The effects of increasing land use intensity on soil nematodes: A turn towards specialism

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Abstract
1. The ecosystem services that humans obtain from the soil are strongly linked to the soil’s biota. There is ample evidence that intensive agriculture has a negative effect on the soil’s biological diversity. While in other ecosystems, habitat specialists are at a higher risk of extinction due to human impacts than generalists, we have no evidence of whether this holds true for soil biota. We calculated the realized niche width for soil nematodes using co-occurrence data. We compared these with ecological traits. We then calculated an index of community specialization and tested whether land use intensity leads to decreases in the index of community specialization, taxon richness, diversity and to changes in nematode abundance.

2. The resulting realized niche widths did not correlate with ecological traits such as feeding group, body mass or c-p class. While it is possible that there are no relationships between these traits and the realized niche width, it is likelier that food availability, pH tolerance, or host breadth are more important factors in explaining niche width.

3. Contrary to our expectations, the lowest community specialization levels were found in soils with the lowest human intervention (shrubland–woodland ecosystems), while grasslands, dairy farms and arable farms had an overall higher level of specialization. Weather variables and land use intensity explained 66% of the variation in the index of community specialization in sandy soils. We found highest richness and diversity at intermediate levels of disturbance (grasslands and dairy farms). The lowest abundances were found on shrubland–woodland systems. Dairy farms on sand and clay had similar indices of community specialization, whereas peaty soils fostered a higher proportion of habitat specialists.

4. We argue that farmland supposes a stable environment for organisms with shorter life spans. Agricultural management strives to lower disturbances, allowing shorter lived organisms to escape pressures otherwise present in nature, such as drought or nutrient deficiencies during the growing season. In very disturbed...
systems, however, specialists may also suffer from negative effects of land use intensity.

5. This co-occurrence method to assess niche width opens the door to estimating the soil community’s niche breadth, for which resource-based methods are difficult to implement.

**KEYWORDS**
- effects of land use intensity
- Fridley’s co-occurrence method
- generalist species
- index of community specialization
- nematode community
- realized niche width
- specialist species

# 1 | INTRODUCTION

Humans derive multiple benefits from the soil system (Sarakhan et al., 2005). The delivery of these ‘ecosystem services’ depends on a number of soil processes driven by different groups of soil dwelling fauna (Ferris & Tuomisto, 2015; Haygarth & Ritz, 2009; Kibblewhite, Ritz, & Swift, 2008). Soil biota acts as decomposers, nutrient transformers, ecosystem engineers and bio-controllers (Kibblewhite et al., 2008). For example, earthworms, enchytraeids and fungi can act as ecosystem engineers (functional group) by restructuring soil material (ecosystem process) which in turn affects erosion, water quality and water supply (ecosystem services) (Pulleman et al., 2012). Microbes are also important nutrient cyclers and decomposers, and changes in the microbial community can lead to reduced decomposition rates, affecting the provision of food, fibre and water, as well as the capacity of the soil to reduce pollutant concentrations (Bardgett & van der Putten, 2014). The soil food web drives these nutrient transformations, but can also be impacted by (human induced) changes in soil quality and resilience, which in turn can reduce the capacity of soil processes, functions and ecosystem service delivery (Haygarth & Ritz, 2009; Wagg, Bender, Widmer, & Heijden, 2014).

There is little question that a human disturbance affects soil biota. Management practices, chemical stresses (pollution) and soil compaction are some of the most pertinent threats to soil biota (Orgiazzi et al., 2016; Turbé et al., 2010). Land use change has also been documented to impact the diversity of predatory mites, nematodes, earthworms and enchytraeids (Postma-Blauw, Goede, Bloem, Faber, & Brussaard, 2010). Crop rotation and cover crops affect microbial composition (Pankhurst et al., 1995). The application of pesticides and pollutants leads to decreases in the abundance of earthworms, isopods, enchytraeids and collembolans (Bardgett, Speir, Ross, Yeates, & Kettles, 1994; Blakely, Neher, & Spongberg, 2002; Korthals et al., 1996; Paoletti & Hassall, 1999; Yeates, Orchard, Speir, Hunt, & Hermans, 1994). Physical impacts such as tillage and compaction affect root pathogenic fungi, protozoa, collembola and earthworm communities (van Capelle, Schrader, & Brunotte, 2012; Chan, 2001), and this sequence is not at all exhaustive. Across Europe, agricultural intensification has led to a decrease in functional diversity, a shorter food web and a lower community weighted biomass (Tsiafouli et al., 2015).

Species with a narrow niche width (habitat specialists) are often more vulnerable to disturbance and more likely to be endangered than those that can inhabit a broader range of habitats (habitat generalists) (Clavel, Julliard, & Devictor, 2011; Ducatez, Tingley, & Shine, 2014). Population decreases in habitat specialists have been observed in birds (Devictor et al., 2008; Ibarra & Martin, 2015); carabid beetles (Kotze & O’Hara, 2003); bees, Heteroptera, spider communities (Dormann et al., 2007); and even agricultural weeds (Fried, Petit, & Reboud, 2010), all related to an increase in human disturbances. While there have been many attempts to quantify the effect of land use change and land use intensity (LUI) on the diversity of soil biota, none have distinguished these effects on the proportion of generalists and specialists, most probably due to the difficulty in establishing a soil organisms’ niche width (Bardgett, 2002).

