Location of distribution of nematode in Java Island, Indonesia

Procedures

Extraction of nematodes from the root sample

Nematodes were extracted from rice roots using a modified mist chamber method, as described by Hopper et al. (2005). The roots were washed free of adhering soil, cut into pieces approximately 0.5 cm in length, and weighed to obtain 10 g of sample. The roots were put in a funnel with a 0.2 cm diameter sieve, and the funnel was put inside the mist chamber. After 72 hours of misting, the nematode suspension was collected and filtered through a 400-mesh sieve. The suspension was then stored in a 25 mL collection bottle. The samples were kept at 10ºC and were ready for identification.

Extraction of nematodes from the soil sample

Nematode extraction from soil samples was performed using the flotation-centrifugation method described by Caveness and Jensen (1955). After combining a 100 mL soil sample with 900 mL of water and passing it through 20- and 400-mesh sieves, the mixture was transferred into 15 mL Falcon tubes and centrifuged for 5 minutes at 1500×*g*. After discarding the supernatant, the soil sediment was combined with a 40% sugar solution and centrifuged for one minute at 1700×*g*. The supernatant was immediately poured onto a 400-mesh sieve and rinsed. Nematodes retained on the sieve were backwashed into a storage bottle and stored at 10°C.

Nematode population assessment

A total of 15 mL of nematode suspension from each sample was poured into a counting dish and allowed to settle, allowing the nematodes to sink to the bottom of the dish. The extracted nematodes were counted using a hand counter under an OLYMPUS SZ-ST stereomicroscope at up to 40× magnification. Counts were standardized and expressed as the number of individuals per 100 g of soil and per 5 g of roots, respectively.

Preparation of semi-permanent slides

Semi-permanent slides were prepared using a modified Goodey (1973) method, excluding glass wool and paraffin rings. Nematodes were mounted on FAA (formalin-alcohol-acetic acid) solutions, sealed with transparent nail polish, and examined under an OLYMPUS BX51 microscope at 10×–100× magnifications.

Identification based on morphological characters

Nematodes were morphologically identified to the genus level. The identification method involved comparing morphological characteristics with the identification key book, "Plant Parasitic Nematodes in Subtropical and Tropical Agriculture" by Sikora et al. (2018), and relevant scientific publications. At least 10 individuals per genus per sample were examined to confirm diagnostic characters. All identifications were independently cross-checked by three trained nematologists to ensure taxonomic consistency and validated using molecular methods on a subset of samples (data not shown).

Nematode taxonomy and community structure analysis

Nematodes were assigned to trophic groups according to their recognized feeding strategies at the genus level. The classification followed the functional guild system described by Yeates et al. (1999) and Yeates and Bongers (1999), which organizes nematodes into five major categories: plant feeders, bacterivores, fungivores, predators, and omnivores. Since nematodes in this study were identified only to genus, trophic designations were based on feeding habits that are consistently reported for each genus in standard nematode taxonomic and ecological references. All identified genera were categorized into their respective trophic groups, and these classifications were subsequently used in the calculation of biodiversity metrics and ecological indices. The nematode diversity was calculated by the Shannon-Wiener Index (H'), the Evenness Index (E), and Simpson's Dominance Index (D). Statistical analysis was performed using Microsoft Excel. Formulas used to calculate diversity measures analyzed: Shannon-Wiener $(H') = -\sum p_i \ln(p_i)$, Simpson's Dominance $(D) = \Sigma pi^2$, Pielou's Evenness (E): $H'/\ln S$ (Whittaker 1972).

Additional community data were uploaded and analyzed using an online program, NINJA (Nematode Joint Indicator Analysis), to calculate nematode ecological indices, including the maturity (MI), plant parasitic (PPI), enrichment (EI), structure (SI), channel (CI), basal (BI), and compositional metrics, following Sieriebriennikov et al. (2014). The c-p values followed Yeates and Bongers (1999) and Ferris et al. (2001) as implemented in NINJA. One-way ANOVA comparing locations, with index values as the response.

RESULTS AND DISCUSSION

Results

Disease symptoms in rice plants

Disease symptoms in rice plants were observed on the upper part of the plant, including yellowing or chlorotic leaves, chlorosis of leaf tips extending 3-5 cm (Figures 2.B and 2.C) (commonly known as "white tip") caused by *A. besseyi* (Kurniawati and Supramana 2016), and stunted growth. Infected roots showed lesions, shorter roots, and root galls (Figure 2.D). These symptoms were not uniformly distributed throughout fields; the damage they cause occurs in irregular patches. These damaged patches may be small and limited in number, or they may be large and widely distributed throughout the area (Figure 2.A). The same symptoms were reported by Jaabir et al. (2025), paddy infected by plant parasitic nematodes have symptoms such as root lesions, the number of roots decreases, chlorosis, stunted growth, and irregular patch yellowing.

