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RESEARCH ARTICLE

Prevalence and abundance of plant-parasitic nematodes in New Zealand maize fields: effects of territory, soil orders, crop stage, and sampling time

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ABSTRACT

Plant-parasitic nematodes (PPNs) are significant agricultural pests that can reduce maize yields. This study examines the prevalence, abundance, and diversity of PPNs in New Zealand maize fields, focusing on the effects of territory, soil orders, crop stages, and sampling times. Seven PPN genera were identified: *Pratylenchus* spp. (root-lesion), *Helicotylenchus* spp. (spiral), *Meloidogyne* spp. (root-knot), *Heterodera* spp. (cyst), *Paratylenchus* spp. (pin), *Criconemella* spp. (ring), and *Tylenchus* spp. PPNs were present in 98% of the samples, with *Pratylenchus* spp. being the most prevalent (91%), followed by *Helicotylenchus* spp. (38%). Compared to Waikato and Manawatu-Whanganui, Canterbury had the highest nematode populations, particularly of *Pratylenchus* spp. and *Helicotylenchus* spp. Brown and pallic soils supported higher PPN abundances. Sampling during the maize harvesting stage and late autumn resulted in the highest nematode populations and diversity indices. *Pratylenchus* spp. populations often exceeded the economic threshold of 500 *Pratylenchus* kg^{-1} of soil, suggesting a significant threat to maize yield in New Zealand. The findings highlight the need for further research to assess the impact of *Pratylenchus* spp. on maize yield and to develop effective management practices for maize cultivation in the country.

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Introduction

Maize (*Zea mays* L.) is an economically important cereal crop grown worldwide either for human consumption or animal feeds (Millner and Roskruge 2013). In New Zealand, the annual production of maize has fluctuated over the last 10 years between 175,000 and 270,000 metric tons (MT) (Robere and Levin 2023) with forecasts of an increase in coming years (Granwal 2022). Waikato, Gisborne, Bay of Plenty,

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Manawatu-Whanganui, and Hawke's Bay are the top five regions cultivating maize for grain in New Zealand with an area of more than 2500 ha (Anonymous 2020, 2023; Stats 2020; FAR 2022). The average production of these five regions combined was reported to be above 20,000 MT (Stats 2020). In New Zealand, over 45 maize hybrids, developed by different seed producers in New Zealand, have been used in various regions to overcome abiotic and biotic stress issues. None of these hybrids grown in New Zealand have been tested against PPNs (Corsonmaize 2023; Pioneer 2023).

Plant-parasitic nematodes are soil-born microscopic worms known to infest most cultivated crops and are responsible for 14–20% of global annual yield losses (Jung and Wyss 1999; Mesa-Valle et al. 2020). These losses are estimated to be over USD 358 billion (Abd-Elgawad and Askary 2015; Khanal and Land 2023). The yield losses in maize due to PPNs are often mistakenly attributed to other biotic and abiotic factors like nutrient deficiencies. Thus, these yield losses caused by PPN often remain overlooked or are incorrectly identified (Norton 1983; Tylka et al. 2011). A recent study conducted in the United States of America (USA) and Canada indicates that PPNs are among the top ten yield-limiting factors involved in maize cultivation (Mueller et al. 2020). Over 60 PPN species are known to cause damage to maize (Norton 1983). Of these, around 10–12 PPN genera, including *Anguina* spp., *Criconemella* spp., *Ditylenchus* spp., *Helicotylenchus* spp., *Hirschmanniella* spp., *Hoplolaimus* spp., *Meloidogyne* spp., *Pratylenchus* spp., *Radopholus* spp., *Rotylenchus* spp., *Trichodorus* spp., *Tylenchulus* spp., and *Xiphinema* spp. were associated with maize fields (Koenning et al. 1999; Nicol et al. 2011). *Meloidogyne* spp. (root-knot nematode; RKN), and *Pratylenchus* spp. (root-lesion nematode; RLN) cause the most substantial damage (Sikora et al. 2005). Root-lesion nematode species, such as *Pratylenchus hexincisus* has been reported to cause 0.6 MT ha^{-1} yield losses in dryland maize, and *P. scribneri* was estimated to cause yield losses of 0.25 MT ha^{-1} in irrigated maize fields (Smolik and Evenson 1987). Mueller et al. (2016) estimated maize yield losses of over 7.47 million MT due to PPNs in the USA and Canada although maize damage is dependent on the PPN genera present and their abundance within the location (Norton 1983; Koenning et al. 1999; Tylka et al. 2011; Niblack 2014; Simon et al. 2018).

In New Zealand, most of the nematode-related studies were done before the 1990s. However, during the last three decades, inadequate research has been undertaken on PPNs associated with crops, with limited emphasis on maize (Watson and Hill 1985; Knight 1996; Knight et al. 1997). No information about PPN population abundance, distribution, and pathological effects against maize in New Zealand is available. Hence, appropriate evaluation of the prevalence and population abundance of PPN is essential for developing effective management practices to control PPNs in maize fields in New Zealand. It is therefore hypothesised that the prevalence and population density of PPN in New Zealand maize fields exhibit regional variations in species composition and distribution. To test this hypothesis, the objectives were to; (1) determine the prevalence and abundance of major PPN genera in maize fields across New Zealand; (2) analyse the effects of different regions (Canterbury, Waikato, and Manawatu-Whanganui) on nematode populations; (3) investigate the influences of different soil orders, crop stages, and sampling times on PPN populations and diversity.

Materials and methods

Sampling sites selection and survey in maize fields of New Zealand

Soil sampling in maize-growing regions of New Zealand was done between June and November (2022). A total of 384 composite soil samples were collected from 25 fields of maize growing for grains, in three regions: Canterbury (CaR), Waikato (WaR), and Manawatu-Whanganui (MWR) distributed in both the North and South Islands of New Zealand. Locations of the selected fields including the districts, and the number of samples are shown in the Supplementary Information, Table S1. Depending on the size of the sampling field, each field was divided into either 2 or 3 blocks, and composite samples were collected with a minimum of 10 samples and a maximum of 25 samples per field. In the two-blocked fields, 10–16 samples (a double-zigzag pattern) were collected. In contrast, 18–25 samples were collected in a triple-zigzag pattern in the three-blocked fields to cover the entire field (Supplementary Information, Figure S1). At each sampling point, 15 soil cores at a depth of 30 cm were collected randomly using a 2 cm diameter soil sampler (OAKFIELD Apparatus, USA) within a 4 m radius from a sample centre point, averaging around 750 g of soil. Sampling sites and individual sample points within a field were georeferenced using a global positioning system (GPS) unit and were used to generate maps indicating nematode abundance using ArcMap pro 10.8.1 software.

Nematode extraction from soil

The sieving-centrifugal-sugar flotation method described by Jenkins (1964) was used to extract nematodes from the soil samples. Briefly, 100 g of soil from the composite sample was placed in a 9 L plastic bucket and mixed thoroughly with 1 L of tap water. After manually mixing and stirring for at least 30–45 s, the mixture was allowed to settle for 30 s before transferring to nested sieves of aperture 150-µm on top of 38-µm (Glenammer, UK). This process was repeated three times for each sample to recover most nematodes in the soil. The deposit in the bottom sieve (38-µm aperture) was transferred into 50 mL centrifuge tubes and centrifuged at 1750 rpm (576 g - RCF-relative centrifugal force) for 5 min. The supernatant was removed carefully, and the pellet was resuspended and mixed thoroughly with 45% (w/v) sucrose solution (454 g of sugar L^{-1} tap water) before further centrifugation for 1 min at 576 g was done using a centrifuge (Thermo scientific-Multifuge X1R, Germany). The resultant supernatant was transferred to a 38-µm aperture sieve and subsequently washed carefully with tap water dispensed from a wash bottle, with extracted nematodes collected into a 50 mL sterile specimen bottle with a lid. Samples were kept at 4°C until morphologically identified (Kularathna et al. 2019). Identification was performed using an inverted compound light microscope (Olympus CKX53, Japan) at ×40 and/or ×100 magnification and the PPN were identified at the genus level based on morphological descriptions (Fortuner 1988; Mai et al. 1996). Non-PPN were quantified collectively, but they were not identified at the genus level.

