Population dynamics and interactions between plant parasitic and non-parasitic nematodes: An empirical analysis

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ABSTRACT

Non-linear regression models were used to estimate the effect of own and other taxa previous population levels, nitrogen application, and crop rotation on population dynamics of Mononchidae, Dorylaimidae, microbivorous (Rhabditidae), lance (*Hoplolaimus galeatus*), spiral (*Helicotylencus dihystera*), stubby root (*Paratrichodorus minor*), lesion (*Pratylenchus zeae*), and cotton root-knot (*Meloigogyne incognita*) nematodes using data from the Cullars rotation, which is the oldest soil fertility experiment in the Southern United States. Because field experimental data was used, a spatial component was included as populations in one plot were proved to be related to the population level of their neighbors. Own previous levels were found to be very important for all eight groups of nematodes (all groups' current population relied heavily on its own previous population value) and all the groups had an interaction effect with at least one other group. Lesion and cotton root-knot nematodes were found to be competitive while Mononchidae, Dorylaimidae, microbivorous and lance nematodes were non-competitive. All the populations showed high seasonality patterns having lower populations during winter, to then remain steady until September–October when there is a significant increase in the population of cotton root-knot, Dorylaimidae, microbivorous, and lesion nematodes. Nitrogen had a positive effect on Mononchidae, microbivorous, spiral, and cotton root-knot nematodes. The use of clover after cotton in the rotation crop program proved to be significantly better in reducing plant parasitic nematodes compared to other treatments.

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1. Introduction

Agriculture is shifting from a classical/rigid farming system to the use of integrated crop production systems in order to become more efficient managing pests, financial risks, and environmental concerns. Integrated Pest Management is an important tool within these programs as it has been observed to impact positively agricultural yields and/or profits (Chavez et al., 2013; Fernandez-Cornejo, 1998; White and Wetzstein, 1995). In this context, knowledge of population dynamics of soil-borne organisms is critical to developing flexible, information-based farming systems that manage these organisms for maximum expected present value of profit over time.

Many published studies present statistical analyses of population dynamics of nematodes. However, the majority of these tend to use very simple procedures such as comparing the average of populations at different periods of time, or they base inferences on simple correlations. Multiple regression analysis is a statistically more powerful approach as it allows determination of partial effects of many variables that are believed to affect a dependent variable, thus better estimating impacts of treatments and decision variables. Examples of simple (one explanatory variable) linear regression models for the analysis of population dynamics of nematodes are (Jeger et al., 1993; McSorley and Gallaher, 1993), while examples of application of multiple regression models are (Bell and Watson, 2001; McGraw and Koppenhöfer, 2009; Taylor and Rodríguez-Kábana, 1999). An example of a dynamic decision model based on population dynamics estimated with a multiple regression model was published by Taylor and Rodríguez-Kábana (1999). Their decision model was based on dynamic population models for the root-knot nematode (*Meloidogyne arenaria*), Southern blight ("white mold") fungus (*Sclerotium rolfsii*), and microbivorous (Rhabditidae) nematodes estimated on the basis of fall observations in field experiments continued over several years.

This article adds to the literature as it extends the population modeling approach introduced by Taylor and Rodríguez-Kábana (1999) to plant parasitic nematode species:

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Helicotylenchus dihystera (spiral), *Hoplolaimus galeatus* (lance), *Paratrichodorus minor* (stubby root), *Pratylenchus zeae* (lesion), *and Meloigogyne incognita* (cotton root-knot) as well as to non-parasitic taxa within the Mononchidae, Dorylaimidae, and microbivorous (Rhabditidae) nematodes. In addition, the proposed statistical model is improved by including a spatial autocorrelation component in order to account for location effects between experimental samples. Dynamic models are estimated with field observations made approximately monthly from January of 1993 to April of 1996. Use of monthly observations, as opposed to annual observations, permits us to more closely examine the contemporaneous and dynamic interactions of the various genera of nematodes, and to analyze the seasonality of population growth and decline.

The main objective of this study is to estimate the effect of the relevant factors affecting population dynamics of each of the aforementioned taxa. The hypothesis of this study is that nematode population dynamics are greatly affected by: crop rotation, seasonality, and its own and other nematode taxa previous population number.

2. Materials and methods

2.1. Experimental design

Nematode counts were taken from plots in the "Cullars Rotation", which is the oldest soil fertility experiment in the Southern United States, and the second oldest continuous cotton experiment in the World (Auburn University, 2004). The experiment is located on Marvyn loamy sand (fine-loamy, siliceous, thermic Typic Kanhapludults) and, for our data set, used conventional tillage with moldboard plowing, disking, and regular cultivation. Soil samples for nematode analyses were obtained from four (A, B, 1, and 3) of the fourteen soil fertility regimes replicated three times in an ordered block design (see Fig. 1). The 3-year rotation sequence for all plots on the blocks was: (1) cotton followed by crimson clover, (2) corn grain followed by rye harvested the following season, and (3) soybean double cropped. Ten soil core-subsamples were taken from the rhizosphere of plants along the middle of each subplot at approx. 0.5 m spacing and to a depth of 25 cm with a 2.5-cm inner diameter Oakfield® soil probe (Model LS, Ben Meadows Co., Atlanta, GA). The cores were mixed thoroughly, and 100 cm³ of the mix was removed for nematode analysis using the "salad bowl" incubation technique (Rodriguez-Kabana and Pope, 1981). The soil fertility treatments for which nematode samples were taken all had lime, phosphorous and potassium added, but differed in nitrogen fertilization (N or no-N) and legumes (with or without) (see Fig. 1). Five subplots in each 6.1 × 30.2 meter plot were sampled. A total of 1680 observations (60 subplots during 28 periods) were used.