Nematode analysis

A total of five trophic groups have been found in the total of the samples studied: plant feeders, bacterivores, fungivores, predators, and omnivores. The analysis of diversity shows that the nematodes in paddy fields in Java Island are constituted mainly by plant feeders. Very low numbers of fungivore genera were recorded (Figure 3).

In the root and soil samples collected from 16 different rice fields, a total of 26 nematode genera were identified (Table 2). Fourteen genera were identified as free-living, including *Aphelenchus, Chronogaster, Chrysonema, Clavicaudoides, Dorylaimus, Filenchus, Laimydorus, Mesorhabditis, Mononchus, Neotobrilus, Oscheius, Rhabdolaimus, Semitobrilus,* and *Tobrilus.* Plant-feeder nematodes were detected as 12 genera, including *Aphelenchoides, Criconemoides, Mesocriconema, Helicotylenchus, Tylenchorhynchus, Fergusobia, Hirschmanniella, Pratylenchus, Meloidogyne, Rotylenchulus, Psilenchus,* and *Tylenchus.*

Most plant-feeding nematodes were found in roots. In contrast, free-living nematodes are most commonly found in soil samples. However, the plant-feeders' nematodes, specifically *Hirschmanniella* and *Meloidogyne*, were observed to have the highest Mean Abundance (MA), Relative Abundance (RA), and Prominence Value (PV) in the roots. This indicates that they are the primary root-parasitic species, according to their behavior, feeding as an endoparasite on rice root tissues, causing lesions and necrosis. Their dominance suggests dominant plant-parasite interactions that directly impact crop health, particularly in rice fields.

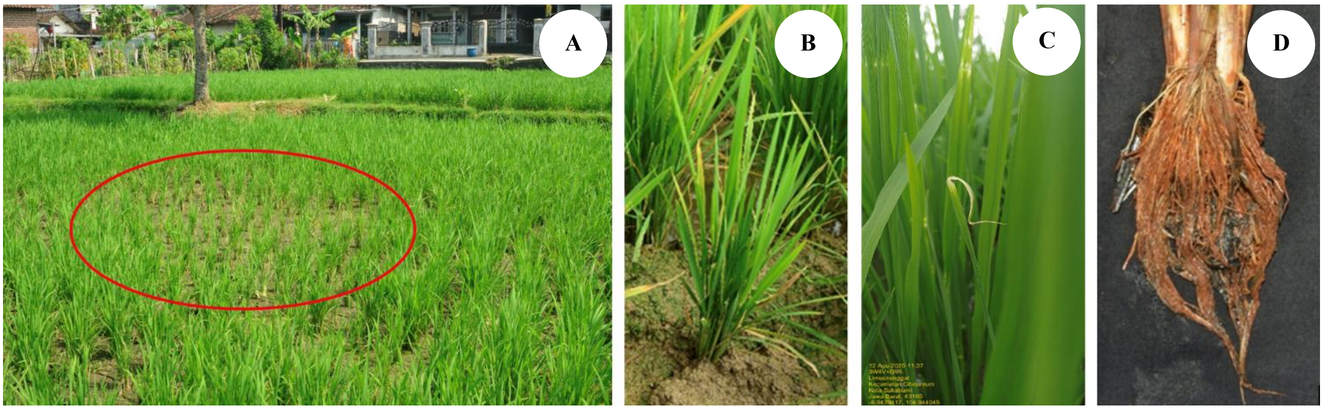

Figure 2. Symptoms of nematode infestation in rice plants. Symptoms on the aerial parts (A, B, and C), while Indicate symptoms on the roots (D)

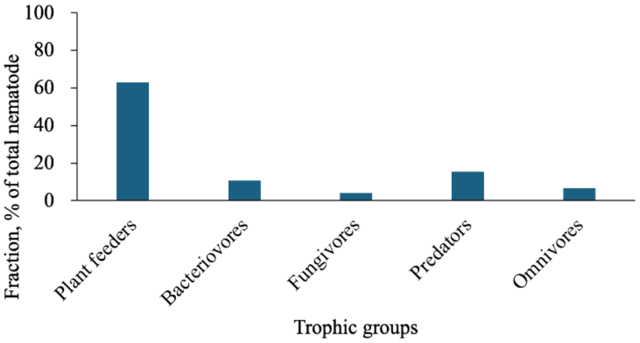

Figure 3. Composition of nematode trophic groups in rice rhizosphere

In contrast, soil samples are dominated by *Helicotylenchus* and *Meloidogyne*. Meanwhile, free-living nematodes were observed in high numbers in the soil, specifically *Neotobrilus* and *Tobrilus.* However, fungivores such as *Aphelenchus* and *Filenchus* occurred rarely, implying that bacterial-based decomposition dominates over fungal pathways in these environments. The soil nematode communities reflect an ecosystem highly influenced by rice monoculture.