Statistical analysis

Genus-specific prevalence data was recorded as the presence (1) or absence (0) of each genus at each survey site and were mapped. Nematode prevalence percentage was

calculated using the following formula:

$$\text{Prevalence } \% = \frac{\text{Number of samples positive for a nematodes genus}}{\text{Total number of samples}}$$

The abundance data for nematodes was checked for normality using the Shapiro–Wilk test. The results indicated that the data were not normally distributed ($p < 0.05$), even after applying log and square root transformations. A non-parametric Kruskal-Wallis's test followed by a Dunn post hoc test was done in R v. 4.3.1 (Development Core Team R 2013) using the packages of 'rcompanion' (Mangiafico 2024), 'FSA' (Ogle et al. 2023), and 'PMCMRplus' (Pohlert 2023). Graphical representation was done using the R packages 'ggplot2' and 'gridExtra' (Wickham 2016; Auguie 2017).

Nematode abundance and diversity indices from the survey were analysed with the set of categorical variables including region, districts, fields, crop stage at sampling and time of sampling, and soil orders of the sampled fields (obtained from https://smap.landcareresearch.co.nz). The crop stages in fields were categorised as the 'maize seedling' stage, 'maize stubbles' just after the maize harvesting stage, 'ploughed' after harvesting, and 'grass' subsequent maize cultivation. The sampling time points are categorised as June/July, August/September, and October/November.

Results

Prevalence of plant-parasitic nematodes in maize fields of New Zealand

Seven PPN genera were identified, including RLN (*Pratylenchus* spp.), spiral (*Helicotylenchus* spp.), RKN (*Meloidogyne* spp.), cyst (*Heterodera* spp.), pin (*Paratylenchus* spp.), ring (*Criconemella* spp.), and *Tylenchus* spp. Non-PPN was detected in all 384 samples, with at least one PPN genus found in 378 samples, representing a 98% prevalence of PPNs across New Zealand maize fields. *Pratylenchus* spp. was the most prevalent genus at 91%, followed by *Helicotylenchus* spp. at 38%, other genera had lower prevalence percentages (Figure 1A). In each sampled region, RLN dominated, representing 95% in Manawatu-Whanganui (MWR), 94% in Canterbury (CaR), and 85% in Waikato (WaR). Spiral was the second most prevalent genus in all regions, with prevalence rates of 45% in WaR, 35% in CaR, and 31% in MWR. *Meloidogyne* and *Paratylenchus* spp. were prevalent only in CaR at 31% and 6%, respectively, while *Criconemella* spp. was recorded only in WaR at 2% (Figure 1B–D).

Pratylenchus spp. prevalence varied across districts. Districts like Ashburton in CaR and Otorohanga, Waikato, and Waipa in WaR reported 100% prevalence, while Matamata-Piako in WaR had the lowest prevalence at 74%. Field-level analysis (Figure 2) revealed that 15 out of 25 sampled fields showed a 100% prevalence of RLN. The prevalence of other PPN genera varied across fields. Spiral nematodes were prevalent in 17 of 25 fields, while *Tylenchus* and cyst nematodes were found in select fields across all regions (Supplementary Information, Table S2). The findings highlight the widespread distribution of PPNs in New Zealand maize fields, with variations in genus prevalence across regions and districts.

Figure 1. Plant-parasitic nematodes prevalence in maize fields of New Zealand. **A,** in New Zealand, **B,** in the Canterbury region, **C,** in the Manawatu-Whanganui region, and **D,** in the Waikato region. Cyst- Heterodera spp., RLN- *Pratylenchus* spp., Pin- *Paratylenchus* spp., Ring- *Criconemella* spp., RKN- *Meloidogyne* spp., Spiral- *Helicotylenchus* spp., and Tylen- *Tylenchus* spp. Numbers in each data point indicate the prevalence percentages (number of samples detected with the nematode genus out of the total samples in an area). Total soil samples in New Zealand-384, Canterbury-176, Manawatu-Whanganui-81, and Waikato-127.

Abundance and diversity indices of plant-parasitic nematodes in maize fields of New Zealand

Regional comparison

Non-PPN and PPN abundances significantly differed across CaR, WaR, and MWR regions (Figure 3A, B; $x^2_{(2)} = 63.05$, $p < 0.001$ for non-PPN; $x^2_{(2)} = 59.52$, $p < 0.001$ for PPN). The CaR exhibited higher nematode populations, with non-PPN at 9702 nematodes kg^{-1} of soil, compared to WaR (5641 kg^{-1}) and MWR (5452 kg^{-1}). Similarly, PPN populations were highest in CaR (2292 kg^{-1}), followed by WaR (1339 kg^{-1}) and MWR (736 kg^{-1}). Abundances of RLN and spiral nematodes significantly differed between regions (Figure 3C, D; $x^2_{(2)} = 31.71$, $p < 0.001$ for RLN; $x^2_{(2)} = 6.10$, $p = 0.047$ for spiral), with CaR maize fields exhibiting higher abundances of RLN and spiral nematodes than WaR and MWR. The Simpson diversity index (1-D) and evenness (E) differed significantly between the regions (Figure 4A, B; $x^2_{(2)} = 6.25$, $p = 0.044$ for 1-D; $x^2_{(2)} = 7.49$, $p = 0.024$ for E). Both diversity indices were higher in CaR than in WaR and MWR. The

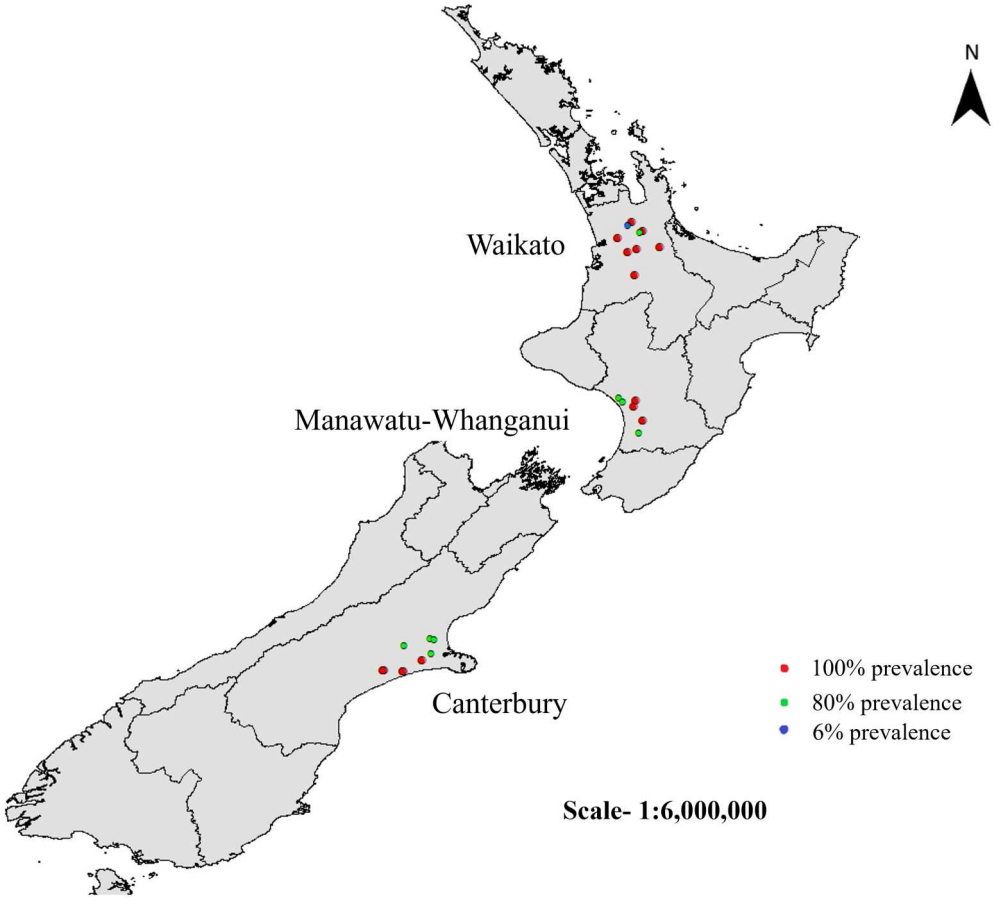

Figure 2. Root-lesion nematode (*Pratylenchus* spp.) prevalence in each sampled maize field in New Zealand. Red dots indicate 100%, green dots indicate 85-95%, and a blue dot indicates 6% of samples are detected for at least one *Pratylenchus* spp. nematode of a particular site (prevalence percentages of a site).

number of PPN genera in the maize fields between the three regions differed significantly (Figure 4C; $x^2_{(2)} = 12.74$, $p = 0.002$).

