



Review Article

Spatial Distribution of Nematodes to Improve their Sampling and Management Decision

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Abstract | Sound sampling of nematodes is basic to their related research and management. Several models of nematodes have been applied to characterize their possible spatial and temporal distribution patterns. These models can provide several advantages such as determining sample size optimization and nematode transformation counts necessary to meet assumptions for parametric statistical analysis. Basically, they can help in unraveling the complexities of ecosystem dynamics into quantifiable metrics. Yet, their merits and demerits, discussed herein, should be considered by researchers and stakeholders. As they should be tailored to fit the intended goal of application, related modifications to derive more accurate and appropriate conclusions for nematode management are reviewed in this study. For instance, iteration improved sample size of *Meloidogyne incognita* to be 389 instead of 402 using the same assumptions of sampling accuracy and nematode density in both cases. Also, alternative analyses to help decision-maker in affording proper nematode-management schemes are suggested. Although single models have been used in nematode studies, it is better to apply more than one model in a study to complement each other and demonstrate more facets of their distributions.

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Introduction

Challenges for advanced agricultural systems comprise producing sufficient food while decreasing negative effects on the environment and utilizing our resources as best we can in durable approaches. Such challenges necessitate sound solving of problems linked to the full spectrum of losses and limitations in crop yields. Plant-parasitic nematodes (PPNs) can inflict substantial agricultural losses globally. A recent revision of such losses caused by

PPNs for the 40 life-sustaining crops with significant values for food and export reported an average of 13.5% losses; equalled USD 358.24 billion annually (Abd-Elgawad and Askary, 2015; Abd-Elgawad, 2020a; 2022). Although various aspects of PPN biology and ecology are basic to optimize nematode management, major challenges are materialized in interpreting the intricacy of agroecosystem structures and dynamics into quantifiable metrics. Therefore, in the last few decades, novel technologies and spatial/temporal statistics were established to provide definite

tools for analyzing point distributional patterns. They can upgrade detection and identification of spatial heterogeneity such as clustering or gradient (Perry *et al.*, 2002). Campos-Herrera *et al.* (2013) reviewed a few of these patterns that have general applications; for nematodes and other organisms. The reviewed patterns are also implied in issues related to catching where multitrophic reactions disclose, and how to characterize and explicate them.

The present study focuses on nematode distribution patterns in terms of their reflections on the economic significance of these nematodes especially from the standpoint of pest management. The study briefly addresses the basic models of the frequency distribution of nematode counts from a sample as a rationale for practical applications of additional related models. Other developed models to tackle ecological and biological issues of nematode distribution along with their merits and demerits are also presented. Related modifications of applying nematode distribution models to derive more accurate and appropriate conclusions for nematode management are discussed herein.

Using basic mathematical models in nematology

Although sampling precision and accuracy are keys to sound nematode research and effective management decision, much experimentation pass over these terms without giving satisfactory attention. For sound nematological research, Salama and Abd-Elgawad (2010) reviewed basic models of the three possible relations between the variance (O^2) of nematode counts and their arithmetic mean (μ) of a population. These are: (1) Positive binomial as a comparative model when the variance is significantly less than the mean ($O^2 < \mu$), (2) Poisson series as the basic framework when the variance is almost equal to the mean ($O^2 = \mu$), and (3) Negative binomial as the most flexible of several possible equations when the variance is significantly larger than the mean ($O^2 > \mu$). These models are rigidly probability distributions and are converted to frequency distributions by multiplying each probability by the nematode-sample size. Advantageously, when the frequency distribution of nematode numbers in a sample fits one of these models, then: (1) the spatial dispersion of the population (ecological meaning) can be depicted in mathematical terms, (2) errors of population parameters can be assessed, (3) spatial and temporal shifts in nematode population density can

be compared, and (4) the effect of ecological factors can be estimated (Herve *et al.*, 2005; Duncan and Phillips, 2009; Salama and Abd-Elgawad, 2010; Rumiani *et al.*, 2021). In this context, Wheeler *et al.* (1994) found that *Meloidogyne hapla* populations were best depicted by the negative binomial distribution, showing clumped distribution of its populations. Also, Poisson distribution was applicable to two *Pratylenchus penetrans* populations, indicating their random spatial distribution (Campbell and Noe, 1985; Wheeler *et al.*, 1994). As nematodes are usually not evenly distributed, the related positive binomial is not of relevant usage for characterizing natural nematode distribution patterns. Nonetheless, positive binomial may be used for setting probability levels in detecting a nematode-infested unit for a range of lot/sample sizes over several infestation levels (Salama and Abd-Elgawad, 2003).