The distribution and mean abundance of data show that plant-feeding nematodes were the dominant trophic group across all 16 sites in soil rice fields (Table 3). Among them, *Meloidogyne* had 50.57% prevalence overall and reached its highest abundance at sites 9 and 10, *Aphelenchoides* had 48.28% prevalence overall and reached its highest abundance at site 2, and *Hirschmanniella* had 41.38% prevalence overall and reached its highest abundance at site 7. The widespread distribution of *Helicotylenchus* (40.23%) and *Tylenchorhynchus* (24.14%) further underscores the persistence of ectoparasitic nematodes in the rhizosphere, which feed externally on root epidermal cells and exacerbate plant stress. In contrast, predatory nematodes such as *Tobrilus* had 42.53% prevalence overall and the highest abundance at site 12, while *Neotobrilus* reached its highest abundance at sites 1 and 2. The presence of *Clavicaudoides* and *Mononchus* at fewer sites with low densities suggests limited predator activity in several locations, possibly due to waterlogging or reduced oxygen conditions.

Bacterivorous nematodes, particularly *Chronogaster* (19.54%) and *Mesorhabditis* (16.09%), were well-represented across several sites (notably sites 3, 6, 8, and 12), indicating high bacterial decomposition and organic matter turnover under anaerobic paddy conditions. Omnivores (*Chryrsonema*, *Dorylaimus*, and *Laimydorus*) and fungivores (*Aphelenchus* and *Filenchus*) showed very low abundance and sporadic occurrence, suggesting that fungal-based decomposition and higher trophic-level interactions are less active compared to bacterial pathways in these systems.

The root nematode community was dominated by plant-feeding nematodes, particularly from the Pratylenchidae family, which exhibited both the highest prevalence and abundance across sites (Table 4). *Hirschmanniella* showed the most dominance, with a prevalence of 73.56% and notably high mean abundances at several sites, particularly sites 1 and 6. This genus is a migratory endoparasite that thrives in flooded rice conditions, where it penetrates root cortical tissues, causing lesions, necrosis, and reduced water and nutrient absorption. Its high frequency across nearly all sites confirms its status as the primary root parasite in paddy ecosystems of Java. *Meloidogyne*, another root-infecting nematode, had a prevalence of 55.17%, indicating relatively high abundance in sites 2 and 12.

Other ectoparasitic plant-feeders, including *Helicotylenchus*, *Fergusobia*, and *Tylenchus*, were detected at relatively low frequencies (<11%), indicating a minor contribution to root parasitism. Their low occurrence may also reflect competitive exclusion or ecological dominance by the more aggressive *Hirschmanniella* and *Meloidogyne* populations, which occupy similar feeding niches within the rice rhizosphere. The low prevalence of *Pratylenchus* (4.60%) and *Rotylenchulus* (4.60%) further supports this pattern, suggesting that these genera play only a limited role in the root nematode complex under submerged paddy conditions, as they are typically more abundant in upland rice systems or drier soils where aeration favors their reproduction and host interaction. Predatory nematodes, represented solely by *Tobrilus* (6.9%), appeared in very low abundance and were limited to a few sites, indicating that predatory regulation within root tissues is minimal. Bacterivores, especially *Mesorhabditis* (1.15%) and *Rhabdolaimus* (4.60%), were also detected in small numbers.

Nematode community structure

The diversity of nematodes varies randomly among different trophic groups, as well as with location (Figure 4). When analyzing the feeding type composition of nematode communities on Java Island, plant feeders were found to be the most common. Plant-feeders nematode was the dominant trophic group, with more than 50% of the total nematodes found in all locations: Banten (53.2%), Bogor (74.5%), Bojonegoro (60.5%), Klaten (64.7%), Malang (62.0%), Subang (60.9%), Sukabumi (65.7%), and Sukoharjo (61.8%).

In the composition of plant-feeder nematode communities, migratory endoparasites were the dominant group in all locations (Figure 5). The highest rate was observed in Bogor (79.9%) and the lowest in Sukoharjo (55.1%). Semi-endoparasites were detected at rates of 5.4% in Bojonegoro, 7.6% in Banten, 5.4% in Bogor, 8.0% in Subang, 12.0% in Klaten, 10.5% in Malang, 4.9% in Sukabumi, and 20.3% in Sukoharjo. Ectoparasites were found at 7.40% in Bogor, 11.10% in Subang, 11.30% in Sukabumi, 18.80% in Malang, and 19.90% in Bojonegoro. Epidermal/root hair feeders were prominent in Subang (7.4%), Sukoharjo (9.3%), Bogor (5.5%), Banten (11.9%), and Bojonegoro (9.7%), while sedentary parasites were found in low proportions in Sukabumi (3.1%), Malang (4.4%), and Bojonegoro (4.1%). These results showed that migratory endoparasites were dominant in all locations, while other feeding groups varied depending on the location.