District-level comparison

The abundance of non-PPN and PPN differed significantly between the eight districts (Figure 5A, B; $x^2_{(7)} = 86.15$, $p < 0.001$ for non-PPN; $x^2_{(7)} = 170.25$, $p < 0.001$ for PPN). The fields in Otorohanga and Waipa districts were analysed together because only one field was sampled in Otorohanga, and the Waipa fields are located nearby. The district of Ashburton (CaR) had a higher mean abundance of non-PPN at 12071 kg^{-1} of soil, while the Manawatu (MWR) had the lowest at 3571 kg^{-1} of soil. Selwyn (CaR) had a higher abundance of PPN at 3675 kg^{-1} of soil. Waimakariri (CaR) and Manawatu (MWR) districts showed substantially lower PPN abundances of 331 and 303 kg^{-1} of soil, respectively. The population of RLN and spiral nematodes varied significantly between the districts (Figure 5C, D; $x^2_{(7)} = 95.56$, $p < 0.001$ for RLN; $x^2_{(7)} = 141.33$,

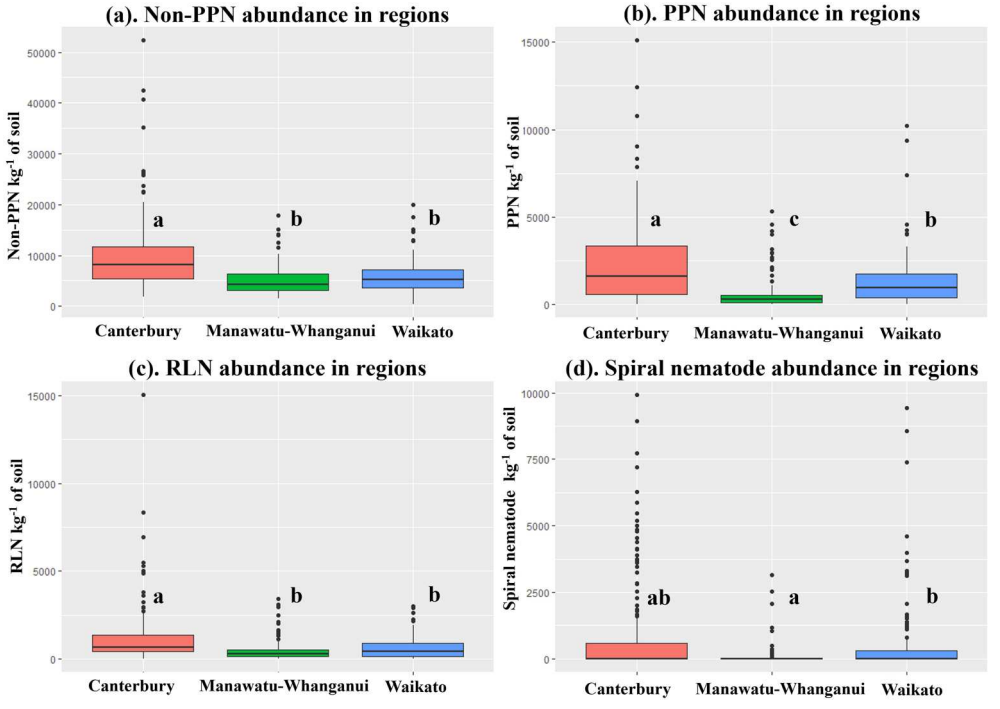

Figure 3. Nematode abundance in maize fields of three regions in New Zealand, **A,** Non-plant-parasitic nematodes abundance, **B,** Plant-parasitic nematode abundance, **C,** Root-lesion nematodes abundance, and **D,** Spiral nematode abundance presented as boxplots (median; 25 and 75% quartiles; max, min of 1.5× interquartile range and outliers). Non-PPN- non-plant-parasitic nematodes, PPN- plant-parasitic nematodes, and RLN-root-lesion nematodes, within each figure, statistically significant differences are indicated by different lettering in data points ($p < 0.05$).

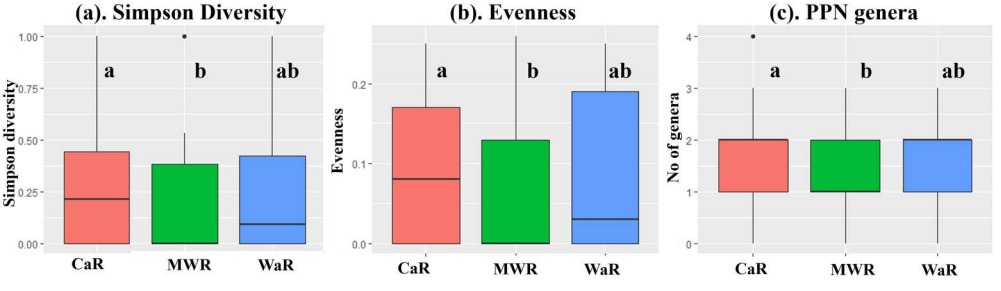

Figure 4. Diversity indices and the number of genera of plant-parasitic nematodes in three regions of New Zealand, **A,** Simpson biodiversity index, **B,** Evenness, and **C,** The number of plant-parasitic nematodes genera presented as boxplots (median; 25 and 75% quartiles; max, min of 1.5× interquartile range and outliers). CaR- Canterbury region, MWR- Manawatu-Whanganui region, and WaR- Waikato region. Within each figure, statistically significant differences are indicated by different lettering in data points ($p < 0.05$).

$p < 0.001$ for spiral). Ashburton had higher RLN populations (1700 kg^{-1}), while the Manawatu district had the lowest population (293 kg^{-1}). Selwyn had a greater mean abundance of the spiral nematode at 2392 kg^{-1} of soil than any other district surveyed, and

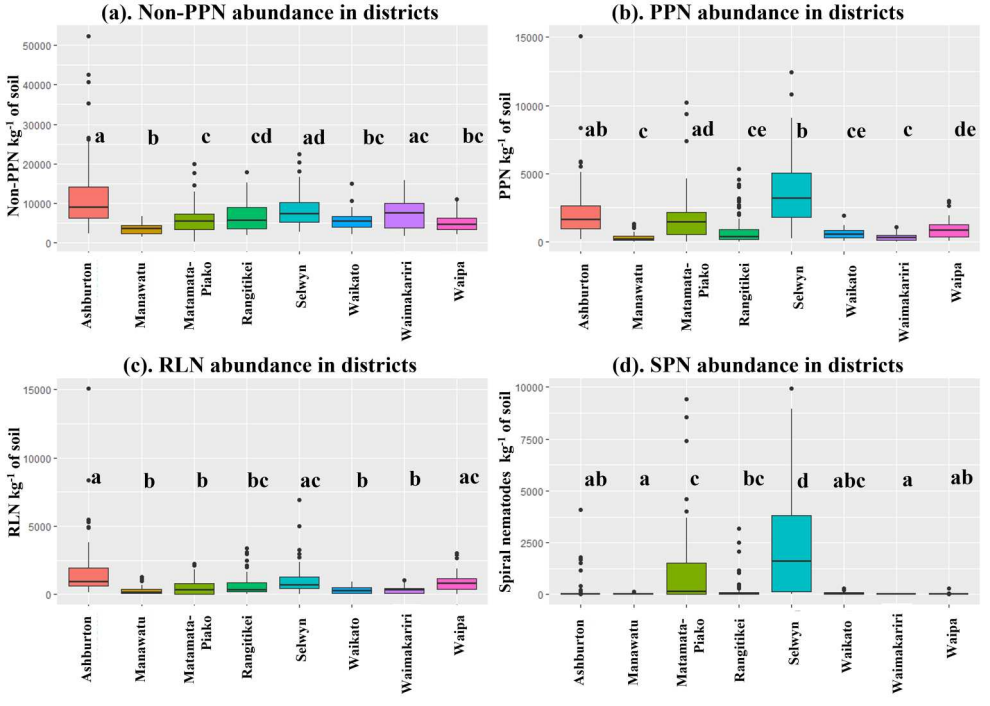

Figure 5. Comparative nematode abundance in maize fields in districts of New Zealand, **A,** Non-plant-parasitic nematodes abundance, **B,** Plant-parasitic nematode abundances, **C,** Root-lesion nematodes abundance, and **D,** Spiral nematode abundance presented as boxplots (median; 25 and 75% quartiles; max, min of 1.5× interquartile range and outliers). Non-PPN- non-plant-parasitic nematodes, PPN-plant-parasitic nematodes, RLN-root-lesion nematodes, and SPN-spiral nematodes; Within each figure, statistically significant differences are indicated by different lettering in data points ($p < 0.05$).

no spiral nematodes were detected in Waimakariri. Diversity indices varied significantly between the districts (Figure 6A, B; $x^2_{(7)} = 80.60$, $p < 0.001$ for 1-D; $x^2_{(7)} = 107.48$, $p < 0.001$ for E). Waikato had the highest mean for both indices at 0.399 and 0.165, respectively. The number of PPN genera varied significantly between the districts ($x^2_{(7)} = 138.76$, $p < 0.001$). Waikato (2.5) and Selwyn (2.3) had higher mean PPN genera than all districts, while the lowest was in the Waimakariri district (0.87, Figure 6C). District-level nematode abundance and diversity data are summarised in supplementary information in Table S3.