Models applied to measure spatial structure of nematodes: their merits and demerits

Sampling plans reviewed by Duncan and Phillips (2009) remains chiefly current as general sampling and extraction techniques have shifted little in the subsequent years (Abd-Elgawad, 2017). Therefore, employing models applied to other organisms to characterize also the nematode distribution patterns have been reported and developed (Been and Schomaker, 2013; Campos-Herrera *et al.*, 2013; Berg *et al.*, 2014; Gorny *et al.*, 2020; Abd-Elgawad, 2021). Such applicable models in nematology can help in unraveling the complexities of ecosystem dynamics into quantifiable metrics via their indices of nematode dispersion. Also, they may open new advantageous avenues such as developing nematode-optimum sample size and use nematode-data transformation to meet assumptions necessary for parametric statistical analyses (McSorley *et al.*, 1985; Duncan *et al.*, 1989; Abd-Elgawad, 1992; Abd-Elgawad and Hasabo, 1995; Ghaderi *et al.*, 2012; Rumiani *et al.*, 2021).

Statistical methods for quantifying the spatial/temporal ordering of ongoing nematode population data rely mainly on fitting the above-mentioned frequency distributions, but applying other fine-tuning models have been a continuous process in nematology. These may comprise using definite models to establish the relationship between mean and variance of the sampled nematodes such as Taylor's power law, TPL (Taylor, 1961), mapping and quantifying spatial autocorrelation (Campbell

and Noe, 1985; Cressie, 1989, 1993), developing two-dimensional maps of spatial patterns for rather immobile organisms (Campos-Herrera *et al.*, 2013; Diggle, 2013), and applying X, Y coordinates in a two dimensional space (Perry, 1995, 1998) to quantify nematodes-distribution patterns (Spiridonov *et al.*, 2007; Kabir *et al.*, 2018; Abd-Elgawad, 2020). Gorny *et al.* (2020) stressed that assumptions are often made on spatial and spatio-temporal distributions, lags, and related nematode-population parameters. Such assumptions are intended to circumvent the potential for high spatial variability and the considerable expenditure of resources as well as time devoted to gather, transfer, and analyze nematode samples to identify and quantify their populations. Because these assumptions can influence both accuracy and precision of assessing nematode populations and, eventually, management decisions (Robertson and Freckman, 1995; Steinberg and Kareiva, 1997; Duncan and Phillips, 2009), several options were adopted to solve such issues. From these options, TPL model was utilized to assess an index of nematode distribution. Consequently, this model could compute the optimal sampling intensities of a polyspecific nematode community (6-8 samples per 2 × 2 m row plot) for estimating populations within 50% of the coefficient of variation of the mean (Wheeler *et al.*, 1994). These intensities comprised nematode species with both clumped (*M. hapla*) and random (*P. penetrans*) distributions of their populations. In another study, the equation of TPL was regrouped to solve for sampling accuracy via defining several levels of accuracy and precision linked to a fixed, cost-determined, sample size (Abd-Elgawad, 2017). Such levels may furnish the decision-maker with more informative inputs on sampling techniques. On the other hand, information on the spatiotemporal attributes of soil-borne disease epidemics is functional for deducing pathogen introduction circumstances and epidemic development. Thus, this information may comprise shifts in nematode population levels and patterns as a reflection of field management as well (Campbell and Noe, 1985; Abd-Elgawad *et al.*, 2016; Contina *et al.*, 2018). Furthermore, analysis of spatial patterns may test assumptions about links among pathogen taxa such as affinity or co-occurrence (Pethybridge and Turechek, 2003), ecological biology, or impacts of abiotic factors such as edaphic elements on spatial patterns, crop losses, and multitrophic interactions among the existing taxa (Campos-Herrera *et al.*, 2013).

Notably, TPL was published (Taylor, 1961, 1970) as rule of thumb. It is used as a model primed for nematology by Ferris (1984) to offer certain services based on calculating nematode dispersion indices (McSorley *et al.*, 1985; Duncan *et al.*, 1989; Abd-Elgawad, 1992; Abd-Elgawad and Hasabo, 1995; Ghaderi *et al.*, 2012; Rumiani *et al.*, 2021). It states that: the variance (S^2) of a population is proportional to a fractional power (b) of the arithmetic mean (X): $S^2 = aX^b$ or $\log S^2 = \log a + b \log X$ (i), where a and b are population parameters, a depends chiefly on the sample size and b is an index of nematode dispersion (McSorley *et al.*, 1985). When parameters a and b of TPL are known, the sample size N (or N^*) can be calculated from:

$$N = (1/E)^2 a (\bar{x})^{b-2} \text{ or } N^* = (t_{\alpha/[n-1]}/D)^2 a (\bar{x})^{b-2}$$