Traditional methods of calculating a species fundamental niche width (the set of environmental conditions a species can potentially live and reproduce in) require measuring the ‘variance in performance measured in common garden or controlled experiments’ (Futuyma & Moreno, 1988; Venail et al., 2008). There are two reasons why this approach is not appropriate for soil biota: firstly, due to the high physical and chemical heterogeneity and microclimatic characteristics at small scales in the soil, which result in a myriad of niches (Bardgett, 2002; Ettema & Wardle, 2002); and secondly, more than 5,000 species (belonging to more than 770 genera) of soil and fresh water dwelling nematodes have been described world-wide (Andrassy, 1992). Selecting and manipulating the soil variables that limit species occurrence and setting up individual controlled experiments would become a daunting (time and resource consuming) task.

There are examples, however, of classifications of soil organisms according to traits that are often associated with niche widths. Nematode families, for example, have been classified into the c-p scale, from colonizers to persisters (Bongers, 1990). Bongers (1990) considered nematodes that rapidly increase in number under favourable conditions, with a short life cycle, high colonization ability and a high tolerance to disturbance as colonizers. At the other end of the spectrum are the ‘persisters’, nematodes with a low reproduction rate, a long life cycle, a low colonization ability and sensitive to disturbance. This classification has served as a starting point to calculate diverse ecological indices to assess, for example the successional stage, disturbance level or nutrient status of the soil (Bongers,
Colonizers fit the typical description of generalists, while persisters are better associated with specialism. There is, however, a lack of consensus regarding the directionality of the relationship between biological traits and specialization (Büchi & Vuilleumier, 2016). This classification into the c-p scale might not be representative of the niche width of the different nematode families, since other factors (such as pH tolerance, host breadth, resting phase) might also limit niche width.

A different method of estimating niche width is calculating the realized niche width (RNW; the set of conditions a species occupies) rather than the fundamental niche width, using diversity metrics or multivariate techniques (Devictor et al., 2010; Futuyma & Moreno, 1988). This approach is not biased by the choice of measured variables or the availability and ease of collection of environmental data (Fridley, Vandermast, Kuppinger, Manthey, & Peet, 2007), problems that are often found when using resource-based methods (see Gaston, Blackburn, & Lawton, 1997 for a review). One such approach uses large-scale co-occurrence matrices under the assumption that extreme specialist species will occur always in the company of the same species, while extreme generalists will occur in very different communities (Fridley et al., 2007; Manthey & Fridley, 2009; Zelený, 2009). Co-occurrence, resource and trait-based methods can lead to similar niche width estimates, but deviations can occur when one species is limited by a resource that is not limiting to others (Carboni, Zelený, & Acosta, 2016; Pannek, Manthey, & Diekmann, 2016).

While co-occurrence methods provide no direct insight into the underlying mechanisms that determine the target species’ niche width, they offer the opportunity to study the effects of LUI on communities’ overall specialism by calculating an index of community specialization (I_CS) which can be used as an indicator of agricultural intensification (Fried et al., 2010). In this paper, we calculated the RNW of different nematode taxa using data gathered in multiple habitats in the Netherlands. We explored its relationship with the aforementioned c-p scale, as well as other functional traits, in order to understand what determines nematode niche width. We then studied nematode richness, abundance, diversity, and the I_CS in different habitats in the Netherlands. Finally, we assess the effects of LUI on these four indices and hypothesize that with increasing LUI, there will be a decrease in the I_CS, diversity and richness.

2 | MATERIALS AND METHODS

2.1 | Dataset

Most of the data used for this study were gathered as part of the Netherlands Soil Monitoring Network (NSMN [Rutgers et al., 2009; Table 1]. This monitoring network incorporated abiotic and biotic measurements taken in sites representative of the more common land use/soil texture categories in the Netherlands (Rutgers et al., 2008, 2009). Due to the overwhelming number of samples belonging to dairy farms on sand (115 out of the NSMN 458 sites), and to prevent bias in the niche width calculation deriving from an uneven site selection (Fridley et al., 2007), the dataset was complemented with data (195 sites) from survey studies carried out in the Netherlands in different habitats (Table 1). For sites with several replicates, only one was chosen at random to be part of the dataset. Soil samples were taken from the top 10–20 cm, and nematode extraction was done using an Oostenbrink elutriator. Further information on the sampling procedures can be found in the literature cited in Table 1.