Field-level comparison

The results revealed differences in abundance between maize fields (Figure 7A–D). Non-PPN populations differed significantly between maize fields ($x^2_{(23)} = 192.33$, $p < 0.001$), ranging from 2750 to around 20,000 kg^{-1} of soil, with Dorie having the highest population at 19,775 kg^{-1} of soil and the lowest mean abundance at Tahuna (2778 kg^{-1} of soil). The PPN population differed significantly between maize fields ($x^2_{(23)} = 241.92$, $p < 0.001$), ranging from 150 to 4500 kg^{-1} of soil in the 24 fields that were sampled. The PPN mean abundance was higher at the Lincoln maize field of Selwyn district in CaR at 4503 kg^{-1} of soil and the lowest PPN

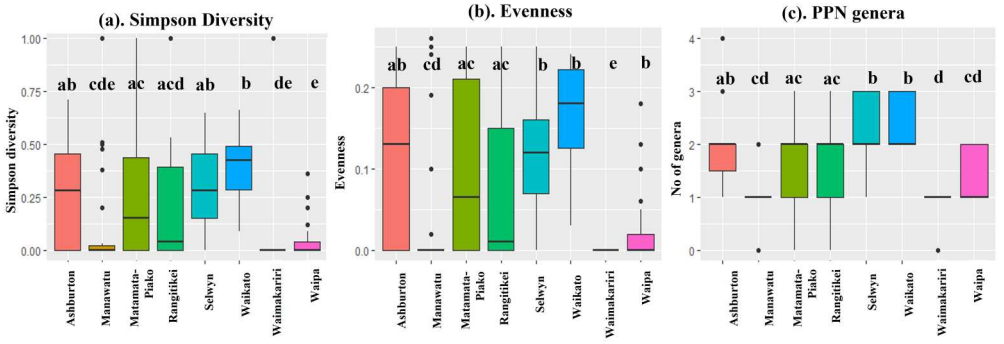

Figure 6. Diversity indices and the number of plant-parasitic nematodes genera in districts of New Zealand, **A,** Simpson biodiversity index, **B,** Evenness, and **C,** The number of plant-parasitic nematodes genera presented as boxplots (median; 25 and 75% quartiles; max, min of 1.5× interquartile range and outliers). Within each figure, statistically significant differences are indicated by different lettering in data points ($p < 0.05$).

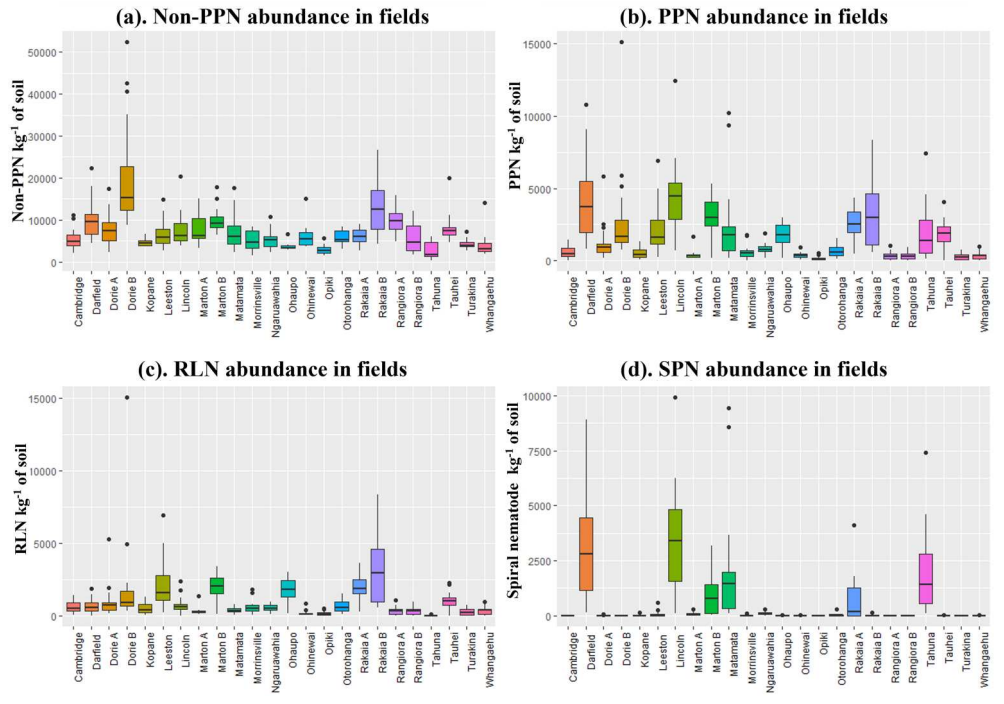

Figure 7. Nematode abundance in maize fields in New Zealand, **A,** Non-plant-parasitic nematodes abundance, **B,** Plant-parasitic nematode abundance, **C,** Root-lesion nematodes abundance, **D,** Spiral nematode abundance presented as boxplots (median; 25 and 75% quartiles; max, min of 1.5× interquartile range and outliers). Non-PPN- Non-plant-parasitic nematodes, PPN- Plant-parasitic nematodes, RLN-root-lesion nematodes, and SPN-spiral nematodes

abundance was recorded in the Opiki maize field of Manawatu district in MWR at 150 kg^{-1} of soil. Over 50% of the sampled fields showed PPN abundance exceeding 1000 PPN kg^{-1} of soil.

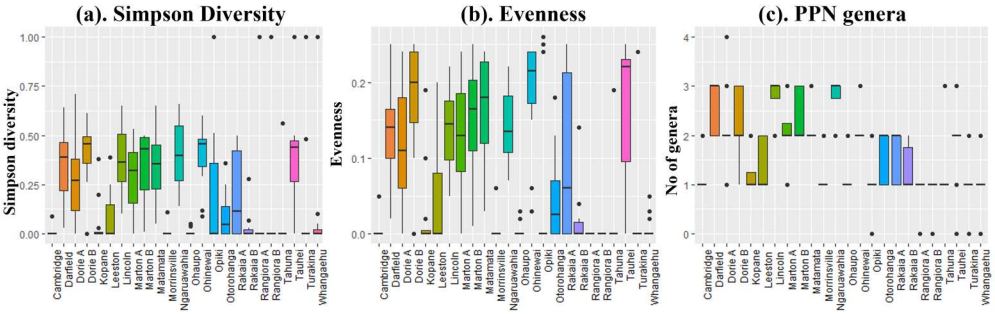

Figure 8. Diversity indices and the number of genera of Plant-parasitic nematodes between maize fields of New Zealand, **A,** Simpson biodiversity index, **B,** Evenness, and **C,** The number of plant-parasitic nematode genera presented as boxplots (median; 25 and 75% quartiles; max, min of 1.5× interquartile range and outliers).