(ii) where N or N^* is the number of samples, $t_{\alpha/[n-1]}$ is the appropriate Student's t value for confidence limits of $1 - \alpha$ and $n - 1$ degrees of freedom, and sampling reliability is defined in terms of the standard error to mean ratio (E) or the ratio of the half-width of the confidence interval to the mean (D) of the samples. Thus, TPL is useful in determining transformations (Taylor, 1970) and developing nematode sampling plans (Ferris, 1984; McSorley *et al.*, 1985; Duncan *et al.*, 1989). Insights on applying TPL could offer further conclusions for the outputs of nematode data. Duncan *et al.* (1989) distinguished between two groups of citrus orchards based on the slope value of TPL. This value for the orchards with smaller patches of *Tylenchulus semipenetrans*-infected trees was different ($P < 0.05$) from that from large-patch orchards. For optimum sample size, TPL calculations revealed that 12 citrus trees (samples) are adequate in the geographic survey and 11 trees in the temporal for *T. semipenetrans* levels of 1,000 juveniles and males/100 cm^3 soil (at $E = 0.20$). On the contrary, such sample size in sporadically infested orchards was assessed to be 69 trees (Duncan *et al.*, 1989). Also, Abd-Elgawad (2016) introduced improvements via iteration process for accurate calculation of nematode-optimum sample size (Table 1). Consequently, minimum number of *Meloidogyne incognita* samples, for example, needed to achieve a 25% level of reliability as defined in terms of confidence interval half-width to mean ratio (D) was 402 and 389 samples before (McSorley *et al.*, 1985) and after (Abd-Elgawad, 2016) iteration, respectively (Table 1). Moreover, rearranging the TPL formulae to solve for the ratio of the half-width of the confidence

interval to the mean of the nematode numbers rather than sample size was suggested to select an acceptable level of sampling reliability (Table 2).

The mechanism through which TPL comes out is still deliberately talked over or argued in the literature (Campos-Herrera *et al.*, 2013; Xiao *et al.*, 2015; Xu and Cohen, 2021). On the other hand, TPL usage is confirmed to be compatible with orders of many organisms and applicable to their distribution patterns in nature (Taylor, 2019). For instance, application of TPL revealed that its exponents varied systematically with potential drivers concerning distribution patterns in time and space of fishes in the North Sea and therefore gains useful ecological acquaintance of the targeted system (Cobain *et al.*, 2019). Hence, these authors stressed that its usage backed the notion of detecting community spatio-temporal structures and dynamics as impacted by driving biotic/abiotic factors. In addition to being a descriptive model, there have been other practical utilizations of TPL in biology and ecology (Taylor, 2019).

Table 1: Minimum number of nematode samples needed to achieve a 25% level of reliability as defined in terms of standard error to mean ratio (E) or confidence interval half-width to mean ratio (D) with iteration*.

Mean count per sample	Number of samples via E	Student's t-value	Number of samples via D	Reference
<i>Criconebella</i> spp.: The power law parameters $a = 3.076$, $b = 1.218$				
10	8	2 (assumed)	33	Abd-Elgawad and Hasabo, 1995
		2.037 (n=33)	34	
		2.035 (n=34)	34	
100	1	2 (assumed)	5	
		2.776 (n=5)	10	
		2.262 (n=10)	7	
		2.447 (n=7)	8	
		2.365 (n=8)	8	
<i>Melioidogyne incognita</i> : The power law parameters $a = 4.77$, $b = 2.12$				
10	101	2 (assumed)	402	McSorley <i>et al.</i> , 1985
		1.966 (n=402)	389	
		1.966 (n=389)	389	
5	93	2 (assumed)	370	
		1.966 (n=370)	358	
		1.967 (n=358)	358	

*The t-value is either assumed as 2 for 95% confidence interval or iterated using its tabulated value from: <http://www.danielsoper.com/statcalc3/calc.aspx?id=10> (Abd-Elgawad, 2016).

Table 2: Percentage level of accuracy as defined in terms of the standard error to mean ratio (E) and the ratio of the half-width of the confidence interval^k to the mean (D) for stratified random sampling of *Melioidogyne* spp. in fields of berseem clover in Egypt.

