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Global Overview of the Functional Roles of Soil-living Nematodes in Terrestrial Communities and Ecosystems¹

DENNIS L. C. PROCTER²

Abstract: The role of soil-living nematodes in different ecosystems can be largely predicted by the intensity of nonbiotic stresses imposed by different temperature and moisture regimes. Assuming that tropical lowland rain forest experiences the most biologically equitable climate, increasing climate-related stress occurs as one proceeds through intervening biomes to low latitude lowland desert, high latitude desert, and alpine desert. Soil nematodes, being mostly relative generalists, show only moderate diversity and low densities in tropical lowland rain forests because of competition from many other more specialized organisms. On the other hand, nematode diversity and densities increase and remain relatively high as one proceeds to the most extreme ecosystems because nematodes show greater adaptability than do many other taxa to climate-induced stress. However, cold allows nematodes greater "ecological release" than does drought because nematodes, being essentially aquatic organisms, require moisture for activity. Thus, cold ecosystems have the greatest nematode diversities and densities.

Key words: adaptability, competition, density, diversity, ecological release, ecosystem function, global overview, nonbiotic stress.

There is a growing realization that soil-living nematodes, previously largely neglected, have important roles in ecosystem function and, therefore, soil fertility, through both energy flow and nutrient mobilization and utilization. With the rapid worldwide degradation of soils, particularly in much of the developing world, rational management urgently requires increased knowledge of the ecology of these soils, including the interactions of the soil flora and fauna.

Free-living nematodes are present in virtually all soils, including those subject to extreme cold, hot, and dry conditions that exclude many other invertebrate groups. In some extreme soil environments nema-

todes may be the dominant below-ground animals in terms of standing crop and production, as shown by Procter (15) for High Arctic tundra. Similarly, studies by Ingham et al. (7,8) have demonstrated the importance of nematodes in semi-arid grassland soils as below-ground herbivores and in mineral mobilization (e.g., nitrogen). However, despite their almost universal occurrence, and evident importance in some ecosystems, the taxonomic composition and functional roles of nematode faunas in natural soil systems are largely unknown.

Existing knowledge of soil-living nematodes in natural ecosystems was summarized and synthesized by Procter (16). The synthesis was used as a basis for developing hypotheses outlining the trends in species composition, densities, and ecological roles as one proceeds from low-latitude tropical ecosystems to high latitude ecosystems. Procter predicted that nematode species richness, density, and biomass are often higher at high latitudes (and elevations)

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² The International Centre, University of Calgary, 2500 University Drive N.W., Calgary, Alberta, Canada T2N 1N4.

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than at lower latitudes and, furthermore, dominate some high latitude invertebrate faunas. Furthermore, microbe-feeding nematodes predominate in these ecosystems. Tolerance of harsh physical conditions, which exclude many other less adaptable invertebrate taxa, combined with food chains dominated by decomposers, explain these nematode populations. By contrast, nematodes contribute relatively little to tropical soil invertebrate faunas but, unlike at high latitudes, include a high proportion of highly specialized, higher plant-parasitic nematodes (1; Procter, unpubl.). Competition by the many specialized tropical organisms, e.g., termites (Procter, unpubl.), may account for the relative unimportance of soil-living nematodes in the tropics. Nematodes are most abundant and diverse in temperate regions (14,16,19) where higher plant-feeding nematodes are particularly important. Partial "ecological release" from competing organisms, which are reduced by adverse environmental conditions combined with human agricultural activities, account in part for the importance of nematodes in the middle latitudes.

In this paper Procter's scheme (16) has been extended and refined to improve its ability to explain and predict the role of soil nematodes in different ecosystems. Essential to the revised thesis is the supposition that soil nematodes are better adapted than most soil invertebrates to environmental stress, whether induced by moisture, temperature, or nutrients. Their anhydrobiotic and cryobiotic capabilities enable nematodes to survive extreme physical conditions. Rapid recovery from cryptobiosis and high intrinsic rates of increase aid utilization of intermittently favorable environments. Generalist feeding habits confer superior adaptiveness in resource-poor habitats. Parthenogenetic reproduction by some species removes the need for a minimum population density for establishment and persistence. Conversely, as generally r-selected animals compared with many other soil-living invertebrate taxa, nematodes are less well adapted to physically unstressed environments, where se-

lection favors more competitively specialized invertebrate taxa.