2.2. Population model specification

The functional form of the population model used for the empirical analyses is an augmented version of the model introduced and developed by Taylor and Rodríguez-Kábana (1999). The mathematical form of this population model is:

$$(P_{it} + 1) = A_{im} \prod_{j=1}^{n} \left[(P_{j,t-1} + 1)^{b_{ij}} \right] e^{\left(\sum_k g_{ik} X_{ik} \right)} (u_{it}) \qquad (1)$$

where P_{it} is population level of the ith organism at time t; Π is the mathematical operator designating the product of the expression in brackets taken over all organisms ($i = 1, 2, \ldots, n$); X_{ik} is a set of k explanatory variables for the ith organism, including nitrogen application; A_{im} is a set of monthly multiplicative intercepts to be estimated; b_{ij} and g_{ik} are other parameters to be estimated; and u_{it} is a random error term.

Since observations throughout the year were used to estimate the population models and since seasonality of nematodes is expected, the multiplicative intercept was allowed to vary depending on the month. As discussed in Taylor and Rodríguez-Kábana (1999), the multiplicative random error of this functional form does not allow for negative population levels and the multiplicative error specification allows higher populations of nematodes to randomly vary more compared to lower populations. Binary variables, X_{ik}, were included to represent the crop rotation sequence, nitrogen application, and whether the subplot was planted to a legume. The "+1" was added as it is possible to have organisms in period t even with zero organism in period $t − 1$ and also because it allows Eq. (1) to be transformed into linear in parameters making the results easier to interpret. This transformation yields:

$$p_{it} = a_i + \sum_{j=1}^{n} b_{ij} p_{j,t-1} + \sum_k g_{ik} x_{ik} + u_{it} \qquad (2)$$

where $p_{it} = \log(P_{it} + 1)$, $p_{j,t-1} = \log(P_{j,t-1} + 1)$, $x_{ik} = \log(X_{ik})$, and $a_i = \log(A_{im})$.

An improvement to this model was made by adding a spatial lag of the dependent variable to the right-hand side of Eq. (2). The spatial lag enters the model as part of the error term. Spatial data contains information on the location of each one of the observations and how they interact with one another. There is spatial autocorrelation in a system if observations that are closer to each other in space have related values. This does not mean that nematodes "move" from one plot to another, it just means that plots that are contiguous share characteristics (such as soil, water, latitude/longitude, *etc.*) that make them similar. Tobler (1970) expressed this concept as "Everything is related to everything else, but near things are more related than distant things". All the population models expressed in Eq. (2) tested positive for spatial correlation. The spatially lagged dependent model, also known as spatial autoregressive (SAR) model, is appropriate when it is believed that the values of the dependent variable in one unit i are directly influenced by the values of the dependent variable found in i's neighbors, and that the effect is not just some type of clustering (Ward and Gleditsch, 2008). A binary distance matrix (neighbors = 1, not neighbors = 0) was used for statistically implement the neighbor effect into the regression model. Accounting for the spatial relationship, Eq. (2) becomes:

$$p_{it} = a_i + \sum_{j=1}^{n} b_{ij} p_{j,t-1} + \sum_k g_{ik} X_{ik} + v_{it} + \theta w_i p_{it} \qquad (3)$$

Where the previous random error term in Eq. (2) has been disaggregated into a stochastic component, v_{it}, and a spatial component, $\theta w_i p_{it}$, in which θ is the parameter to be estimated and w_i is the distance/connectivity matrix.

Interactions for a set of organisms can best be mathematically examined using matrix algebra (Chiang and Wainwright, 2005), which for a set of equations based on Eq. (3), can be written as,

$$\boldsymbol{P}_{(t)} = \boldsymbol{A} + \boldsymbol{B} \boldsymbol{P}_{(t-1)} \qquad (4)$$

where $\boldsymbol{P}(t) = \begin{bmatrix} p_{1t} & p_{2t} & p_{3t} & \ldots & p_{nt} \end{bmatrix}'$; $>\boldsymbol{A} = \begin{bmatrix} a_1 & a_2 & a_3 & \ldots & a_4 \end{bmatrix}'$; and where $\boldsymbol{B} =$

$$\begin{bmatrix} b_{11} & b_{12} & b_{13} & \ldots & b_{1n} \\ b_{21} & b_{22} & b_{23} & \ldots & b_{2n} \\ . & & & & . \\ . & . & & & . \\ . & & . & & . \\ . & & & & . \\ b_{n1} & b_{n2} & b_{n3} & \ldots & b_{nn} \end{bmatrix}$$

Another advantage of this system of equations is that the "community matrix" often referred to in theoretical biological literature (Taylor and Rodríguez-Kábana, 1999) is simply the matrix $(\boldsymbol{B} − \boldsymbol{I})$,