Each sample was categorized according to its land use and soil texture category, resulting in a combination of arable farms, organic and conventional dairy farms, horticulture, city parks, extensively managed grasslands, heathland, dune systems, and coniferous and deciduous forests in a combination of loess, sandy, clayey, loamy and peaty soils (Table 1). We split the dataset (655 sites) into two sets, one was used to calculate the RNW of the target nematode taxa (preliminary set; 229 sites), and the other to test the hypotheses (test set; 426 sites, of which different subsets were selected for further analysis depending on the question at hand). Site selection for the preliminary set is further discussed in the Section 2.4 of the methods.

2.2 | Weather data

Soil biota goes through seasonal changes in abundance and composition. In arable and grass fields, microbial and nematode biomasses are highest in the early summer (Buchanan & King, 1992) and lowest in the winter (Bardgett, Leemans, Cook, & Hobbs, 1997; Bardgett, Lovell, Hobbs, & Jarvis, 1995). Water content in the soil can affect nutrient availability, and strong rainfall can lead to nutrient losses through leaching (Bhadoria, Kaselowsky, Claassen, & Jungk, 1991; Kuchenbuch, Claassen, & Jungk, 1986). The effects of temperature and rainfall on the soil’s condition may further depend on soil texture (Bhadoria et al., 1991) or the presence of vegetation (Green, Harding, & Oliver, 1984).

To account for differences in sampling season and year, each data point was complemented with information on the long-term (3 months) and short-term (a week) weather prior to sampling. Average daily temperature (°C), number of freezing days and cumulative precipitation (mm) for the two periods of interest were extracted from the Royal Netherlands Meteorological Institute (KNMI) from the closest available weather station. Due to strong collinearity between short- and long-term weather, only long-term average daily temperature, long-term cumulative precipitation and log-transformed short-term cumulative precipitation were used as explanatory variables in the models (Equations 2 and 3). For five of the sites in the test set, exact coordinates were not available, so rather than local weather data, we used national averages.

2.3 | Nematode data

Nematode taxa were classified according to Bongers (1988). Identification was not always possible beyond the family level. If members of a specific family were rarely identified to genus level, further calculations were done at family level (this was the case for Criconematidae, Dolichodoridae, Neodiplogasteridae, Qudsianematidae, Rhabditidae,
Thornenematidae and Trichodoridae). If, however, members of a family had been identified to genus level more often than to family level, the nematodes identified into family level were allocated to the genera (within said family) present in the same site. Calculations were done at genus level. This was done to prevent an overestimation of taxon diversity. Prodorylaimus and Mesodorylaimus were grouped prior to analysis. Dauer larvae were analysed as a separate taxon, since they represent a common response to a stressor or environmental cue.

| Soil type | Land use | Sites in preliminary set | Sites in test set | Reference |
|-----------|----------|--------------------------|-------------------|-----------|
| Clay      | Arable farm (conventional) | 10             | 37                | Rutgers et al. (2009) |
|           | City park                                    | 1              |                   | Rutgers et al. (2009) |
|           | Dairy farm                                   |                |                   | Bongers et al. (1989) |
|           | Conventional                                 | 10             | 49                | Rutgers et al. (2009) |
|           | Organic                                      | 10             |                   | Keidel (1998)         |
|           | Forest                                       | 2              |                   | Bongers et al. (1989); Rutgers et al. (2009) |
|           | Horticulture                                 | 10             |                   | Rutgers et al. (2009) |
|           | Semi-natural grassland                       | 2              |                   | Rutgers et al. (2009) |
| Loam      | Forest                                       | 23             |                   | Bongers et al. (1989); de Goede and Bongers (1994) |
|           | Coniferous                                   | 1              |                   | de Goede and Bongers (1994) |
|           | Deciduous                                    | 10             |                   | Rutgers et al. (2009) |
| Loess     | Dairy farm                                   | 7              |                   | Rutgers et al. (2009) |
|           | Conventional                                 |               |                   |                       |
|           | Organic                                      | 4              |                   |                       |
| Peat      | Arable farm (conventional)                   | 6              | 28                | Rutgers et al. (2009) |
|           | Dairy farm                                   |                |                   |                       |
|           | Conventional                                 | 10             |                   |                       |
|           | Organic                                      | 10             |                   |                       |
|           | Horticulture                                 | 1              |                   | Rutgers et al. (2009) |
|           | Semi-natural grassland                       | 10             |                   | Rutgers et al. (2009) |
| Sand      | Arable farm                                   |                |                   |                       |
|           | Conventional                                 | 10             | 14                | Rutgers et al. (2009) |
|           | Organic                                      | 10             |                   |                       |
|           | City park                                    | 10             |                   | Rutgers et al. (2009) |
|           | Dairy farm                                   |                |                   | Bongers et al. (1989) |
|           | Conventional                                 | 10             | 89                | Rutgers et al. (2009) |
|           | Organic                                      | 10             | 12                |                       |
|           | Dune systems                                 |                |                   | de Goede et al. (1993) |
|           | Coastal                                      | 10             | 6                 | Bongers et al. (1989) |
|           | Inland                                       | 5              |                   | Verschoor et al. (1998) |
|           | Forest                                       |                |                   | Bongers et al. (1989) |
|           | Coniferous                                   | 10             | 38                | de Goede and Bongers (1994) |
|           | Deciduous                                    | 10             | 81                | Rutgers et al. (2009) |
|           | Heathland                                    | 10             | 16                | Rutgers et al. (2009) |
|           | Horticulture                                 | 10             |                   | Rutgers et al. (2009) |
|           | Semi-natural grassland                       | 10             | 33                | de Goede and Ogg (1998, unpublished); Keidel (1998); Rutgers et al. (2009) |