Central to the present thesis is the proposal that the role of soil nematodes in different ecosystems can be largely predicated on the presence and intensity of non-biotic stresses imposed by different temperature and moisture regimes. Holdridge et al. (5) devised a life zone classification of terrestrial biomes based on variation in temperature and precipitation, as modified by latitudinal and altitudinal gradients (Fig. 1). The biomes are arranged along continua of increasing stress caused by increasing cold, dryness, unpredictability, and their interactions. In these terms tropical lowland rain forest may be considered the least stressed biome, having a climate characterized by a relatively constant mean annual temperature between 24 and 30 C, evenly distributed precipitation averaging at least 8,000 mm annually, and a potential evapotranspiration ratio of less than 0.25 (5). On the assumption that tropical lowland rain forest experiences the most biologically equitable climate, it is presumed that most (but not all) major taxa of terrestrial organisms, including nematodes, require relatively little physiological adaptability to function effectively within this biome. On the other hand, nematodes, both as individuals and more particularly as a group, show greater adaptability than do many other taxa to the increasing climate-related stress that occurs as one proceeds through intervening biomes to low latitude lowland desert, high latitude desert, and alpine desert.

In the context of the revision of Procter's biogeographical scheme (16) presented here, in which environmental stress is emphasized over strict latitudinal and altitudinal zonation, it is important to note that there are more biomes in the tropics than elsewhere and that many of these tropical biomes experience considerable environmental stress related to both low moisture and low temperatures. Consequently, some tropical biomes much more closely resemble the highly stressed biomes characteristic of other latitudes in physi-