Table 2. Community analysis of nematodes on roots and soil rice fields in Java Island, Indonesia

Family	Genera	C-p class	P-p class	Roots					Soil				
				MA	RA	PD	PV	RF	MA	RA	PD	PV	RF
Plant-feeders													
Aphelenchodidae	*Aphelenchoides*	0	2	0	0	0	0	0	3.34	13.36	6.93	12.46	48.14
Criconematidae	*Criconemoides*	0	3	0.01	0.02	1.00	0.65	1.07	0.16	0.64	1.75	2.37	5.30
Criconematidae	*Mesocriconema*	0	3	0.14	0.22	2.40	3.23	5.75	0	0	0	0	0
Dolichodoridae	*Helicotylenchus*	0	3	0.16	0.26	1.56	5.81	5.00	4.69	18.73	11.66	10.39	73.94
Dolichodoridae	*Tylenchorhynchus*	0	3	0	0	0	0	0	1.53	6.11	6.33	6.23	31.12
Heterodidae	*Meloidogyne*	0	3	23.28	37.94	42.19	30.97	313.36	4.52	18.04	8.93	13.06	63.50
Neotylenchidae	*Fergusobia*	0	2	0.26	0.43	3.83	3.87	10.07	0	0	0	0	0
Pratylenchidae	*Hirschmanniella*	0	3	37.18	60.60	50.55	41.29	433.54	1.89	7.53	4.56	10.68	29.30
Pratylenchidae	*Pratylenchus*	0	3	0.05	0.09	1.25	4.69	2.58	0	0	0	0	0
Rotylenchulidae	*Rotylenchulus*	0	3	0.07	0.11	1.50	4.60	2.58	0	0	0	0	0
Tylenchidae	*Psilenchus*	0	2	0	0	0	0	0	0.03	0.14	1.50	0.59	2.27
Tylenchidae	*Tylenchus*	0	2	0.08	0.13	2.33	1.94	4.33	0.11	0.46	1.67	1.78	4.38
Predators													
Nygolaimidae	*Clavicaudoides*	3	0	0	0	0	0	0	0.13	0.51	1.83	1.78	4.81
Mononchidae	*Mononchus*	4	0	0	0	0	0	0	0.20	0.78	2.43	2.08	6.89
Tobrilidae	*Neotobrilus*	3	0	0	0	0	0	0	2.97	11.85	15.18	5.04	67.09
Tobrilidae	*Semitobrilus*	3	0	0	0	0	0	0	0.46	1.84	2.86	4.15	11.46
Tobrilidae	*Tobrilus*	3	0	0	0	0	0	0	1.84	7.35	4.32	10.98	28.20
Bacteriovores													
Chronogastridae	*Chronogaster*	3	0	0	0	0	0	0	0.60	2.39	3.06	5.04	13.52
Rhabditidae	*Oscheius*	1	0	0	0	0	0	0	0.03	0.14	1.50	0.59	2.27
Rhabdolaimidae	*Rhabdolaimus*	3	0	0.03	0.06	0.75	2.58	1.61	0.16	0.64	2.80	1.48	6.71
Rhabdolaimidae	*Mesorhabditis*	1	0	0.01	0.02	1.00	0.65	1.07	1.22	4.87	7.57	4.15	30.37
Omnivores													
Crateronematidae	*Chrysonema*	4	0	0	0	0	0	0	0.02	0.09	2.00	0.30	2.14
Dorylaimidae	*Dorylaimus*	4	0	0	0	0	0	0	0.11	0.46	3.33	0.89	6.99
Thornenematidae	*Laimydorus*	4	0	0.07	0.11	1.00	3.87	2.63	0.32	1.29	2.55	3.26	9.05
Fungivores													
Aphelenchidae	*Aphelenchus*	2	0	0	0	0	0	0	0.03	0.14	3.00	0.30	3.17
Tylenchidae	*Filenchus*	2	0	0	0	0	0	0	0.01	0.05	1.00	0.30	1.07

Note: MA: Mean Abundance, RA: Relative Abundance, PD: Population Density, PV: Prominence Value, RF: Relative Frequency

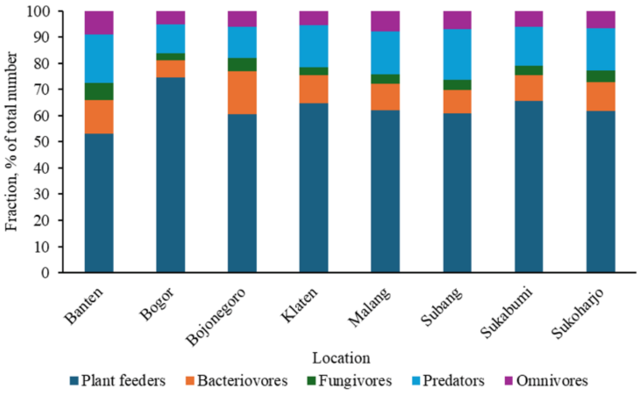

Figure 4. Feeding type composition of nematode assemblage on Java Island, Indonesia

According to the feeding-type composition of free-living nematode communities, predators were the most dominant group (Figure 6). Predators reached the highest rates in almost all districts, particularly in Subang (48.9%). In other locations, especially in Bojonegoro, the rate is the lowest (30.0%). Bacterivores were the second most prevalent group, after predators, with the highest proportions in Bojonegoro (41.5%) and the lowest in Subang (22.6.%). Omnivores and fungivores were detected at lower rates in all locations, with omnivore rates ranging from 15.6% (Bojonegoro and Klaten) to 20.4% (Malang) and fungivore rates between 8.5% (Klaten) and 13.6% (Banten). These results indicated that the predator nematode is dominant in paddy field ecosystems and that environmental conditions influence the distribution of nematode feeding types.