| Total     | 229    | 426 |

**TABLE 1** Land use type, soil texture and number of independent sites used to calculate nematodes’ realized niche width (preliminary set), to study the variables that affect the nematode’s index of community specialization (test set) and related references.
Nematode taxa were assigned a c-p value (Bongers & Bongers, 1998), feeding group (Yeates, Bongers, DeGoede, Freckman, & Georgieva, 1993), functional guild (Ferris et al., 2001), and meta-bolitic footprint (Ferris, 2010), which were extracted from Nemaplex (Ferris, 1999; last accessed November 2018). For average body mass values, we used values reported by Mulder and Vond (2011), which include the weight of males, females and juveniles extracted from soils belonging to the NSMN. The averages reported by Ferris (2010) are unlikely to be representative of our sample, since they are based on average female weights (which in the case of endoparasitic nematodes cannot be extracted following the procedures in the present work) and have recently been reported to grossly overestimate the average size of nematodes extracted from the soil (Zhao et al., 2019). Filenchus, Aphelenchoides and Ditylenchus were classified as fungus feeders. Body mass was log-transformed prior to analysis.

2.4 | Realized niche width

To quantify the nematodes’ RNW, we used the protocol developed by Fridley et al. (2007) with some adjustments. Our data selection for the preliminary set is a fair representation of Dutch habitats. The Netherlands uses up to 60% of its land for agriculture, and only slightly above 12% of the country is considered to be woodland or nature (CBS, 2016). To prevent bias towards one or another habitat (Fridley et al., 2007), the preliminary set was made out of no more than 10 sites per land use/soil texture category (Table 1; resulting in a total of 229 sites), under the assumption that different soil textures and land use types and management styles (organic vs. conventional) provide distinct habitats for soil life (Freckman & Ettema, 1993; de Goede & Bongers, 1994; Jiao et al., 2015; Quist, 2017; Quist et al., 2016).

This protocol is known to be biased when the community is or appears saturated, that is when an increase in landscape (gamma) diversity does not lead to an increase in local (alpha) diversity (Manthey & Fridley, 2009; Zelený, 2009). To check this, we calculated average alpha and gamma diversities in 100 random subsets of 20 sites each from the preliminary set, which showed a significant positive relationship (F-statistic = 22.55, adjusted $r^2 = .18$, $p$-value <.001). Following recommendations from Manthey and Fridley (2009), we quantified RNW using Jaccard’s pairwise dissimilarity (Jaccard, 1912). Jaccard’s dissimilarity can range from 0 (all species are the same in the compared sites) to 1 (no overlap in the species composition).

Nematode taxa present in at least 10% of the sites were considered target taxa. For each target taxon, we selected all sites in which it was present. Then, a random subset of 20 sites was used to calculate pairwise Jaccard’s dissimilarity after presence/absence standardization (calculated using function ‘vegdist’ function from the ‘vegan’ package for R [Oksanen et al., 2018]). This random selection procedure was repeated 100 times, and we took the average Jaccard’s dissimilarity in these 100 repetitions as the target taxon’s RNW (theta [θ] in the initial protocol [Fridley et al., 2007]). As a consequence, taxa present in more sites will have a more accurate estimate of RNW.

We analysed differences between RNW and the aforementioned traits using either Spearman’s rank order correlation (using the ‘cor.test’ function in R [Core Team, 2017]) for continuous variables or Kruskal–Wallis’ rank sum test (Hollander & Wolfe, 1999) in the case of categorical variables (using the ‘kruskal.test’ function in the same R package; [R Core Team, 2017]).

Nematode taxa were then classified as either generalists (higher RNW) or specialists (lower RNW) by splitting the RNW values into two groups using Jenks’ natural breaks optimization (Jenks, 1967). This division into groups is intended to facilitate the calculation of the $I_{CS}$. Nematodes classified into specialists simply have a narrower niche width than those classified as generalists. Goodness of variance fit (GVF), a measure based on sum of squares deviation between values and mean, which ranges from 0 (worst fit) to 1 (perfect fit), was used to evaluate the split. Both tests were carried out using the ‘clazıint’ package for R (Bivand, 2017).

2.5 | Nematode diversity indices

To monitor the nematode community, we calculated nematode abundance (in number of nematodes per 100 g fresh weight), nematode richness (defined as the number of taxa present in a site), nematode diversity and the $I_{CS}$.