The RLN mean abundance differed significantly between maize fields ($x^2_{(23)} = 202.77$, $p < 0.001$) and it was higher in the Rakaia-B, in Ashburton, CaR with 3210 kg^{-1} of soil, and the lowest in Tahuna (Matamata-Piako, WaR) with 6 kg^{-1} of soil. The mean RLN abundance was greater than 1000 kg^{-1} of soil in 30% of the sampled fields. Greater than 500 RLN kg^{-1} of soil was observed in 63% of the fields. Spiral nematode abundance differed significantly between maize fields ($x^2_{(23)} = 307.15$, $p < 0.001$) and it was higher in Lincoln with an average of 3432 kg^{-1} of soil followed by Darfield (3101), Matamata (2081), Tahuna (1928), and Marton B (1017) fields having numbers above 1000 kg^{-1} of soil. Spiral nematode population was not detected in Dorie B, Rangiora A & B, Opiki, Turakina, and Cambridge fields. Nematode abundance varied between each sampling point within a field and this trend was observed in most of the field. For instance, Figure 9 shows the RLN abundance in the Dorie field, where the nematode abundance was below 500 RLN kg^{-1} of soil in 7 sampling points, while 14 sampling points had 500–1000 RLN kg^{-1} of soil and 4 sampling points had above 1000 RLN kg^{-1} of soil. Diversity indices differed significantly between maize fields (Figure 8A–C); 1-D ($x^2_{(23)} = 190.74$, $p < 0.001$); E ($x^2_{(23)} = 229.18$, $p < 0.001$); and PPN genera ($x^2_{(23)} = 253.42$, $p < 0.001$). Field-level nematode abundance and diversity data are summarised in supplementary information, Table S4.

Effect of soil orders on nematode population in maize fields

The abundance of non-PPN and PPN between the soil orders differed significantly (Figure 10A, B; $x^2_{(9)} = 128.41$, $p < 0.001$ for non-PPN; $x^2_{(9)} = 132.07$, $p < 0.001$ for PPN). The population of the non-PPN was substantially higher in soil order pallic with 11,285 kg^{-1} of soil and the lowest was recorded in organic soil order at 2778 kg^{-1} of soil. The PPN population was higher in brown (2842) and pallic (2564) soil orders than in others. Organic (1939), recent (1745), ultic (1351), allophanic (1266), and granular (1024) orders were recorded with PPNs above 1000 PPN kg^{-1} of soil. The lowest PPN population at 532 and 360 kg^{-1} of soil were reported in soil orders raw and melanic, respectively.

The abundance of the RLN and spiral nematodes between soil orders differed significantly (Figure 10C, D; $x^2_{(9)} = 151.84$, $p < 0.001$ for RLN; $x^2_{(9)} = 86.94$, $p < 0.001$ for spiral).

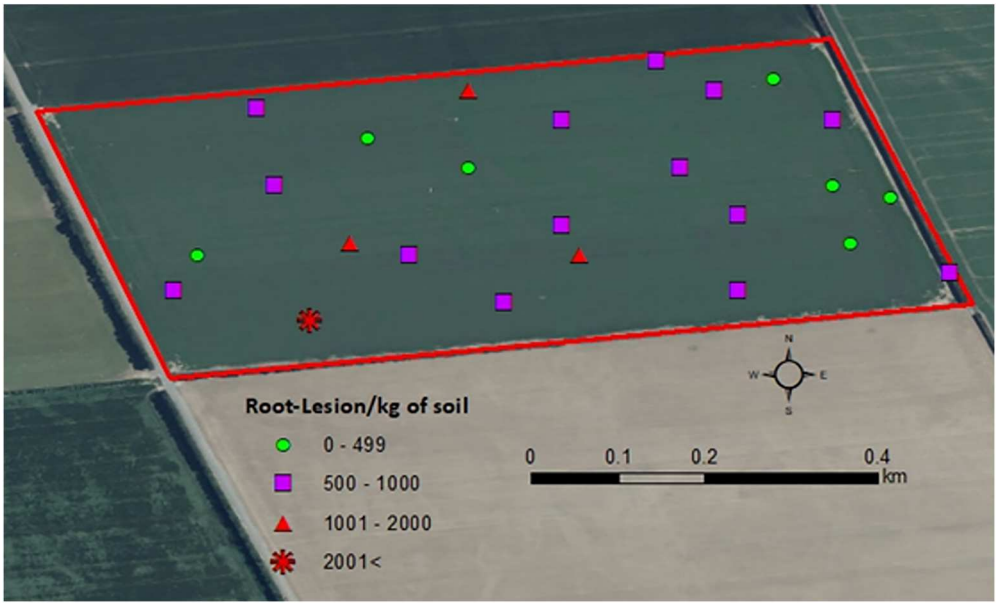

Figure 9. *Pratylenchus* spp. abundance within a field at Dorie in Ashburton, Canterbury.

The abundance of RLN was higher at 2394 kg^{-1} of soil in brown soil and the lowest in organic order at 6 kg^{-1} of soil. The spiral nematode means abundance was higher in the organic soil order 1928kg^{-1} and lower in soil order ultic (4) granular (3), and N/A samples (2 kg^{-1} of soil). Diversity indices and number of PPN genera differed significantly between the soil orders (Figure 11A–C; $x^2_{(9)} = 52.51$, $p < 0.001$ for 1-D; $x^2_{(9)} = 75.13$, $p < 0.001$ for E; $x^2_{(9)} = 82.89$, $p < 0.001$). The 1-D and E were higher in pallic soil at 0.296 and 0.127, respectively. The lowest 1-D (0.031) and E (0.011) in the organic soil, respectively. The number of PPN genera was higher in pallic (2.15) and lowest in organic (1.11) soil orders. Nematode abundance and diversity data related to the soil orders are summarised in supplementary Table S5.

Effect of crop stage at sampling on nematode population in maize fields

The abundance of non-PPN and PPN with crop stages at sampling had a significant relationship (Figure 12A, B; $x^2_{(3)} = 45.30$, $p < 0.001$ for non-PPN; $x^2_{(3)} = 31.00$, $p < 0.001$ for PPN). The mean abundance of non-PPN was higher in the grass fields (13 614 kg^{-1} of soil) and lowest in the seedling stage fields (6288 kg^{-1} of soil). The mean abundance of the PPN was higher in fields with maize stubbles after harvest (2473 kg^{-1} of soil), and the lowest abundance at the seedling stage (1346 kg^{-1} of soil). The abundance of the RLN and spiral nematodes showed a significant relationship with crop stages at sampling (Figure 12C, D; $x^2_{(3)} = 16.41$, $p = 0.001$ for RLN; $x^2_{(3)} = 42.87$, $p < 0.001$ for spiral). The RLN population was higher in harvested (1417 kg^{-1} of soil) and grass fields (1333) than in ploughed (805) and seedling stage fields (639). The mean abundance of the spiral nematode was higher in harvested fields (1054 kg^{-1} of soil) than in any other fields sampled while having the lowest abundance in grass

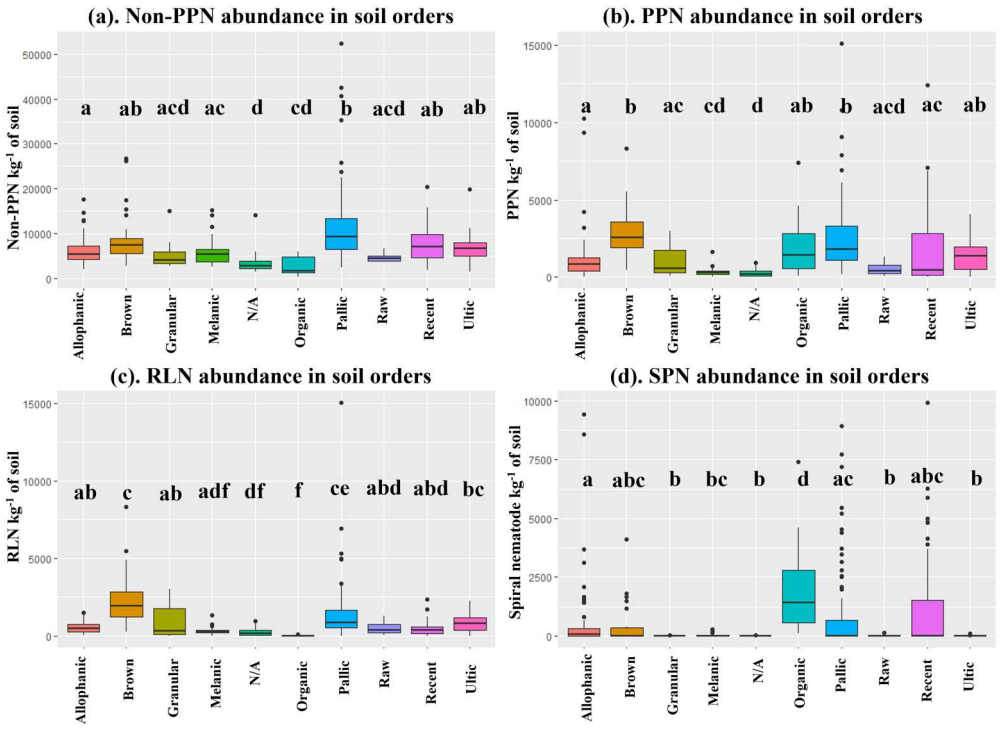

Figure 10. Nematode abundance among soil order in New Zealand maize fields, **A,** Non-plant-parasitic nematodes abundance, **B,** Plant-parasitic nematode abundances, **C,** Root-lesion nematodes abundance, and **D,** Spiral nematode abundance presented as boxplots (median; 25 and 75% quartiles; max, min of 1.5× interquartile range and outliers). Non-PPN- Non-plant-parasitic nematodes, PPN- Plant-parasitic nematodes, RLN-root-lesion nematodes, and SPN-spiral nematodes; Within each figure, statistically significant differences are indicated by different lettering in data points ($p < 0.05$).

