INFLUENCE OF SOIL PHYSICO-CHEMICAL PARAMETERS ON NEMATODE COMMUNITIES IN BANANA-*Grevillea robusta* AGROFORESTRY SYSTEMS IN KIRINYAGA, CENTRAL KENYA

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A Thesis submitted in partial fulfilment of the requirements for the award of the degree of

Master in Agroforestry

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DECLARATION

This thesis is my original work and has not been submitted for award of a degree in any other University.

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DEDICATION

To those who rejoice in fighting for the less privileged

To those who care about the welfare of smallholder farmers

To those who are passionate about soil health

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LIST OF ACRONYMS

AEZ - Agro Ecological Zone

AMF - Arbuscular Mychorrhizal Fungi

CAN : Calcium Ammonium Phosphate

CCA : Canonical Correspondence Analysis

CI : Channel Index

CS : Cropping System

DAP : Di-ammonium Phosphate

EI : Enrichment Index

LH : Low highland

LM : Low midland

m asl : meter above sea level

MI : Maturity Index

NPK : Nitrogen, Phosphorus and Potassium

OM : Organic Matter

PPI : Plant Parasite Index

SI : Structure Index

TN : Total Nitrogen

TOC : Total Organic Carbon

UM : Upper midland

ABSTRACT

Banana remains an essential crop mainly cultivated in the tropical and subtropical regions. In Africa, its production is carried out by small scale farmers under different cropping systems for both home consumption and market. However, banana production is hampered by low soil fertility, inadequate banana management practices, pests and diseases resulting in low yields. To overcome these challenges, farmers resort to emerging technologies such as improved fallow, cover crops, integrated pest and soil fertility management, agroforestry with fast growing tree species. Using soil nematodes as an indicator of soil health, this study was carried out to determine the influence of soil physico-chemical properties on soil nematode community in grevillea-banana agroforestry systems in Kirinyaga County, Central Kenya. Soil samples were collected in banana sole stands, *Grevillea robusta* sole stands and grevillea-banana intercrops in three agro-ecological zones during the dry and rainy seasons. These soil samples were analysed for their physico-chemical properties, nematode extraction, identification to genus level and calculation of nematode community and ecological indices.

Soil physio-chemical properties, namely soil moisture content, soil bulk density, soil organic matter, total nitrogen, phosphorus and exchangeable bases, were significantly different among agro-ecological zones, cropping systems and between seasons. The overall nematode density, comprising bacterivore, fungivore, omnivore, predator and herbivore nematode trophic groups increased significantly during the wet season compared to the dry season. The highest population density of bacterivore nematodes was recovered in banana sole stands in the highland zone at 170.2 individuals/ 200 cc sol whereas the least was found in grevillea-banana intercrops in the midland zone at 35.3 individuals/ 200 cc soil. The population density of fungivore nematodes was significantly affected by interactive effects of agro-ecological zones and cropping systems, being higher only in banana sole stands and grevillea-banana intercrops in the lowland zone at 28.5 and 16.4 individuals/ 200 cc soil, respectively; in

grevillea sole stands in the midland zone at 16.3 individuals/ 200 cc soil; and in grevillea sole stands and grevillea-banana intercrops in the highland zone at 18.8 and 17.7 individuals/ 200 cc soil, respectively. The density of predator, omnivore and herbivore nematodes were significantly higher in banana sole stands in the lowland zone at 20.66, 56.66 and 371.67 individuals/200 cc soil, respectively. The population density of herbivore nematodes was significantly higher in banana sole stands compared to grevillea sole stands and the intercrops in all the agro-ecological zones. The Shannon's diversity index and taxonomic richness were significantly higher in the highland zone at 1.99 and 11.8 compared to the midland (1.72 and 8.83) and the lowland zones (1.78 and 9.57). Nematode population was more diverse and evenly distributed in grevillea-banana intercrops and grevillea sole stands than in banana sole stands. Enrichment and Channel indices revealed highland and lowland zones to be nutrient-rich and dominated by bacterial decomposition pathway while the midland zone is nutrient-poor and dominated by a fungal decomposition pathway. The Structure Index and Maturity Index were significantly low in banana sole stands compared to grevillea sole stands and grevillea-banana intercrops. These results suggest that intercropping banana with grevillea trees is more sustainable than growing banana in monoculture since intercrops maintained a healthy soil whereas the banana monoculture favoured the build-up of the population of parasitic nematodes.

Key words: Nematode, banana, *Grevillea robusta*, agroforestry system

CHAPTER ONE

INTRODUCTION

1.1 Background

Banana remains an essential crop cultivated in various agro-ecological conditions up to elevation of 1,800 m above sea level (m asl) of more than 100 countries in the tropical and subtropical regions (Karamura and Frison, 1998). It is the fourth most important crop in terms of production after rice, wheat and maize, and the second most exported fruit after citrus globally (Lassois *et al*., 2009).

Banana production in Africa is carried out by small scale farmers under different cropping systems where beer banana, cooking banana and plantains are cultivated for both home consumption and markets (Lassois *et al*., 2009; Komatsu *et al*., 2010). In subsistence systems, bananas and plantains are grown alongside a diverse range of food crops such as roots and tubers, vegetables, legumes, grains, coffee and cocoa, fruit, and agroforestry trees (Viljoen, 2010). Recently, market oriented plantations have been established in the Great Lakes Region of Africa, with Uganda producing majority of cooking banana (Bagamba *et al*., 2010) while desert banana is mainly produced in the East and Central Highlands of Kenya (Reddy *et al*., 2007).