We calculated taxon diversity using the Shannon–Weaver index ($H'$), such that $H' = \sum_{i=1}^{S} p_i \times \ln p_i$, where $p_i$ is the proportional abundance of taxon $i$ (in number of nematodes per 100 g fresh weight) and $S$ is the total number of taxa identified per site (the site’s richness; Hill (1973)). We used the function ‘diversity’ from the vegan package (Oksanen et al., 2018).

The $I_{CS}$ was calculated such that:

$$I_{CS} = \frac{s_i}{s_i + g_i}$$

where $s_i$ is the abundance of specialist nematodes in site $i$, and $g_i$ is the abundance of generalist nematodes in site $i$.

We selected (from the test set) land use/soil texture combinations with 10 or more replicates and tested whether different land use/soil texture combinations have a different $I_{CS}$ using the Kruskal–Wallis’ rank sum test for categorical variables (Hollander & Wolfe, 1999) (using the aforementioned function in R). We assessed differences between the groups using Dunn’s test for multiple comparisons with Bonferroni adjustment for $p$-values using the ‘posthoc.kruskal.dunn.test’ function within the PMCMR package (Dunn, 1964; Holm, 1979; Pohler, 2014).

2.6 | Effects of land use intensity on the nematode community

While the test set did not permit complete combinations of all land use categories and soil textures, it did allow to test differences in nematode diversity indices due to LUI in (a) sandy soils, where data were available for land use classes with ascending LUI (shrubland–woodland [131 sites], semi-natural grasslands [33 sites], dairy farms
[101 sites] and arable farms [14 sites]; and (b) within dairy farms on soils with different textures (32 sites on clayey soils, 16 on peaty soils and 61 on sandy soils), where nutrient availability acted as proxy for LUI, since a higher cattle density results in an increase in available phosphorus and organic matter in the soil (Mulder, Zwart, Wijnen, Schouten, & Breure, 2003).

Data were analysed following the protocols proposed by Zuur, Ieno, and Elphick (2010) and Zuur and Ieno (2016). Collinearity between explanatory variables was assessed using correlation plots. Variance inflation factors (VIF) were calculated for the remaining independent variables using the ‘corvif’ function for r, which was below 3 for all variables, and none were removed (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The initial models were such that:

\[
\text{Response} \sim \text{LUI}_i + \text{LTAvgT}_i + \text{STCPP}_i + \text{LTAvgT}_i \times \text{LUI}_i + \text{LTCPP}_i \times \text{LUI}_i
\]

\[
\text{Response} \sim \text{Ctot}_i + P - A|_i + \text{LTAvgT}_i + \text{LTCPP}_i + \text{STCPP}_i + \text{LTAvgT}_i \times \text{LTCPP}_i + \text{Ctot}_i + \text{LTCPP}_i \times \text{PAL}_i
\]

where Response is either ICS, abundance, richness or diversity; LUI is the LUI category in sandy soil; LTAvgT and LTCPP are the long-term average temperature and cumulative precipitation; STCPP is the short-term cumulative precipitation (log-transformed); Ctot is total carbon (% determined by thermogravimetric analysis); and PAL is the extractable phosphorus (determined using an ammonium lactate extraction and expressed in mg P \(_2\)O\(_5\)/100 g dry soil), in site i.

Model selection processes were done following (Zuur et al., 2009), starting with all variables under study and ecologically motivated interactions, terms were dropped using the AIC criterion. Model assumptions were verified by plotting residuals versus fitted values, versus each covariate in the model and versus each covariate not in the model, as well as exploring diagnostic plots.

Since ICS is restricted from 0 to 1, we used beta regressions (Ferrari & Cribari-Neto, 2004) to test the relationship between ICS and explanatory variables in Equations (1) and (2), using the ‘betareg’ package in R (Cribari-Neto & Zeileis, 2010). Beta distributions are restricted from 0 to 1, but include neither of these values, and thus, we transformed ICS so that zeroes and ones became numbers close to 0 and 1 respectively, such that:

\[
ICS = \frac{I_{CS} \times (n-1) + 0.5}{n}
\]

where ICS is the ICS without zeroes or ones, ICS is the index of community specialization calculated using Equation (1), and n is the total number of sites in the analysis (Cribari-Neto & Zeileis, 2010).

To study the relationships between the explanatory variables and (a) taxon richness, (b) nematode abundance and (c) taxon diversity, we used for (a) a Poisson generalized linear model, using the ‘glm’ function of the ‘stats’ package (R Core Team, 2017); for (b) a negative binomial generalized linear model, and models were fit using the ‘glm.nb’ function of the ‘MASS’ package (Venables & Ripley, 2002); and in the case of (c), we fit different regressions to test the models presented in Equations (2) and (3). After checking the residual plots, and performing a log-likelihood ratio test to compare models (L. Ratio, p-value), a model allowing for variable variances per land use type (fit using the ‘varbind’ function of the ‘nlme’ package (Pinheiro, Bates, DebRoy, & Sarkar, 2017) such that 1(LUI) was preferable for Equation (2), while a linear regression was used to test Equation (3).