The maturity indices of nematode communities showed relatively small numerical variation among locations (Table 5). The Maturity Index (MI) differed significantly among locations (p: 0.003), with the highest values recorded in Sukabumi (3.07±0.06) and the lowest in Bojonegoro (2.65±0.29). A similar pattern was observed for MI 2-5, which showed highly significant variation ($p<0.001$), with Sukabumi (3.38±0.06) and Malang (3.33±0.02) presenting the highest values. ΣMI also varied strongly among sites ($p<0.001$), ranging from 2.67 to 2.95. The Plant Parasitic Index (PPI) differed significantly (p: 0.016), with Bogor and Klaten exhibiting higher values than Subang. The MI 2-5 focuses on specific maturity groups (cp2-cp5), with all locations having high value (>3), further supporting that its nematode community is composed of more mature types. Meanwhile, ΣMI is the combined index integrates both free-living and plant-parasitic groups to represent total nematode assemblage stability.

Table 3. Prevalence and mean abundance of nematode genera (per 100 g soil) n: 89

Genera	**Prevalence (% of samples)**	**Site**															
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Plant-feeders																	
Aphelenchoides	48.28	8	18	4	11	0	0	0	3	2	10	0	0	0	0	8	0
Criconemoides	9.20	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Helicotylenchus	40.23	2	11	0	0	3	0	0	0	6	3	32	0	3	6	0	0
Tylenchorhynchus	24.14	0	2	0	0	0	0	3	2	10	2	0	0	0	0	0	0
Hirschmanniella	41.38	4	9	0	0	2	1	13	1	1	0	1	2	2	2	0	0
Meloidogyne	50.57	2	2	0	0	7	0	8	1	11	14	2	4	2	7	0	0
Rotylenchulus	3.45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psilenchus	2.30	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tylenchus	6.90	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Predators																	
Clavicaudoides	6.90	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Mononchus	8.05	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Neotobrilus	19.54	31	35	0	0	0	0	0	0	4	8	0	0	0	0	0	0
Semitobrilus	16.09	0	0	0	0	0	0	0	0	0	0	0	0	2	2	5	0
Tobrilus	42.53	0	0	2	3	1	3	0	0	0	0	0	28	2	1	1	0
Bacteriovores																	
Chronogaster	19.54	0	2	1	0	0	0	0	0	0	0	0	6	2	0	1	0
Oscheius	2.30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhabdolaimus	5.75	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Mesorhabditis	16.09	0	0	0	1	0	0	17	1	0	1	0	0	0	0	0	0
Omnivores																	
Chrysonema	1.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Dorylaimus	3.45	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laimydorus	12.64	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0
Fungivores																	
Aphelenchus	1.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Filenchus	1.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 4. Prevalence and mean abundance of nematode genera (per 10 g roots) n: 89

Genera	**Prevalence (% of samples)**	**Site**															
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Plant-feeders																	
Criconemoides	1.15	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Mesocriconema	5.75	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Helicotylenchus	10.34	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Fergusobia	6.90	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
Hirschmanniella	73.56	130	76	44	25	36	103	17	0	29	28	7	22	31	30	13	8
Pratylenchus	4.60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meloidogyne	55.17	3	163	43	15	47	37	19	0	22	1	4	103	2	51	0	0
Rotylenchulus	4.60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tylenchus	3.45	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Predators		0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Tobrilus	6.90	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Bacteriovores		0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhabdolaimus	4.60	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
Mesorhabditis	1.15	130	76	44	25	36	103	17	0	29	28	7	22	31	30	13	8

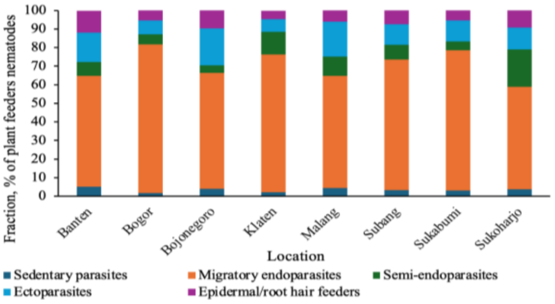

Figure 5. Feeding type composition of plant-feeders nematode assemblage on Java Island, Indonesia

