



Spatial organization of soil nematode communities in urban landscapes: Taylor's Power Law reveals life strategy characteristics

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ARTICLE INFO

Article history:

Received 19 January 2012

Received in revised form 2 November 2012

Accepted 6 November 2012

Keywords:

Spatial organization

Spatial distribution

Soil nematodes

Life history strategy

Colonizer-persister class

Functional guilds

Taylor's power law

Urban soil

ABSTRACT

It is well known that Taylor's power law describes spatial aggregation, but its ecological interpretation remains elusive. Here we used data on spatial organization of soil nematode communities in urban landscapes to test relationships between nematode life history characteristics and the power law aggregation indicator, b . Forty seven genera of soil inhabiting nematodes were identified from 360 samples taken from turfgrass lawns at three public schools located in each of three northeast Ohio cities in July and October 2007. The nematodes were classified according to their life-styles in three life history classifications: trophic group, colonizer-persister (cp) class, and functional guild, a combination of trophic group and cp-class. Estimates of Taylor's b for 28 more common genera ranged from 1.21 to 2.34. Estimates of b for trophic group, cp-class and functional guild ranged from 1.41 to 2.10, 1.34 to 1.97 and 1.41 to 2.39, respectively. Segregating genera by their trophic group, cp-class and functional guild each accounted for as much inter-genus variation in Taylor's power law as fitting 28 separate regressions. The improvements of fit in parallel line analyses for the three life-style categories over 28 lines for individual genera were highly significant. Bacterial- and plant-feeding groups were more highly aggregated than omnivorous and predatory nematodes. Nematodes in cp-classes 1 and 2 tended to be more aggregated than those in higher cp-classes. The functional guilds were generally more highly aggregated than individual genera, suggesting a higher degree of aggregation at the functional guild level. We conclude that nematode genera vary in their spatial organizations, but membership in a cp-class and functional guild accounts for much of this variability. Thus, Taylor's power law aggregation indicator, b , is sensitive to nematode feeding habits and life strategy traits as they influence a population's pattern of spatial organization.

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1. Introduction

Taylor's power law (Taylor, 1961) has been applied in a wide range of disciplines ranging from complex networks (e.g. Internet traffic), economics and finance (stock market volume and pricing), meteorology and statistical physics where it is known as fluctuation scaling, as well as agriculture and ecology (Eisler et al., 2008). In ecology and agriculture, Taylor's power law is widely used to develop and interpret sampling programs (Taylor, 1984) and in statistics for deriving exact transformations (Healy and Taylor, 1962). The law states that the relationship between sample variance, V , and sample mean, M , is of the form

$$V = a \cdot M^b \quad (1a)$$

or

$$\log[V] = A + b \cdot \log[M] \quad (1b)$$

where b and $A = \log[a]$ are parameters estimated by regression. While it is clear that Taylor's power law describes aggregation in some way, its origins and ecological interpretation remain unclear. Although Eisler et al. (2008) showed the power law to be ubiquitous and they present mathematical models leading to variances proportional to fractional powers of the mean (fluctuation scaling), their models predict $1 \leq b \leq 2$. Like other models they fail to account for the many ecological cases where $b > 2$ (Taylor et al., 1978, 1980, 1983). Lacking the ability to account for $b > 2$, the models lack a convincing ecological interpretation for Taylor's power law.

There are three ways to conduct a power law analysis: *i* ensemble scaling in which multiple simultaneous samples are taken within a set of blocks and the mean-variance pairs are calculated for each block; *ii* spatial scaling in which simultaneous samples at multiple sites are taken at intervals over time and mean and

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variance calculated from the simultaneous samples at each time point to produce a time series of mean-variance pairs; and *iii* temporal scaling where samples are taken at multiple sites over time and the mean and variance at each site computed from the time series to produce mean-variance pairs for each site. Taylor et al. (1978, 1980) performed the first two analyses, finding that in almost every case power law regressions were significant at $p < 0.01$, and in many $p < 0.001$. It appears from their results that simultaneous spatial replication (ensemble method) and a temporal sequence of samples (spatial method) are equivalent. Taylor and Woivod (1982) examined the temporal stability of aphid and moth populations from samples using the last (temporal) method. This approach also produced highly significant power law regressions, but there appears to be no relationship between the spatial and temporal gradients or intercepts (Taylor and Woivod, 1982).

Analysis by Taylor et al. (1978) confirmed the generality of Taylor's power law for 102 species from diverse animal groups. Commensurate with the wide taxonomic range, the sampling scales ranged over six orders of magnitude from ciliates on the surface of a flat-worm to the human population of the United States of America with widely differing sampling methods, each appropriate to the species being sampled. In this collection b ranged from 0.56 to 2.75 with mean $b = 1.45 \pm 0.39$. Examining narrower taxonomic groupings they found that b ranged from 1.29 to 2.95 for 97 species of aphid caught in suction traps, 0.95 to 3.32 for 263 moth species caught in light traps and 1.19 to 2.69 for 111 bird species recorded by direct observation (Taylor et al., 1980). The b value even for a single genus of noctuid moths (*Apamea*) comprising six species ranged from 1.20 to 3.32. Thus, there are differences in the value of b between taxa at several levels of classification but no systematic difference related to the taxonomic characters used to classify species.