When LUI was a significant explanatory variable in the resulting models, we carried out a Wald test to compare two linearly restricted models to assess whether LUI classes were different from one another (Fox, 1997) using the ‘linear.hypothesis’ function from the ‘car’ package (Fox et al., 2012).

3 | RESULTS

3.1 | Nematode realized niche width

There were 45 target taxa (occurring in at least in 23 sites) belonging to 26 families. These target nematode taxa occurred with an average of 19 other taxa per site (alpha diversity) and can co-occur with an average of 69 taxa in 20 sites (gamma diversity). Realized niche width (quantified using Jaccard’s dissimilarity) was 0.63, ranging from 0.524 (Psilenchus) to 0.689 (Heterocephalobus) (Table S1). Realized niche width showed no significant relationships with putative feeding, c-p value, herbivore guild or the average taxon mass (Figure 1).

3.2 | Community specialization

Classification into two groups, namely habitat generalists and habitat specialists, yielded 24 (relative) specialist and 21 generalist taxa (Table S1: Jenks natural breaks optimization GVF = 0.73).

Mean community specialization (Ics) was lowest in forests, followed by heathland, semi-natural grasslands, arable fields and highest in dairy farms (Figure 2; Kruskal–Wallis, \(\chi^2 = 284, df = 10, p\)-value <.01). We observed different mean Ics in different land use/texture classes (Dunn’s test for multiple comparisons with Bonferroni adjustment for p-values; Figure 2). Variations in Ics were driven by an increase in nematodes with a narrower niche width (Figure S1).

3.3 | Land use intensity in sandy soils

After initial model validation, a point with a very large Cook’s distance and high generalized leverage (an extensive dairy farm on sandy soil with 0 generalists) was taken out and the model was re-fit. This had no strong effects on the coefficients, but increased the precision parameter. Further model validation showed no underlying problems. In sandy soils, long-term daily average temperature as well as long-term cumulative precipitation had a significant effect on the proportion of specialist nematodes in the community (beta regression, Pseudo \(R^2 = .66\), log-likelihood of 228.2 on 16 degrees of freedom; Table S2), such that drier, warmer conditions relate to the highest Ics (Figure 3a). Ics was significantly lower in shrubland-woodland systems than in the rest of the land use types (Table 2). This land use type had a higher proportional abundance of generalist nematodes (Figure S2a). Non-target taxa (taxa for which we did not...
calculate a RNW, since they were not present in enough sites) made up a higher proportion of the total population in shrubland–woodland systems (46 taxa) than in semi-natural grasslands (33 taxa), dairy farms (34 taxa) and arable farms (7 taxa) (Figure S2).

Land use intensity explained a significant part of the variation in nematode richness (29% of the variation), which was unaffected by weather. Long-term average daily temperature had different effects on the abundance and diversity of nematodes in soils under different LUIs (Table S2; Figure 3). Increases of temperature led to an increase in nematode abundance in shrubland–woodland systems and a slight decrease in semi-natural grasslands, but had no effects on the nematode abundance in dairy and arable farms. Temperature and LUI explained 48% of the variation in nematode abundance (Table S2). Temperature had a negative effect on nematode diversity in all land uses except for arable farms. This implies that some groups disproportionately benefit from higher temperatures, leading to more...
uneven communities. In arable farms, which harbour the least diverse communities during the coldest months, higher temperatures led to an increase in diversity.

### 3.4 | Land use intensity in dairy farms

Within dairy farms, $I_{CS}$ increased slightly with increasing PAL and precipitation, but there was a significant negative interaction between long-term cumulative precipitation and PAL (beta regression, pseudo $R^2 = .39$; log-likelihood of 105.7 on 10 degrees of freedom; Figure 4a). $I_{CS}$ was significantly higher on peaty soils, which tend to have a lower proportion of generalists than clayey and sandy soils (Table S3; Figure S3).

None of the studied independent variables could explain the variations in nematode richness (Poisson, Null dev. = 55.45 (271 df); Res. Dev. = 52.46 (270 df); Figure 4b). Nematode abundance could be partially explained by soil texture (where clay soils had lowest abundance, sandy soils the highest, and peaty soils had high variability) and total carbon ($C_{tot}$) (NB, Null dev. = 144 (108 df); Res. Dev. = 112 (105 df); Figure 4c). Taxon diversity significantly decreased with increasing PAL (linear regression, adjusted $R^2 = .093; F = 12.1; p-value < .001; Figure 4d).

### 4 | DISCUSSION

In this paper, we estimated the niche width of soil nematodes using co-occurrence data, studied the effects of land use on the nematode community, and the vulnerability of specialist nematodes to LUI. Habitat generalists were similarly abundant in all studied systems, while nematodes with a narrower niche width (opposite to our expectations) dominated agricultural landscapes. The $I_{CS}$ was lowest in forests, and higher in the other land use types. The communities’ specialization in dairy farms increased with increasing PAL, but the overall role of nutrient availability in determining $I_{CS}$ appears to be dependent on external factors such as weather conditions.