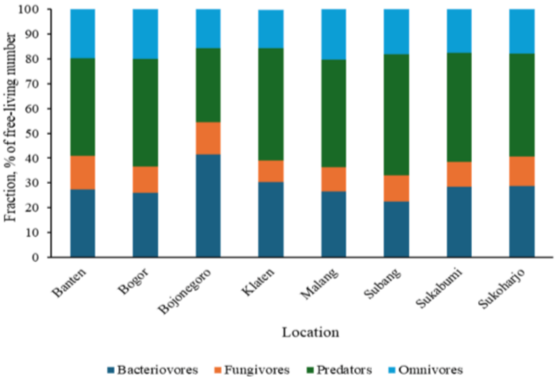

Figure 6. Feeding type composition of the free-living nematode assemblage in all locations

Variation was observed in the CI (p: 0.005), with Bogor (20.51±0.89) and Banten (21.06±1.84) showing the highest values. The BI also differed across locations (p: 0.001), with Bojonegoro (4.52±0.92) and Bogor (4.54±0.27) exhibiting higher values than other sites. In addition, the EI varied (p: 0.008), ranging from 82.62 to 87.50 among locations. The SI showed high differences ($p<0.001$), with Sukabumi and Malang recording the highest values (>96).

The nematode diversity index (H′) ranged from 0.19 to 0.84. The highest values were observed in Malang (0.84) and Sukabumi (0.82), indicating complex nematode communities and stable ecosystems. The lowest value has been established in Banten (0.19), signifying the dominance of specific species due to environmental effects. The evenness (E) score, ranging from 0.10 to 0.32, indicated that the distribution of individuals among species was not yet equilibrated. The dominance index (C) ranged from 0.56 to 0.90 and exhibited a negative relationship with H′, indicating that areas with greater diversity had lower dominance. Malang and Sukabumi exhibited the most stable ecosystem conditions, but Banten and Sukoharjo were susceptible to community disturbances (Figure 7).

The c-p triangle plot prepared using c-p values of nematodes revealed that most of the nematodes in paddy fields in Java Island belonged to the stability axis (c-p 3-5) (Figure 8). All locations, where most of the diversity occurred, are relatively stable and pure but have low nutrients because the points tend to cluster near the left angle, close to the stability axis (c-p 3-5). This data indicates that almost all locations are dominated by nematodes with the K (persister) life strategy, characterized by a long life cycle, sensitivity to disturbance, and a complex food web structure. At the same time, the Bojonegoro samples demonstrated very low levels of enrichment and stress, showing no high organic nutrition input and a dominance of opportunistic bacterivorous nematodes. Bojonegoro is slightly closer to the center of the triangle and exhibits a transition between enriched and stable conditions, possibly due to fluctuations in land management or moderate levels of disturbance.

The food web analysis results for each location indicate variability in the soil ecosystems (Figure 9). Food web analysis, based on the EI and SI, showed that all sites fell into the enriched and structured region of the EI-SI diagram, suggesting active nutrient cycling and relatively intact trophic structure, despite evidence of disturbance in some locations (e.g., low H′ in Banten). These locations exhibited relatively high EI values, indicating active bacterial-mediated decomposition and responsiveness to nutrient enrichment, particularly nitrogen. Their moderate to high SI values further suggested a well-organized soil food web structure supported by the presence of higher trophic groups such as omnivores and predators. No sites were positioned in the degraded quadrant (low EI, low SI), indicating an absence of severely depleted or highly disturbed soil conditions.

Discussion

This study shows that rice fields across Java Island support nematode communities dominated by plant-parasitic groups, particularly *Hirschmanniella* and *Meloidogyne*, with free-living nematodes largely represented by bacterivores. These patterns are consistent with irrigated rice ecosystems, where flooded and nutrient-rich conditions tend to favor bacterial pathways and suppress fungal channels. The lower abundance of fungivores reflects these anaerobic conditions, aligning with established ecological expectations for paddy soils. The increased population of bacterivores suggests that the bacterial-based energy channel plays a more significant role in the decomposition of organic matter within the rice fields (Mikola and Sulkava 2001). In the rice fields, the number of fungi is low under anaerobic conditions because fungi prefer aerobic conditions, which likely reflects the relationships between fungivores and their food resources (Fu et al. 2000).

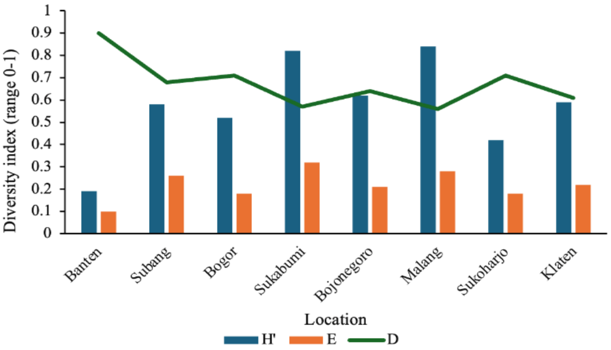

Figure 7. Nematode Shanon-Wiener diversity index (H'), Evenness index (E), and Simpson's dominance index (D) in Java Island, Indonesia