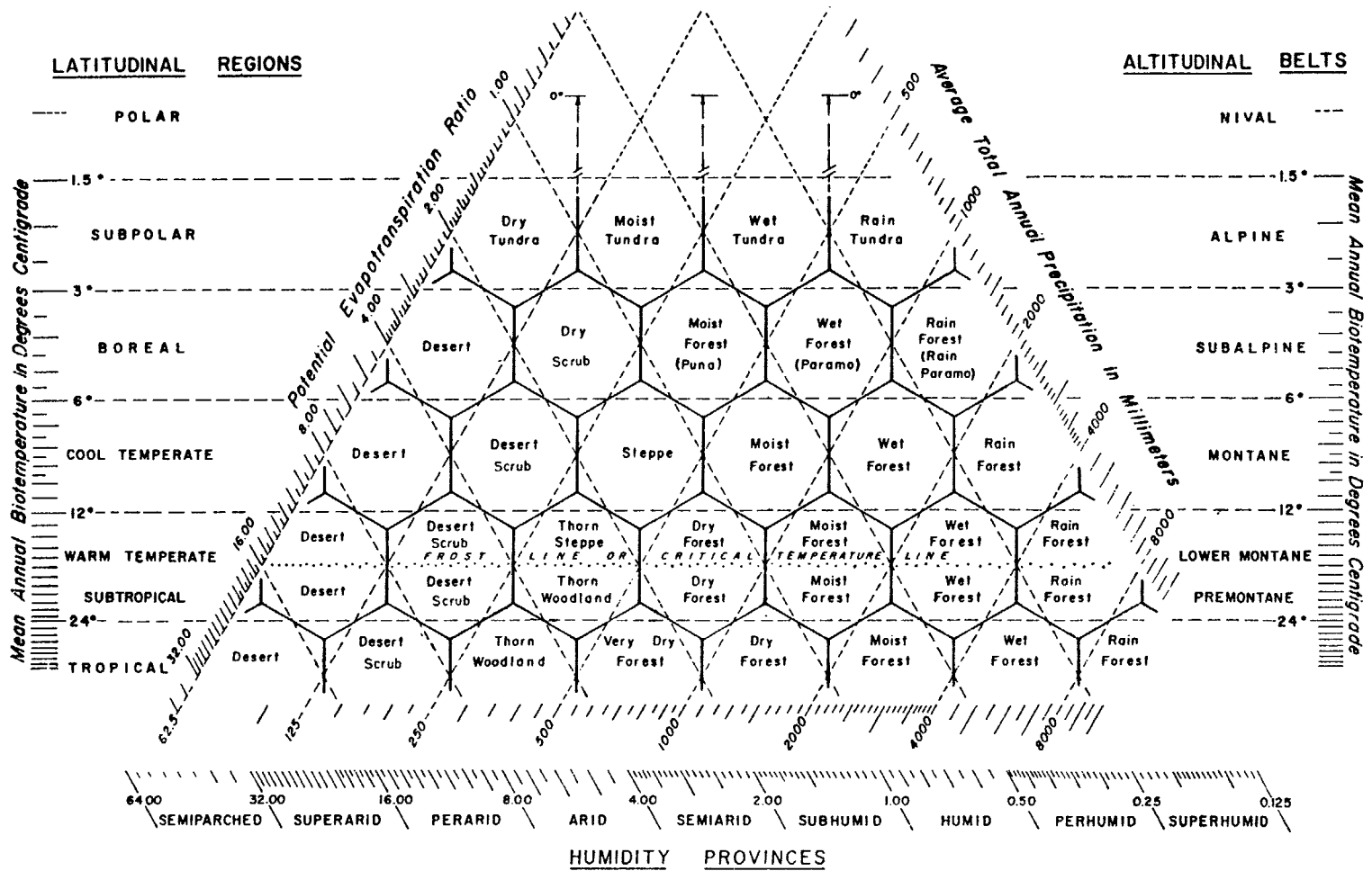


FIG. 1. Holdridge Life Zone Model: Classification of world life zones according to latitudinal region, altitudinal belt, and humidity province (after Holdridge et al., 5).

ogonomy and function than the tropical lowland rain forest considered characteristic of the tropics. This point is emphasized because geographical location is only one determinant of ecosystem function and is a less universal and sensitive predictor of function than is the general level of environmental stress experienced by the ecosystem.

Jordan (10) has outlined a eutrophic-oligotrophic functional classification of ecosystems, reflecting both the direct effects of increasing environmental stresses on the plant communities and their indirect effects through impact on soil nutrient availability and cycling. Generally, ecosystems in the most stressed environments show the lowest plant stature, biomass, species diversity, net primary productivity, and photosynthesis : respiration ratios. Large trees are usually least stress tolerant, in part because they have a large nonphotosynthetic biomass supported by a relatively small mass of leaves. For this reason shrubs are generally more stress tolerant than trees, grasses more tolerant than shrubs, and herbs more tolerant than grasses. Under conditions of very high stress, the only plants that generally survive are those that consist almost entirely of photosynthetic cells, such as algae.

Plants of oligotrophic ecosystems show the greatest development of nutrient-conserving mechanisms. For example, leaf sclerophylly is more developed in dry Mediterranean-type ecosystems (13) and tropical savannas (17) than in rain forests. In desert regions the development of scleromorphic vegetation is extreme (18)—the sparse vegetation has thick leaves with small cells, thick walls, and thick cuticles. The presence of nutrient-conserving mechanisms is a response in part to the tying-up of nutrients in litter and humus, which characteristically accumulate because environmental stress reduces rate of turnover. On the other hand, eutrophic ecosystems show least development of nutrient-conserving mechanisms because environmental conditions allow rapid turnover of nutrients, with consequent little accumulation of litter and humus. In gen-

eral, eutrophic ecosystems, with their young, basically fertile soils (e.g., temperate grasslands), provide more resources for soil-living organisms than do oligotrophic ecosystems with their old infertile soils (e.g., tropical savannas) and well-developed nutrient-conserving mechanisms.