#### 4.1 | Realized niche width

Although the protocol to calculate RNW using co-occurrence matrices was initially developed and applied to tree communities, it has since been used to calculate the RNW of, for example, vertebrates (Ducatez et al., 2014). The suitability of this method to calculate the RNWs of such different organisms resides in the simplicity of the idea behind it: a habitat specialist will occur in the company of species that can inhabit the same habitat. A generalist might appear in this and other habitats in the company of diverse sets of species. It is widely accepted that nematode communities differ from one another under different environmental conditions, even in environments that are already extreme (Kerfahi et al., 2017), implying at least community level habitat specialization. As such, the protocol could also be used to assess the RNW of other soil fauna for which similar trends
have been observed (such as earthworms [Decaëns, Margerie, Aubert, Hedde, & Bureau, 2008], enchytraeids or collembolans [van Dijk et al., 2009]). It is, however, not suitable for communities that are or appear saturated (which might be the case for soil bacteria [Raynaud & Nunan, 2014]) although Zelený (2009) proposed a Beals transformation of the zeroes in the co-occurrence matrix prior to the calculation the niche width of saturated communities.

There were no significant relationships between RNW and the studied traits, (i.e. nematode life-history and feeding groups). While there is a possibility that there is no relationship between these factors, the sample size of the groups in our study may be too small to pick up any sort of significant pattern. The target taxa contained, for example, only three predatory nematodes and five omnivores. A decrease in dispersal ability has been associated with specialism in the past, particularly in the case of seed dispersal (Fridley et al., 2007). Similarly to seeds, smaller nematodes are more likely to be wind-blown than larger nematodes (Ptatscheck, Gansfort, & Traunspurger, 2018), but what this might mean to dispersal rates is not clear. There is no knowledge on how wind dispersal compares to crawling, or how either of these compare to other forms of passive dispersal. Furthermore, while dispersal might play a role in RNW, it might be small compared to that of food availability, pH tolerance or host breadth in the case of plant parasites.

Niche breadth is a result of differences in environmental stability: a stable environment leads to specialization, and a heterogeneous environment will lead to different generalist strategies depending on the time-scale at which organisms experience disturbance (Clavel et al., 2011; Levins, 1968). This means that the same disturbance is experienced differently between below- and above-ground organisms, but also by soil free-living nematode species with different life spans. For example, a species with a 7-day life span (Rhabditis terracoli) or one with a 138-day life span (in Cephalobus dubius) (Gems, 2000) will experience a week of flooding as either the nature of the environment (in the first case) or a temporary disturbance (in the latter), and this event will have a very different impact in their evolutionary history.

### TABLE 2
Differences in the nematode index of community specialization ($I_{CS}$), taxon richness, abundance (nematodes per 100 g of fresh weight) and Shannon diversity between different land use categories in sandy soils

|                       | Shrubland–woodland | SN-grassland       | Dairy farming    |
|-----------------------|--------------------|--------------------|------------------|
| $I_{CS}$              | z-value            | p-value            | $\chi^2$        | p-value          |
| Shrubland–woodland    |                    |                    | -                | -               |
| SN-grassland          | 4.66               | <.001              | -                | -               |
| Dairy farming         | 6.70               | <.001              | 1.35             | .25             |
| Arable farming        | 6.516              | <.001              | 0.008            | .93             |

|                       | z-value            | p-value            | $\chi^2$        | p-value          |
|-----------------------|--------------------|--------------------|------------------|------------------|
| Richness              |                    |                    | -                | -               |
| Shrubland–woodland    |                    |                    | -                | -               |
| SN-grassland          | 4.51               | <.001              | -                | -               |
| Dairy farming         | 8.00               | <.001              | 0.10             | .32             |
| Arable farming        | 0.31               | .78                | 5.58             | .02             |

|                       | t-value            | p-value            | $\chi^2$        | p-value          |
|-----------------------|--------------------|--------------------|------------------|------------------|
| Abundance             |                    |                    | -                | -               |
| Shrubland–woodland    |                    |                    | -                | -               |
| SN-grassland          | 4.96               | <.001              | -                | -               |
| Dairy farming         | 8.14               | <.001              | 0.10             | .75             |
| Arable farming        | 5.63               | <.001              | 0.17             | .68             |

|                       | t-value            | p-value            | $\chi^2$        | p-value          |
|-----------------------|--------------------|--------------------|------------------|------------------|
| Shannon diversity     |                    |                    | -                | -               |
| Shrubland–woodland    |                    |                    | -                | -               |
| SN-grassland          | 2.06               | .04                | -                | -               |
| Dairy farming         | 2.11               | .03                | 1.14             | .28             |
| Arable farming        | -2.49              | .01                | 14.17            | <.001           |

Note: For comparisons between shrubland–woodland and other groups, we present the parameters and p-values of the respective regression models (a beta regression, a generalized linear model, a negative binomial and a Poisson generalized linear model). For comparisons between the rest of the sites, we present the chi-square and p-value for Wald test-based comparisons between the groups.