Table 5. The Maturity Index family of nematodes across in Java Island, Indonesia

Index	Banten	Bogor	Bojonegoro	Klaten	Malang	Subang	Sukabumi	Sukoharjo	p-value
MI	3.04±0.01	2.92±0.02	2.65±0.29	2.95±0.01	3.05±0.05	3.06±0.02	3.07±0.06	3.00±0.00	0.003
MI 2-5	3.27±0.02	3.22±0.03	3.19±0.01	3.24±0.03	3.33±0.02	3.26±0.05	3.38±0.06	3.21±0.06	<0.001
ΣMI	2.85±0.04	2.90±0.01	2.67±0.09	2.91±0.02	2.95±0.05	2.88±0.02	2.90±0.01	2.90±0.04	<0.001
PPI	2.63±0.10	2.88±0.02	2.68±0.14	2.88±0.03	2.88±0.09	2.75±0.08	2.79±0.06	2.81±0.10	0.016
CI	21.06±1.84	20.51±0.89	14.60±6.97	14.29±0.01	13.98±0.52	20.00±0.00	14.68±0.68	20.00±0.00	0.005
BI	3.57±0.44	4.54±0.27	4.52±0.92	2.82±0.33	2.54±0.42	2.99±0.49	2.76±0.25	3.25±0.72	0.001
EI	82.62±1.24	82.98±0.61	87.48±5.47	87.50±0.00	87.73±0.40	83.33±0.00	87.20±0.52	83.33±0.00	0.008
SI	95.69±0.56	94.17±0.39	93.00±0.11	96.48±0.52	96.88±0.62	96.48±0.69	96.60±0.36	96.09±1.01	<0.001

Note: MI: Maturity Index. MI 2-5: Maturity Index 2-5, ΣMI: Sigma Maturity Index, PPI: Plant Parasitic Index, CI: Channel Index, BI: Basal Index, EI: Enrichment Index, SI: Structure Index

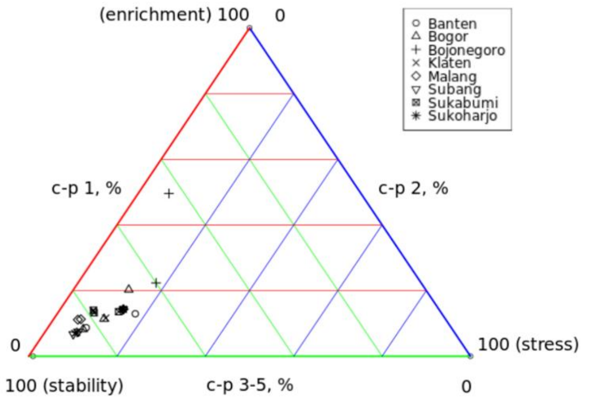

Figure 8. The c-p (colonizer-persister) triangle depicting soil status in Java Island, Indonesia

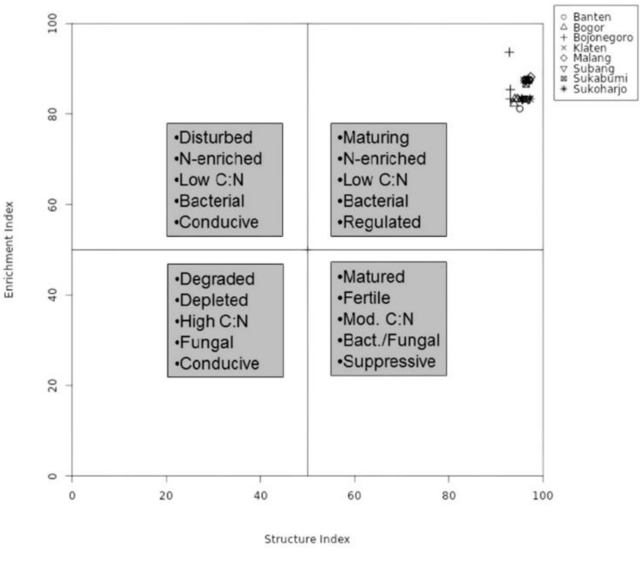

Figure 9. Food web analysis of nematode communities as bioindicators of soil health in Java Island, Indonesia

The maturity and food-web indices demonstrate that the nematode community structure varies considerably across sites, reflecting heterogeneous ecological conditions and distinct levels of disturbance among the regions studied. The differences in the MI and ΣMI (p: 0.003 and p<0.001) suggest that the stability and disturbance level of soil ecosystems differ markedly from one location to another. Higher MI values in regions such as Malang, Subang, and Sukabumi indicate more stable and less disturbed soil ecosystems. In contrast, lower MI values in Bojonegoro reflect a more stressed or disturbed environment. The strong significance of MI 2-5 (p<0.001), which captures changes in nematodes with moderate c-p values, further reinforces evidence of differential ecological pressure across the sites.