The trends in ecosystem characteristics outlined in the preceding paragraphs, combined with the broad adaptability of soil nematodes, provide the basic principles by which the roles of nematodes in different ecosystems can be predicted. Starting with an unstressed ecosystem, as epitomized by tropical lowland rain forest, increasing environmental stress, caused by either increasing drought or declining temperature as the two simplest possible conditions, initially favors progressively increasing nematode species richness, diversity, densities, and biomass. However, these parameters increase at different rates. Diversity, being relatively high in resource-rich unstressed environments, increases least, whereas densities and biomass, initially very low, increase most. These trends continue through to ecosystems subject to high levels of stress before they slow and reverse. The relative contribution of soil nematodes to the total soil invertebrate fauna likewise progressively increases, but without marked slowing in extreme ecosystems because other invertebrates, being generally less adaptable, are progressively excluded. Increasing coldness allows nematodes greater "ecological release" than does increasing dryness, resulting in smaller relative increases in the five parameters in drier ecosystems. There are two main reasons for this difference between dry and cold ecosystems. First, as essentially aquatic animals needing moisture to be active, nematodes are more directly constrained by drought than by low temperature. Second, many competing and cohabiting soil invertebrates are better adapted to dryness than to cold (e.g., termites, ants, beetles, arachnids). However, increasing stress caused by supra-optimal moisture in particular rapidly attenuates soil nematode populations.

Increasing development of nutrient-con-

serving mechanisms along gradients of increasing climatic stress, combined with declining importance of higher plants, results in a progressive functional shift from higher plant-feeding nematodes to lower plant-feeding and microbe-feeding species. This trend continues into the most extreme ecosystems. With increasing dryness, however, the transition from higher plant-feeding species to microbe-feeding species occurs with relatively little intervention by lower plant-feeding nematodes. This is because lower plants such as mosses, liverworts, and fungi are poorly represented in dry ecosystems relative to the often highly specialized higher plants. The trophic progression is less abrupt in cold ecosystems because lower plants, being relatively well adapted to low temperatures, are better represented in cold-stressed ecosystems. The concurrent accumulation of litter and humus with increasing climatic stress, which is much more marked in cold than in dry ecosystems, usually produces very favorable environments for soil nematodes, which respond with very high densities and biomass. The rate of litter and humus accumulation eventually reverses and declines as extreme cold attenuates plant productivity; however, litter and humus continue to be a substantial substrate for all but the coldest ecosystems. Litter and humus accumulation is much more limited and localized in dry ecosystems, but they may assume extreme local importance (beneath widely dispersed plants) for the predominantly microbe-feeding nematodes of very dry ecosystems.

While, for the broad purposes of this scheme, nematodes have been treated as r-selected organisms compared with many other soil-living taxa, they include both r-selected and K-selected species. For example, Johnson et al. (9) considered dorylaimid species as the nematode "K strategists" in forest habitats, being relatively sensitive to forest disturbance. On the other hand, rhabditids are considered extreme "r strategists." The tylenchids as a group are neither extreme "K strategists" nor extreme "r strategists," and they compete well in both stable and disturbed hab-

itats. Applying this classification to Procter's scheme, relatively unstressed biomes such as tropical lowland rain forest should have an abundance of dorylaimid nematodes, whereas highly stressed biomes such as hot desert and arctic-alpine tundra should have many rhabditids. Similarly, early successional seres, especially when primary succession is in progress, should be dominated by r-selected nematodes, with a progression to K-selected species in late successional seres. The early stages of secondary succession, however, may show a relatively rapid influx of tylenchids as intermediate strategists.

The major operational hypotheses of Procter's revised biogeographical scheme, as outlined here, are summarized in Table 1. Included are predicted trends in species richness, taxonomic and trophic diversity, adaptive characteristics, densities, biomass, and proportion of total soil invertebrate biomass in response to increasingly adverse moisture and temperature regimes. The biomes included in the table are some of those from which quantitative samples have been collected in order to test the hypotheses.