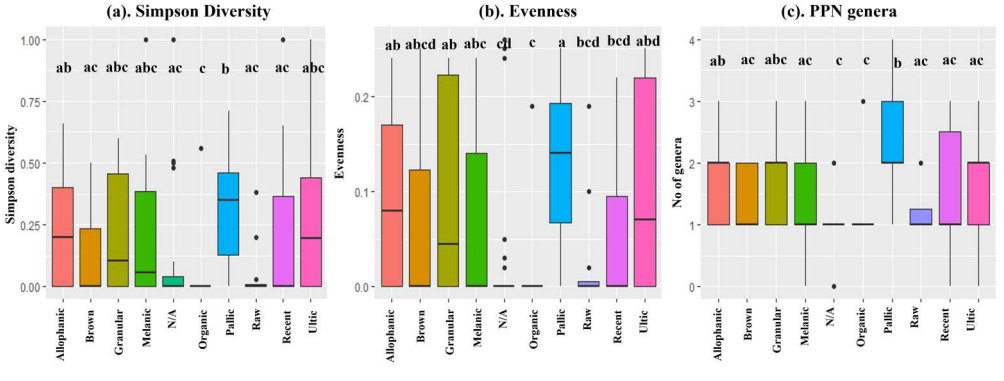

Figure 11. Diversity indices and the number of genera of plant-parasitic nematodes among soil order in New Zealand maize fields, **A,** Simpson biodiversity index, **B,** Evenness, and **C,** The number of plant-parasitic nematodes genera presented as boxplots (median; 25 and 75% quartiles; max, min of 1.5× interquartile range and outliers). Within each figure, statistically significant differences are indicated by different lettering in data points ($p < 0.05$).

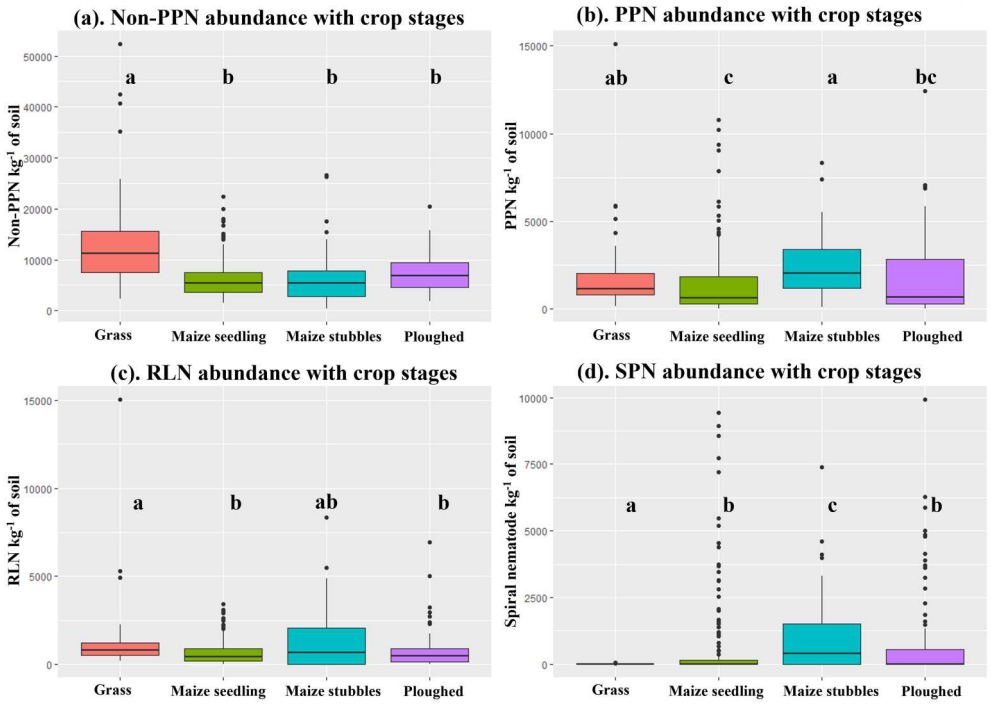

Figure 12. Nematode abundance in crop stages in New Zealand maize fields, **A,** Non-plant-parasitic nematodes abundance, **B,** Plant-parasitic nematode abundance, **C,** Root lesion nematodes abundance, and **D,** Spiral nematode abundance presented as boxplots (median; 25 and 75% quartiles; max, min of 1.5× interquartile range and outliers). Non-PPN- non-plant-parasitic nematodes, PPN-plant-parasitic nematodes, RLN-root-lesion nematodes, and SPN-spiral nematodes; within each figure, statistically significant differences are indicated by different lettering in data points ($p < 0.05$).

fields (2 kg^{-1} of soil). The diversity indices and the number of PPN genera had a significant relationship with crop stages at sampling (Figure 13A–C; $x^2_{(3)} = 34.48$, $p < 0.001$ for 1-D; $x^2_{(3)} = 49.08$, $p < 0.001$ for E; $x^2_{(3)} = 39.64$, $p < 0.001$ for PPN genera). The 1-D (0.332), E (0.148) and the number of PPN genera (2.18) were higher in grass fields than in other fields.

Effect of sampling time on nematode population in maize fields

The abundance of non-PPN and PPN with sampling times had a significant relationship (Figure 14A, B; $x^2_{(2)} = 72.35$, $p < 0.001$ for non-PPN; $x^2_{(2)} = 65.45$, $p < 0.001$ for PPN). The mean abundance of non-PPN was higher in June/July at 11408 kg^{-1} of soil, next to August/September (7765 kg^{-1} of soil) and the lowest abundance was recorded in October/November (5567 kg^{-1} of soil). The mean PPN population in June/July of 2987 kg^{-1} of soil was higher than August/September and October/November 1502 and 1104 kg^{-1} of soil, respectively. The abundance of RLN and spiral nematodes with sampling times had a significant relationship (Figure 14C, D; $x^2_{(2)} = 30.08$, $p < 0.001$ for RLN; $x^2_{(2)} = 23.49$, $p < 0.001$ for spiral). The RLN population was higher in August/September and June/July at 1344 and 1022 kg^{-1} of soil, respectively whereas the

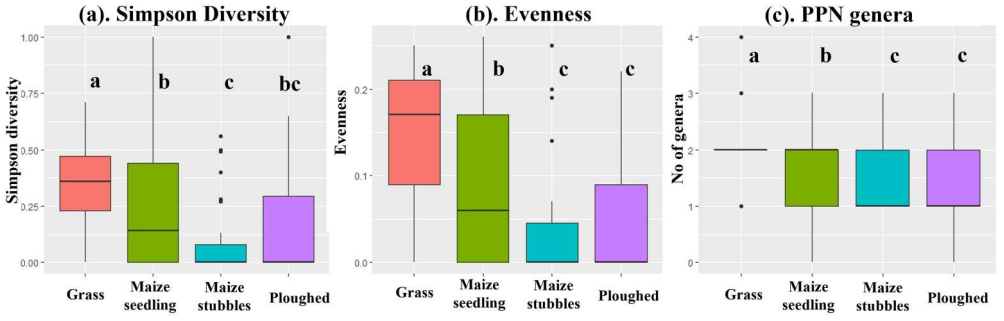

Figure 13. Diversity indices and the number of genera of plant-parasitic nematodes between crop stages in New Zealand maize fields. **A,** Simpson biodiversity index, **B,** Evenness, and **C,** The number of plant-parasitic nematodes genera presented as boxplots (median; 25 and 75% quartiles; max, min of 1.5× interquartile range and outliers). Within each figure, statistically significant differences are indicated by different lettering in data points ($p < 0.05$).