SN-grassland: semi-natural grassland; p-values <.05 are given in bold.
Contrary to previous studies (Carboni et al., 2016; Ducatez et al., 2014; Fridley et al., 2007), community level specialization increased with increasing LUI. Lowest levels of community specialization were observed on shrubland–woodland systems. These are characterized by having a very low human impact, due in part to the poor nutrient availability and acidity of the soils. Nematode habitat generalism might be a reflection of any of these characteristics, a tolerance to a wide pH range or the possibility to survive under different nutrient regimes.

4.2 | Land use intensity on sandy soils

Once we accounted for weather variations, we discovered that the \( l_{CS} \) was still lowest in shrubland–woodland systems, but did not differ significantly between semi-natural grasslands, dairy farms and arable farms in sandy soils. The management of productive soils in the Netherlands strives to provide stable conditions for the plant’s growing season, conditions that will also favour nematode growth by maintaining high nutrient inputs and minimizing impacts such as drought or flooding. In this context, a growing season in a managed system might represent an unstable environment for organisms with life spans longer than a growing season, but a stable one for nematodes, which might explain a more specialized community.

Take for example, the case of Rhabditidae, a taxon classified as a generalist. A flush of nutrients often leads to a rapid increase in the number of Rhabditidae (Ettema & Bongers, 1993). When the nutrients are scarce, the new generation might go into a resting stage (dauer larvae) to wait for better conditions. The ability to go into a temporary developmental stage is one of the expected outcomes of evolution in a system with coarse environmental variability (a disturbance regime that affects only some members of the population at a time) (Levins, 1968). Dauer larvae, which we treated as its own target taxon, had a relatively narrow niche width. This might be a result of farmland management practices, which stimulate the growth of Rhabditidae, and the subsequent appearance of dauer larvae, while conditions in natural systems rarely allow for a flush of Rhabditidae.

To confirm this, we calculated the \( l_{CS} \) without dauer larvae did not observe any change in the observed trends (Figure S4).

4.3 | Land use intensity in dairy farming

Dairy farms on peat soils (with a higher carbon content) had a more specialized community than those on sand or clay. Increased soil carbon content was also related to an increase in nematode abundance, in line with previous results (Briar, Grewal, Somasekhar, Stinner, & Miller, 2007; Ferris, Venette, & Lau, 1996). We used PAL as a proxy for LUI. Although there are other important measurements of LUI other than PAL (i.e. pesticide use or frequency of tillage), we did not have access to such information. Phosphorus application comes either as a
result of a higher cattle density grazing and/or a higher frequency of mechanical manure applications, both of which could lead to compaction of the soil, but also an increase in nitrogen in the soil (Bilotta, Brazier, Haygarth, & Sparks, 2007; Matches, 1992; Mulholland & Fullen, 1991; Scholefield & Hall, 1986). We found a slight positive relationship between PAL and ICS but also an interaction between PAL and long-term cumulative precipitation that led to a decrease in ICS. Manure applications have been shown to lead to an increase in the total number of nematodes (Forge, Bittman, & Kowalenko, 2005), which can lead to unevenness in the nematode community (which will result in a decrease in diversity) if some nematodes are benefited more than others (in line with our results). While previous studies have observed an interaction between the effect of nitrogen additions and rainfall to the nematode communities, such that an increase of these two factors led to a decrease in nematode abundance and a change in composition (Sun et al., 2013), we could find no studies linking PAL and precipitation with any effects on the nematode community, nor can we provide a suitable explanation without further study.

5 | CONCLUSIONS

Co-occurrence-based methods of niche width estimation offer a great opportunity for soil ecology, as well as a potential tool for biological soil quality assessment. Soil biota is often difficult to culture and manipulate, and much of its ecology is still to be discovered. Contrary to our expectations, the highest levels of community specialization were found on farmland systems. The average taxon composition in farmland highlights the environmental homogeneity of such environments (particularly during the growing season), a fact also supported by the decrease in species rarity in these systems. We provide the first look into the RNW of soil nematodes, a soil biota group with a relatively well known ecology, but we suggest that future work should look into the niche width of other soil biota groups. From our work, there are strong indications that below-ground community level specialization is a result of human activity, but that different activities might have different effects on the overall specialization of the community.

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AUTHORS’ CONTRIBUTIONS

C.V. and R.G.M.G. conceived the presented idea and received important feedback from all co-authors; M.R. and A.J.S. provided the data necessary to perform the analyses; C.V. led the writing of the manuscript and the analysis of the data; and R.G.M.G. verified the computations. All authors discussed the methods and results and contributed to the final manuscript.

DATA AVAILABILITY STATEMENT

The data that support this work were mainly collected by the Netherlands National Institute for Public Health and the Environment (RIVM) and are protected by confidentiality agreements. Data not belonging to the NSMN (nationwide soil monitoring network) are published in the provided literature.

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