Although the trends in soil nematode faunas outlined here have been broadly described in terms of the abiotic and biotic characteristics of different biomes, the same principles serve equally well in predicting trends in adjacent communities within biomes. For example, in High Arctic tundra Procter (15) showed that in four contiguous plant communities spanning 50 meters, different levels of moisture and temperature stress affected the nematode populations in a marked and predictable manner. Similarly, within nominally uniform Amazon lowland rain forest, several forms of terre firme forest, caatinga forest, and igapó (seasonally flooded) forest, each of which is clearly subject to different environmental stresses (10), are likely to have different soil nematode populations.

Ecotones are likely to have higher nematode species richness, diversity and biomass than adjacent biomes and communities because of greater diversity of habitats (including plants). Malcevski's study (12) of

TABLE 1. Major hypotheses in Procter's biogeographical scheme of the functional roles of soil-living nematodes in terrestrial ecosystems in response to increasingly adverse moisture and temperature regimes.

	— Increasing dryness →				— Increasing cold →		
	Tropical lowland rain forest	Tropical deciduous forest	Savanna	Hot desert	Montane rain forest	Alpine heath	Alpine tundra
Species richness	High	V. high	High	Low	V. high	High	Medium
Species diversity	High	V. high	High	Low	V. high	High	Medium
Trophic diversity	Medium	High	High	V. low	V. high	High	Medium
Higher plant parasitic	V. high	V. high	High	V. low	V. high	Medium	V. low
Lower plant parasitic	V. low	Medium	V. low	V. low	High	High	High
Microbe feeding	Medium	Medium	Medium	V. high	Medium	High	V. high
Nemas of epiphytes	High	Low	V. low	V. low	V. high	Medium	V. low
Adaptive characters	K	K-r	r-K	r	K-r	r-K	r
Nematode densities	V. low	Medium	Low	V. low	V. high	V. high	High
Nematode biomass	V. low	Medium	Low	V. low	V. high	V. high	High
Invert. biomass, %	V. low	Low	Medium	High	Medium	High	V. high

the soil-living nematodes of the ecotone between savanna and forest in the Ivory Coast supports this hypothesis.

An important component of Procter's scheme (16) is the hypothesis that increasing altitude resembles increasing latitude in its effect on soil nematode faunas. This hypothesis is based on the observation that the altitudinal zonation of vegetation quite closely matches the zonation by latitude from the equator towards the poles, especially in the northern hemisphere (6). In the present scheme altitudinal zonation, like latitudinal zonation, is largely supplanted by the nature and degree of environmental stress in defining nematode populations. Environmental stresses at high altitudes are somewhat different from those at high latitudes. For example, alpine tundra in the tropics is subject to marked diurnal rhythms in temperature, which may be much harsher for life than are the quite equitable summer temperatures experienced by high latitude tundra. Other differences of possible importance include the smaller areas of alpine ecosystems and the shorter distances between them. For instance, alpine tundra is very small in area, relative to arctic tundra, and physically much closer to a variety of other ecosystems, with which it shares similar environmental rhythms. Consequently, compared with arctic tundra, alpine tundra may have

few endemic taxa and may share a relatively large portion of its fauna with nearby ecosystems. Small land masses, such as tropical islands, show even more marked compression of life zones with altitude (called the "Massenerhebung effect") (3), the result primarily of different amounts of precipitation. Endemism is probably even less marked in such adjoining ecosystems.

Tropical mountain biomes pose other biogeographical questions as well. Because the mountain tops in eastern Africa are isolated from other mountain systems, and from each other, by very different environments, they show high levels of endemism of the alpine flora (2). For example, 80% of the species of the alpine flora in eastern Africa occur nowhere else, whereas, on the average, 64% of the species above 3,000 m occur on only one of the mountains of the region (4). For this reason, the high altitude biomes of mountains such as Mt. Kilimanjaro and Mt. Kenya offer the opportunity to test aspects of the equilibrium theory of island biogeography (11) with regard to free-living soil nematodes. Classical questions such as species number and degree of endemism, relative to the area and age of the biome, and distance from a colonizing source can be explored in such systems. An additional point of interest is possible correlation in these pa-

rameters between the nematodes and plants, indicating frequent dispersal together. The Galapagos Islands offer opportunities for similar analyses.

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