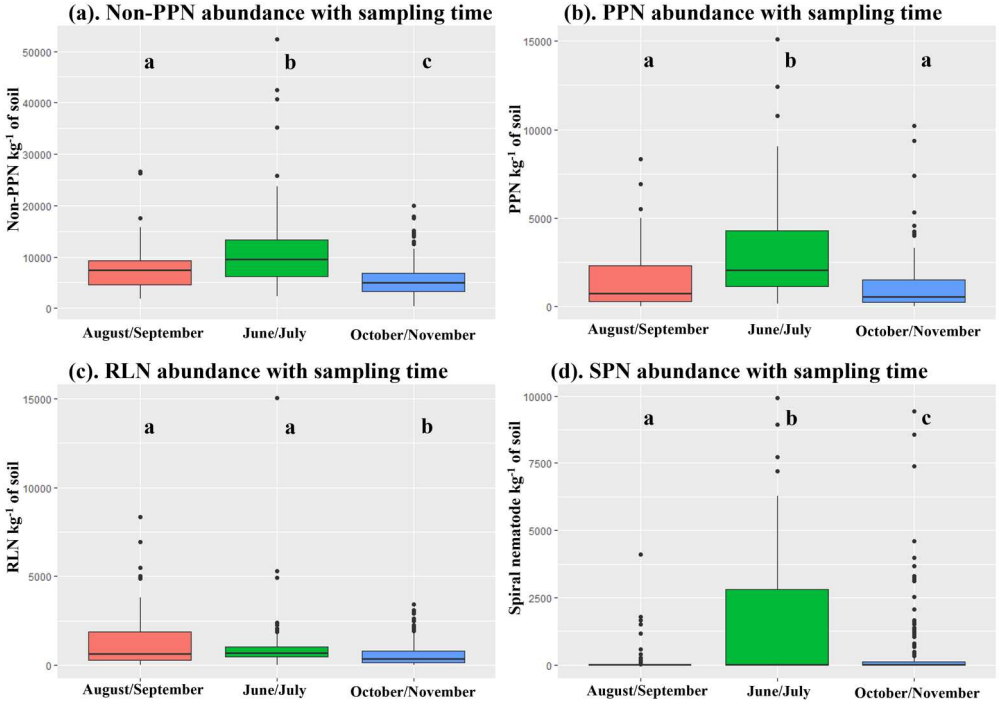

Figure 14. Nematode abundance with sampling time in New Zealand maize fields, **A,** Non-plant-parasitic nematodes abundance, **B,** Plant-parasitic nematode abundance, **C,** Root-lesion nematodes abundance, and **D,** Spiral nematode abundance presented as boxplots (median; 25 and 75% quartiles; max, min of 1.5× interquartile range and outliers). Non-PPN- non-plant-parasitic nematodes, PPN- Plant-parasitic nematodes, RLN-root-lesion nematodes, and SPN-spiral nematodes; Within each figure, statistically significant differences are indicated by different lettering in data points ($p < 0.05$).

lowest population was in October/November (584 kg^{-1} of soil). The population of the spiral nematode was higher in June/July at 1523 kg^{-1} of soil than in October/November (421 kg^{-1} of soil) and August/September (158 kg^{-1} of soil). The diversity indices

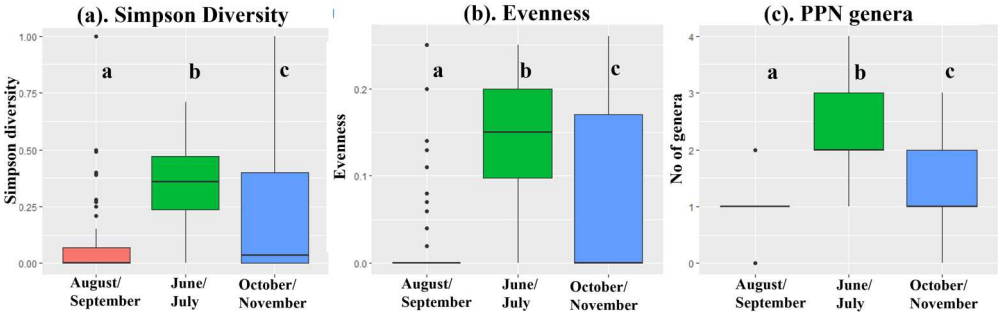

Figure 15. Diversity indices and the number of plant-parasitic nematodes genera in sampling time in New Zealand maize fields. **A,** Simpson biodiversity index, **B,** Evenness, and **C,** The number of plant-parasitic nematodes genera presented as boxplots (median; 25 and 75% quartiles; max, min of 1.5× interquartile range and outliers). Within each figure, statistically significant differences are indicated by different lettering in data points ($p < 0.05$).

and number of PPN genera with sampling times had a significant relationship (Figure 15A–C; $x^2_{(2)} = 69.37$, $p < 0.001$ for 1-D; $x^2_{(2)} = 79.85$, $p < 0.001$ for E; $x^2_{(2)} = 120.23$, $p < 0.001$ for PPN genera). All three indices were higher at the June/July sampling time. Nematode abundance and diversity data related to the crop stage and sampling time are summarised in supplementary Table S6.

Discussion

This survey serves as the primary comprehensive examination of PPN associated with maize fields in New Zealand, marking a substantial contribution to the identification of problematic nematode populations in this important arable crop. Particularly, this study is also the most extensive PPN survey conducted in New Zealand in the last three decades.

Survey results revealed that PPNs were found in 98% of samples, indicating their widespread prevalence in New Zealand maize fields. All sampled fields had one or more of the seven PPN genera: RLN (*Pratylenchus*), spiral (*Helicotylenchus*), RKN (*Meloidogyne*) (as j2-juveniles), cyst (*Heterodera*) (as juveniles), pin (*Paratylenchus*), ring (*Criconemella*) and *Tylenchus*. Previous studies have indicated the four genera that have been associated with New Zealand maize fields are *Helicotylenchus* spp., *Meloidogyne* spp., *Heterodera* spp., and *Pratylenchus* spp. (Knight et al. 1997). Further, the seven genera identified in this study have previously been reported in association with cereal crops in New Zealand (Knight 1996; Knight et al. 1997; Mercer et al. 2008; Manaaki Whenua – Landcare Research 2013). Similar findings were reported in maize fields in the USA, where spiral, RLN, and *Tylenchus* nematodes were commonly present (Tylka et al. 2011; Simon et al. 2018; Han et al. 2021), aligning with our observations in New Zealand.

Root-lesion nematode (91%) was the most prevalent genus and was widely distributed in all sampled regions; Canterbury, Waikato and Manawatu-Whanganui. The prevalence of RLN was nearly equal across 8 out of 9 districts, with over 80% of samples testing positive for RLN. In comparison, the prevalence of RLN in New Zealand maize fields was higher than the levels reported in maize fields in Iowa (51%) (Tylka et al. 2011), Ohio (80%) (Simon et al. 2018), North Dakota (20%) (Chowdhury et al. 2020), Illinois

(86%) (Han et al. 2021) and Michigan (81%) (Thapa et al. 2023), in the USA, and Sri Lanka (71%) (Thiruchchelvan et al. 2024). In this survey, 30% of maize fields in New Zealand had a mean abundance of RLN above 1000 kg^{-1} of soil. Over 63% of New Zealand maize fields had RLN levels exceeding 500 kg^{-1}, aligning with the economic damage threshold reported for maize fields in the USA, where the threshold is 500 RLN kg^{-1} of soil (Tylka et al. 2011; Simon et al. 2018; Chowdhury et al. 2020). The higher prevalence and abundance of RLN may be linked to farming practices in New Zealand, such as rotating crops or monocropping of maize, which are favourable to the RLN. Mo et al. (2021) indicated that monocropping is favourable for the widespread prevalence of PPNs, with RLNs the most prevalent and widely dispersed in maize fields. They also indicated that nematode distribution differed among hosts, ecological regions, and soil types, as observed in this study.