The PPI (p: 0.016) indicates variation in plant-parasitic nematode dominance between locations. Higher PPI values in Bogor and Klaten suggest greater parasitic pressure on crops, likely influenced by differences in host plant availability, cropping systems, and local agroecological conditions. The CI (p: 0.005) highlights differences in organic matter decomposition pathways (fungal vs. bacterial) among locations. High CI values in Banten and Bogor reflect a fungal-dominated decomposition channel, whereas lower CI values in Malang and Klaten indicate a shift toward bacterial-driven decomposition. These differences are closely linked to moisture levels, aeration, and organic matter inputs unique to each location. The BI (p: 0.001) demonstrates that the degree of ecological stress or disturbance differs across locations. Higher BI values (as seen in Bojonegoro and Bogor) suggest a dominance of stress-tolerant nematode groups and possible environmental degradation or anthropogenic disturbances. The EI was consistently high across all regions, indicating substantial microbial turnover and responsiveness of enrichment opportunists. Such patterns are commonly observed in fertilizer-dependent rice systems, though here they should be viewed as inferred ecological responses, not direct measurements of nutrient dynamics. Similarly, the generally high SI suggests that top-down regulatory groups (e.g., omnivores, predators) persist despite disturbance. This combination, high EI with moderately high SI, supports the interpretation of rice fields as productive, enriched, and reasonably structured ecosystems, consistent with patterns reported in other tropical rice studies. This pattern aligns with previous findings that nitrogen availability strongly stimulates bacterial growth, subsequently increasing bacterivorous nematode populations and accelerating nutrient turnover (Ferris et al. 2001; Li et al. 2022).

The nematode diversity observed reflects substantial variation in soil ecosystem stability on Java Island. High H′ values in Malang and Sukabumi indicate complex nematode assemblages with multiple trophic roles, a hallmark of mature and stable systems as described by Bongers (1990). In contrast, extremely low diversity and high dominance in Banten suggest a community strongly shaped by disturbance, where a few r-strategist taxa proliferate. The c-p triangle further supports this interpretation: most sites clustered near the stability axis (c-p 3-5), indicating communities dominated by persister groups that require relatively stable conditions and longer life cycles, whereas Bojonegoro occupied a transitional position, suggesting fluctuating conditions or moderate levels of disturbance. Food-web analysis using the EI-SI framework (Ferris et al. 2001) aligned with these findings. All locations fell within the enriched and structured quadrant, reflecting active nutrient cycling driven largely by bacterial decomposition (high EI) while still maintaining trophic integrity supported by omnivores and predators (high SI). Significantly, no location fell into the degraded (low EI-low SI) quadrant, indicating the absence of severely depleted soil food webs. Taken together, the EI-SI patterns combined with the dominance of c-p 3-5 groups indicate that Java's rice fields function as enriched yet relatively structured systems, shaped by recurrent nutrient inputs but buffered by hydrological stability that maintains higher trophic groups. These patterns are consistent with the ecological theory that flooded agroecosystems can exhibit moderate disturbance signatures yet retain resilient and functional nematode communities.

The patterns observed across Java's rice fields reflect broadly comparable ecological conditions, shaped by similar cultivation practices and irrigation regimes typical of flooded rice agriculture. Some locations exhibit signs of greater ecological balance or stress, but inferences regarding management or soil quality should be interpreted with caution, given the absence of direct measurements. These findings provide a baseline for future work incorporating soil chemistry, organic matter inputs, hydrological metrics, and management records to more definitively test the mechanisms underlying nematode community variation.

The combined ecological indices collectively demonstrate that while Java's rice systems are shaped by similar hydrological and management practices, specific regions, particularly Bogor, Malang, and Sukabumi, exhibit more stable and mature soil ecosystems. In contrast, Banten and Bojonegoro emerge as areas of concern, showing clear indicators of disturbance and reduced soil ecological quality. These site-specific insights are highly relevant for designing region-tailored soil health interventions, such as adjusted fertilizer regimes, organic matter enhancement, improved water management, and strategic crop rotation, to optimize nematode community balance and sustain long-term rice productivity.

In conclusion, rice fields across Java Island are characterized by nematode communities dominated by plant-parasitic genera, particularly *Hirschmanniella* and *Meloidogyne*, and by bacterivore-driven free-living groups indicative of strong bacterial decomposition pathways. This study provides an integrated assessment of plant-parasitic and free-living nematode assemblages across major rice-growing regions of Java, revealing significant ecological heterogeneity among sites. Plant-parasitic genera consistently dominated flooded rice ecosystems, while free-living communities were primarily bacterivorous, reflecting anaerobic, nutrient-rich soil conditions. Nematode-derived indices showed strong regional contrasts in food-web maturity, enrichment dynamics, and ecological stress, with Malang, Subang, and Sukoharjo representing relatively stable systems, and Banten and Bojonegoro showing clear disturbance signatures. Strengthening soil food-web resilience in these regions is likely to reduce plant-parasitic nematode pressure and support more sustainable rice production across Java.

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