In his original paper announcing the variance-mean power law, Taylor (1961) proposed that the gradient b of the power law is an index of aggregation that measures an intrinsic property of populations. Later studies (Taylor et al., 1978, 1980) supported this proposition and showed that b varies far less than expected by chance among different populations of the same species (Taylor et al., 1988). In fact, b is remarkably stable when the (statistical) population is well defined and the sampling method standardized (Taylor et al., 1998). But b is not always isotropic (Trumble, 1985; Taylor, 1987); it has been observed to change with life stage (Elliott, 1981, 1982, 1983, 1986; Boag et al., 1994), with time of day (Elliott, 2002) or year (Boag et al., 1989), in different parts of the same habitat (Elliott, 2004) and over a range of scales (Clark et al., 1996). Elliott (2002) concluded that the parameters of the power law are life-stage specific and that these changes are "an essential part of the behavioral dynamics of species."

Clearly the interpretation of Taylor's power law is complex. It is neither a taxonomic character nor immutable even though it can be highly isotropic when sampling is consistent and carefully defined (Taylor et al., 1998). Apparently the variance-mean relationship is malleable and responsive to environmental and ontogenetic factors and sensitive to life history characteristics under certain circumstances. But, the full ecological significance of Taylor's power law is still unknown half a century after its discovery. A number of attempts have been made to derive from first principles, either analytically or by simulation, a power relationship between variance and mean, and from this infer the power law's ecological meaning (e.g. Taylor and Taylor, 1977; Anderson et al., 1982; Perry and Taylor, 1989; Yamamura, 2000; Kilpatrick and Ives, 2003; Kendal, 2004; Ballantyne, 2005). So far, all such attempts have met with limited success because the models either predicted a narrow range of b consistently or generated a broad range of b unpredictably. By contrast with these theoretical approaches, this paper takes a

comparative empirical approach to the interpretation of Taylor's power law.

Spatial organization of organisms and their life history strategy traits are closely related (Kotliar and Wiens, 1990) with mobility, a key determinant of spatial organization (Taylor and Taylor, 1977; Thrush, 1991). Differences in feeding and dispersal strategies influence the distances traveled by organisms over short and long-time scales, resulting in distinct spatial distributions as they track resources (Duffy and Hay, 1994; Holmquist, 1998). Thus, within the same ecological system, it is expected that species groups with similar life histories will be similarly distributed across different spatial scales (Tanaka and Leite, 2003).

Power law parameters have been applied to assess spatial distribution of several species of plant parasitic nematodes (e.g. Green, 1979; McSorley et al., 1985; Ferris et al., 1990; Mukhopadhyaya and Sarkar, 1990), but rarely for free-living nematodes and never for an ensemble representing a range of life-history strategies. Power law parameters have also been used to estimate required sample size or find a proper transformation for nematode abundance data (Ferris et al., 1990; Boag et al., 1992; Neher and Campbell, 1996). But data of soil nematode distributions have not hitherto been used to test ecological questions.

Soil nematodes may serve as useful model systems for understanding relationship between Taylor's power law and life-strategy of organisms. Not only are soil nematodes the most abundant ($\sim 10^6 \text{ m}^{-2}$) and diverse metazoans (commonly $>30 \text{ taxa m}^{-2}$) in most soils (Yeates, 1979), they can also be divided into two well defined functional classification systems which reflect different aspects of their life-strategy (Bongers, 1990; Ferris et al., 2001). The first functional classification is called colonizer-persister (cp) scale. Motivated by a need to develop indicators of environmental health, Bongers (1990) proposed that the life history strategy of nematodes reflects the quality of their soil habitat. He established the cp classification of nematodes to reflect their life history strategies and proposed that this classification system be assigned to terrestrial nematodes at the family level on a continuum equivalent to the r - K continuum. Colonizers (r) are characterized as nematodes that rapidly increase in number under favorable conditions (e.g. addition of organic matter), have a short-life cycle, and produce large numbers of small eggs. Persisters (k) are characterized with a low reproduction rate, a long life-cycle, production of fewer but larger eggs, low colonization ability and higher sensitivity to disturbance. The cp-classes range from 1 to 5, the low cp-classes having characteristics similar to r -strategists and high cp-classes similar to K -strategists. The current cp-class scale does not consider spatial distribution or organization of nematodes even though spatial behavior is frequently very different for early and late succession organisms in general. The second functional classification is called the soil nematode functional guild (Ferris et al., 2001), defined by their cp-class and their trophic groups (bacterivores, fungivores, omnivores, predators, and plant feeders; Bongers, 1990; Yeates et al., 1993; Bongers and Bongers, 1998).

Considering the general empirical evidence of Taylor's power law and the known variation in distribution and abundance of soil-inhabiting nematodes, we collected spatial distribution data in urban landscapes to interpret the ecological meaning of Taylor's power law. We determined whether the value of Taylor's power law aggregation indicator b is sensitive to the life-strategy of soil nematodes, as measured by cp-scale and functional guild by comparing the spatial organization of soil nematodes at the genus, trophic group, cp-class, and functional guild levels. We hypothesized that a statistical model that includes nematode life-history status (trophic group, CP-class, or functional guild) will explain more variation in Taylor's b than a model based on taxonomic status (genus).

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