In this study, the mean abundances of non-PPN, PPN, RLN, spiral nematodes, and related diversity indices were higher in CaR maize fields than in WaR and MWR of New Zealand. These regional nematode population differences could be influenced by many factors such as soil and ecological conditions in the respective area (Kable and Mai 1968; Castillo et al. 1996; Kandji et al. 2003; Govaerts et al. 2007; Fleming et al. 2016; Karuri et al. 2017). The CaR in the South Island of New Zealand has a range of climatic differences and soil physiochemical properties compared to WaR and MWR which are in the central and southwestern parts of the North Island (NIWA 2023) (Supplementary Information Table S7). The diversity and abundance of PPN could have been influenced by changes in climatic conditions, particularly rainfall, as demonstrated in previous studies (Castillo et al. 1996; Govaerts et al. 2007; Karuri et al. 2017). Moisture plays a significant role in the proliferation and potential damage of RLN, as increased soil moisture during the rainy season supports their growth (Mielie 2014). In this study, maize fields in CaR had a higher RLN abundance compared to the other two regions, which were sampled during the rainy season.

In the North Island, specifically in WaR and MWR, maize has been cultivated continuously for over three years, with some areas practising back-to-back maize cultivation for more than a decade. In the CaR region, most maize growers have extensively practised crop rotation by rotating maize with ryegrass, pasture, wheat, white clover, potato, peas, and winter crops. In this study, one location (Rakaia B in Ashburton) was the exception in CaR, as it did not implement crop rotation practices, thereby resulting in a high population density of 3000 kg^{-1} RLN. It has been reported that crop rotation has an impact on reducing nematode populations and their overall damage by breaking the nematode population cycles through the incorporation of nematode-resistant rotation crops (Arjun et al. 1983; Wang and McSorley 2005; Thompson et al. 2010; Tylka et al. 2011; Simon et al. 2018). However, in the current study, RLN abundance was higher in the CaR even with crop rotations. This could be due to the following reasons; In New Zealand, limited studies have been conducted to evaluate the potential threats of PPNs in maize or agriculturally important crops. Therefore, maize growers are not aware of the detrimental impact that these nematodes pose to maize. Due to this void of information, growers have not factored in nematodes when developing their crop rotation regimes. This speculation has been reported by Simon et al. (2018), indicating that a similar trend was noted in Ohio maize fields, where RLN occurrence and abundance were higher when maize was rotated with wheat, soybean, and then maize.

Simon et al. (2018) suggested that these crops are hosts for a RLN population buildup. This study revealed that farmers in CaR rotate crops using crops such as pasture, ryegrass, wheat, peas, white clover, and potato which are also known to cause RLN population buildup (Forge et al. 2000; Fleming et al. 2016; Rohan 2018; Simon et al. 2018; Orlando et al. 2020; Gil et al. 2021).

In this study, sampled fields have been categorised into different groups based on soil orders, crop stage, and time of sampling to compare their effect on nematode populations. Nematode population and diversity indices were influenced by all these factors. For example, the mean abundance of RLN was significantly higher at 2394 kg^{-1} in brown soil orders compared to other soil orders. In contrast, the lowest RLN prevalence and abundance were observed in the organic soil order while the spiral nematode abundance was higher in the organic soil order than in other soil orders. According to Tylka et al. (2011), soil type could be one of the driving factors affecting nematode populations. This observation is supported by Thapa et al. (2023), who reported that RLN is most prevalent in muck soil and noted that nematodes such as RLN, spiral, needle, dagger, and ring have preferences for different soil types. In this study, the mean abundance of the non-PPN, PPNs, and diversity indices as well as the number of PPN genera was influenced by soil orders of sampled fields. For instance, higher PPN and non-PPN abundance were observed in pallic and brown soil orders while the lowest abundance was seen in organic soil. This is consistent with findings by Simon et al. (2018), who reported that soil series in Ohio, USA maize fields significantly influenced the occurrence and abundance of PPN genera. Fleming et al. (2016) also reported that soil types substantially affect PPN populations, abundances or number of PPN genera, and the diversity indices in cereals and grass fields, supporting the results of the current study. Differences in key soil properties may explain the significant differences in nematode populations and densities between soil orders observed in this study. Soil properties such as texture, organic matter content, moisture levels, and nutrient availability can influence nematode habitat suitability and food resources (Koenning et al. 1996; Yeates et al. 1997; Neher 1999; Metwally et al. 2019). For example, brown soils which showed higher nematode abundance, typically have better drainage topsoil and subsoil horizons with loamy soil texture (Hewitt 2013) that could provide a favourable environment for nematodes. In contrast, the higher moisture retention and organic matter with peat soil texture in organic soils (Hewitt 2013) could be the reason for the lower nematode abundance. Future research should aim to quantify these soil properties in different orders to better understand their impact on nematode populations and diversity.

The sampling period for the current study spanned through late autumn, winter, and spring seasons in New Zealand. Soil samples collected at different times showed that late autumn at harvesting yielded higher abundances of RLN and spiral nematodes compared to samples collected at the seedling stage in late spring or early summer. Previous studies by Chowdhury et al. (2020), Simon et al. (2018), Han et al. (2021), and Thapa et al. (2023) have demonstrated that sampling at different stages of plant growth and harvest can alter nematode abundance. Additionally, Tylka et al. (2011) and Thapa et al. (2023) suggested that sampling PPNs in maize fields during autumn and spring is optimal for recovering most PPNs, including RLN, needle, and lance nematodes, as we have found in this study. Additionally, fields sampled at the seedling stage in WaR and MWR, located in the North Island, were geographically and ecologically different from CaR in the South Island,

which may have caused discrepancies in nematode abundance. These findings suggest that nematode populations and diversity are influenced not only by soil orders but also by the timing and conditions of sampling. Future studies should investigate the population and diversity of PPNs in New Zealand maize fields across different growth stages and time points throughout the year to provide a comprehensive understanding of their dynamics.

In the current study, the majority of the fields exhibited uneven distribution of nematodes within each field, as depicted in Figure 9. This uneven distribution is attributed to various soil physicochemical properties, as highlighted in previous research (Overstreet et al. 2014; Thiellier and Kularathna 2023). This pattern suggests that nematode distribution within fields may be more closely related to soil properties rather than climate factors such as rainfall, temperature, relative humidity, and sunshine hours. This is because soil properties are typically heterogeneous and not evenly distributed across fields. This finding indicates that future research works need to focus on the interactions between soil characteristics and nematode occurrences. Some dominant nematode species damaging maize in New Zealand occur at densities above the specified thresholds previously shown to cause damage (Tylka et al. 2011; Simon et al. 2018; Chowdhury et al. 2020; Thapa et al. 2023). The RLN abundance observed in this study was remarkably higher than in previous reports. The exclusion of root samples may have led to an underestimation of RLN populations, as recovery rates can differ between soil and root tissues for endoparasitic species like *Pratylenchus* (Fleming et al. 2016). Including root samples could have provided a more precise estimate of RLN abundance. Given the potential impact of this pathogen on maize yield, further research is needed to assess its full impact, explore cultivar susceptibility, and develop sustainable management strategies for maize production in New Zealand.

Conclusions

The study revealed a high prevalence of PPN in maize fields, with 98% of samples testing positive. Seven PPN genera were identified, with *Pratylenchus* spp. being the most prevalent (91%), followed by *Helicotylenchus* spp. (38%). Canterbury exhibited the highest nematode populations and diversity, particularly for *Pratylenchus* spp. compared to Waikato and Manawatu-Wanganui. Soil orders influenced nematode populations, with brown and pallic soils supporting higher abundances, especially of *Pratylenchus* spp. The crop stage at sampling significantly affected nematode populations, with higher abundances observed in harvested maize fields. The highest nematode populations and diversity indices were recorded in late autumn, compared to early spring and early summer. The abundance of *Pratylenchus* spp. in New Zealand maize fields was significantly higher than the reported threshold for maize fields elsewhere (500 *Pratylenchus* spp. kg^{-1} of soil). This study highlights the need for targeted management plans to mitigate the impact of PPN, particularly *Pratylenchus* spp., in New Zealand maize production.

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Disclosure statement

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Author contributions

NT took the lead in writing the manuscript. All authors provided critical feedback and helped shape the research, analysis, and manuscript.

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