Cost of samples (US \$)	Finance based number of samples	Mean nematode count per sample ^y	Level of accuracy/reliability ^z	
			D	E
Taylor's power law parameters: $a = 3.483$, $b = 1.729$				
150	15	40	63%	29%
200	20	30	55%	26%
250	25	20	51%	25%
300	30	20	48%	23%
400	40	10	44%	22%
200	20	1	87%	42%
250	25	1	77%	37%
750	150	1	30%	15%

^kThe t-value at 95% confidence interval was obtained from: <http://www.danielsoper.com/statcalc3/calc.aspx?id=10>. ^yBased on a sample size of 100 gm soil (Abd-Elgawad and Hasabo, 1995; Abd-Elgawad, 2016, 2017). ^zThe fractional values rounded up to nearest two decimals (i.e. percentage).

Such a reliability/ accuracy of nematode sampling is especially significant for decision-maker in case of limited fund. Therefore, to define exact levels of accuracy linked to a fixed, cost-determined, sample size could be calculated (Abd-Elgawad, 2016). These levels may also furnish the decision-maker with more informative data on sampling approaches and their accuracies (Abd-Elgawad, 2017). However, such statistical manipulations should lead to identical confidence profile that is below, at, or above the economic threshold level, in most cases. As identification of new nematode species/strains/races is tremendously continuing via accurate and rapid morphological, biochemical and molecular tools (Shao *et al.*, 2023) where modern trend is further facilitated by setting deep learning patterns for their automatic identification (Shabrina *et al.*, 2023), quite high confidence interval should be assured. Hence, Abd-Elgawad (2017) reported a 99% confidence band above action threshold of *Tylenchulus semipenetrans* population with mean= 2500 at a precision of 80% or more as attainable probability levels due to emerging trends in gathering/processing samples and identifying their nematodes. Ultimately, such high levels of sampling precision and accuracy may be tailored with the current advances and evolutions in processing soil sampling rate to extra sizes of nematode samples.

Table 3: Comparison of index of aggregation (I_a)* values of four different studies on entomopathogenic nematode (EPN) distributions using different approaches in various regions.

EPN studied population	Form of measured EPNs	I_a value	Comments (location)	Reference
<i>Heterorhabditis bacteriophora</i> -infective stage juveniles (IJs) applied uniformly, in one, or nine patches on Kentucky bluegrass	EPN-infected <i>Galleria mellonella</i> larvae over time	All mean values were less than one but differed ($P \leq 0.05$) until 20 weeks, no more, after EPN application	The values suggest a more even distribution than a random one (New Jersey/ USA)	Wilson <i>et al.</i> , 2003
Natural populations of <i>Steinernema feltiae</i> and <i>S. affine</i> in grassland plots	IJs assigned to one of 4 groups of increasing physiological age	The values ranged 1.27-1.45 with group II as the most aggregated one.	All values indicate aggregated distribution (Merelbeke/ Belgium)	Spiridonov <i>et al.</i> , 2007
<i>H. bacteriophora</i> or <i>S. carpocapsae</i> -infected <i>G. mellonella</i> larvae applied within 24 h of initial IJ emergence to cultivated fields and adjoining grassy border plots	<i>H. bacteriophora</i> and <i>S. carpocapsae</i> -IJs recovered from <i>G. mellonella</i> larvae baits applied several times after the cadavers	Range < 1 to > 2. Mean values differed between EPN species in bait traps and between soil management regimes at 48 h and 16 days after placing the cadavers, respectively	Spatial distributions after dispersing from a grassy border into the adjacent planted field plots were more aggregated for <i>H. bacteriophora</i> than for <i>S. carpocapsae</i> (Ohio/ USA)	Bal <i>et al.</i> , 2017
Natural populations of <i>H. indica</i> in citrus and mango grove	EPN-infected <i>G. mellonella</i> larvae	0.913	I_a refers to even, close to random, distribution (Giza/ Egypt)	Abd-Elgawad, 2020

* I_a = the observed value of distance to regularity/ the mean randomized value (Perry, 1995).

Campos-Herrera *et al.* (2013) reviewed geostatistical models as a different set that can simultaneously utilize sample values and locations to illustrate spatial patterns and assess values at unsampled locations (Clark, 2001). Geostatistical models can effectively use global positioning systems (GPS) to define the location/site of each sample unit (Goovaerts, 1999). Unfortunately, this set of models does not supply tests to estimate the statistical significance of the established patterns. On the contrary, Analysis by Distance IndicEs (SADIE) manifested in a software package (Perry, 1995, 1998; Winder *et al.*, 2019) can estimate the statistical probability level of spatial links between organisms or the same organism at different times (Perry, 1995). Although SADIE is more realistic measure than the empirical TYL, it is still of more limited use than TYL in nematology. Therefore, examples of its useful applications are given (Table 3).

Admittedly, these distribution models with their related indices can better be applied to complement each other and demonstrate more aspects of their established patterns. In this context, Gorny *et al.* (2020) simultaneously used two indices to fix adequate sampling protocols and to define certain sites for nematicidal application. For nematode interaction with other soil microorganisms, Wu *et al.* (2019) utilized SADIE to record regulation of entomopathogenic nematodes (EPNs) by the soil fungus *Fusarium solani*. Thus, using such indices of

dispersion to boost biocontrol potential or to save unnecessary costs in nematicidal usage is ideally consistent with IPM. Moreover, spatial patterns are more depictive of nematode distributions in samples collected far apart which will be more influenced by different microhabitats than samples taken near to each other. This notion could be supported by utilizing SADIE analyses and semi-variogram together to better understand spatial patterns and spatiotemporal dynamics of PPNs (Gorny *et al.*, 2020) and EPNs (Stuart *et al.*, 2015). To ease its applications, SADIE software program including its main indices and graphical demonstrations were made available and reviewed (Winder *et al.*, 2019). SADIE was also combined with other techniques to examine soil food webs in citrus groves for developing novel biocontrol approach within an IPM plans (Campos-Herrera *et al.*, 2012, 2013).

Complementary approaches (Lavigne *et al.*, 2010; Li *et al.*, 2012) are also important to optimize detection of spatial heterogeneity especially when SADIE cannot tackle it effectively. Such approaches are useful when clusters of the targeted organism are located on elongated or square domains and close to the edges of the studied areas. In such cases, these techniques can distinguish clusters with small radius and in smaller sample size than that of SADIE. They can also be adapted to suit the absolute position or the value of the counts.

Overall advantages of determining nematode distribution patterns

Initially, it goes without saying that the above-mentioned pros and cons for different models of nematode distribution should be taken into account. Additionally, distribution patterns of plant nematodes are always derived from sound sampling to generally achieve one or more of the following advantages: (i) Select plant species/genotype that best fit to certain sites/locations, (ii) Manipulate variable rate techniques for applying the exact volume of nematicides, (iii) Unravel the complexities of nematode-ecosystem dynamics into quantifiable metrics, (iv) Distinguish relationships between various organisms in the sampled area, (v) Exploit such relationships in time and space for alert integrated pest management (IPM) schemes (Abd-Elgawad, 2021). Stuart and Gaugler (1994) speculated that EPN aggregated distribution can have substantial ramifications at the natural polyspecific community levels by shifting the dynamics of predation, parasitism, and competition. Moreover, the related temporal and spatial (horizontal/vertical) distributions may be compared with other relevant biotic and physical force(s) for better design of IPM schemes, and (vi) Certain models can function for nematode-count transformation to meet not only assumptions for parametric statistical analysis but also to achieve sound and accurate treatment comparisons.

Conclusions and Recommendations

Plant-parasitic nematodes deserve sound management approaches. Research on spatial and temporal distribution patterns of the nematodes based on their authentic dispersion indices will optimize such approaches. It offers realistic marks to unravel the complexities of ecosystem dynamics into quantifiable metrics. These patterns can enable to leverage variable rate techniques for the used nematicides and accurately depict relationships between organisms in space and time for careful IPM while basically serve in the precise nematode-count transformation to perfect treatment comparisons.

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Novelty Statement

Advanced agricultural systems can manipulate spatial distributions of nematodes to improve their sampling and management decision. The application of concepts and models related to nematode distribution patterns presented herein may be harnessed to tackle ecological and biological issues of nematodes and lower unwanted environmental effects.

Author Contribution

Mahfouz M. M. Abd-Elgawad: Suggested the idea, collected the literature necessary for the manuscript, wrote and reviewed the manuscript. Also, the author read and approved the manuscript.

Abbreviations

IPM, Integrated pest management; RKNs, Root-knot nematodes; E , the standard error to mean ratio; D , the ratio of the half-width of the confidence interval to the mean; I_a , the observed value of distance to regularity divided by the mean randomized value; TPL, Taylor's power law; S^2 , variance of a population; X , arithmetic mean; a and b , population parameters of Taylor's power law; PPNs, Plant-parasitic nematodes; EPNs, Entomopathogenic nematodes.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Conflict of interests

The author has declared no conflict of interest.

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