The productivity of banana plantation in the Great Lakes Region has been limited by both biotic and abiotic stresses, resulting in low yields (van Asten *et al*., 2004). The most common threats to these banana production systems include low soil fertility, diseases and pests and inadequate banana management practices (Okumu *et al*., 2011; Nyombi, 2013; Alou *et al*., 2014). Soil fertility has declined as a result of continuous farming without fallow, inadequate cultural practices such as low level of organic amendment incorporation and cultivation on steep slopes leading to soil erosion (van Asten *et al*., 2004). Lack of certified banana planting

materials has contributed to the spread of major diseases and pest which include banana bunchy top disease, black sigatoka, *Fusarium* wilt and recently banana *Xanthomonas* wilt (Tushemereirwe, 2004; Tinzaara *et al*., 2009). Pests on the other hand include banana black weevil, fruit flies, thrips aphids and nematodes and farmers seem not to be aware of their effects (Njau and Mwangi, 2010). These pests and diseases can occur together and exacerbate the banana yield decline in some regions.

Banana pests such as nematodes result in 30 to 60 % yield losses (Oka, 2010). For instance, Speijer and Kajumba (2000) recorded a yield decline from 7.1 to 3.5 tons ha^{-1} due to infection by plant parasitic nematodes in central Uganda. This yield reduction was attributed to reduction in water and nutrients uptake and anchorage insufficiency caused by root damages (Oka, 2010). Besides, other soil borne diseases can be facilitated through the injuries caused by these nematodes and aggravate the damage (Kandji *et al*., 2003). Nematode infestations are hardly noticed by farmers until yield decline becomes detectable (Njau and Mwangi, 2010). In fact, the nematode early infestation phase can induce a long vegetative phase with a slight reduction in the bunch size without any observable symptom. The later stages of the infestation can only be realized late when the pest has already infested a great number of banana mats, inducing economic losses (Quénéhervé, 2009).

The most damaging nematode species in banana belong to the genera *Radopholus, Pratylenchus, Meloidogyne* and *Helicotylenchus* (Quénéhervé, 2009; Chávez and Araya, 2010) but their abundance and species richness are influenced by the banana cultivars and climatic conditions (Chitamba *et al*., 2013; Kamira *et al*., 2013; Daneel and Jager, 2015; Daneel and De Waele, 2017). The major damages caused by these nematodes result from the destruction of root cortical tissues that can induce root pruning and eventually plant toppling alongside the symptom characteristic of root damage (leaf yellowing, plant stunting).

Apart from the plant-parasitic nematodes with their economic importance in terms of crop yield reduction (Gantait *et al*., 2011), the soil ecosystem harbours a multitude of free-living nematodes that are involved in biological processes (Neher, 2001). In natural as well as disturbed ecosystems, bacterial and fungal feeders affect and regulate both the organic matter decomposition and the recycling of soil nutrients (Thoden *et al*., 2011) whereas the free-living omnivores and predators regulate the population of other organisms (Neher, 2001; Gao *et al*., 2019). Hence, the abundance and diversity of their functional groups are vital for the functioning of agro-ecosystems (Steel and Ferris, 2016). Perturbation in their structure can result in unpredictable damages among others explosion of plant-parasitic nematode population, soil fertility decline and nutrient immobilisation (Yeates and Bongers, 1999; Dong *et al*., 2008; Xiao *et al*., 2014). This perturbation is generally caused by land use and land cover changes, change in microclimatic conditions, introduction of new agricultural practices such as soil amendment and chemical application, improved fallows with fast growing tree species. Since land use and land cover changes have direct implications on soil physical, chemical and biological processes, they are likely to influence the biological composition of soil ecosystems, and more specifically nematodes (Vazquez *et al*., 2019). These mutual interactions have been studied extensively under classic farming setups including fertilization experiments, irrigation trials and forest clearing areas (Matlack, 2001; Dong et al., 2008; Hu and Qi, 2010; Kimenju et al., 2009; Djigal et al., 2012; Thuo et al., 2020). These studies found out inconsistent results with regards to the effect of specific soil physico-chemical properties. The inconsistencies in these studies might be due to the climatic variability among the study areas but also the management practices which are likely to interactively affect the soil nematode population (Yeates and Bongers, 1999). Few studies have assessed the effect of agroforestery practices on nematode populations (Diakhaté et al., 2013; Xiao et al., 2014; Marsden et al., 2020; Rigal et al., 2020). Their results indicates that the influence of agroforestry practices on soil nematode community is dependent on the

different component in place in the agroforestry system and possible interactions between wood species and annual crops on soil properties can promote a healthy soil nematode community (Marsden et al., 2020; Rigal et al., 2020).

Currently, the diversity and abundance of the nematode community in terms of trophic groups and functional guilds is receiving more and more attention since they can be used as indicators in the evaluation of the functioning of soils and their health status in farming systems (Neher, 2001). For instance, nematode community with high diversity, high abundance (but with low herbivores population) and high structure values denote good soil food web conditions and a healthy soil (Gao *et al*., 2019).

1.2 Problem Statement

In Kenya, banana is an important food and cash crop. Its cultivation is carried out by approximately 390,000 small-scale farmers on an average acreage of 0.21 ha under a mixed cropping system (FAO, 2014). Annual production of the crop was estimated at 1,414,176 tons in 2018 (Wahome *et al*., 2021). The incremental banana production that has been reported since the last two decades, as in the case of Imenti South Sub-County, is more as a result of increase in acreage due to land use change favouring banana over other crops (Nyamamba *et al*., 2020) than increase in productivity of the crop.

Nematodes have been identified among the most important pests in banana production areas of Kenya alongside other biotic and abiotic factors. The banana-nematode complex includes *Pratylenchus goodeyi, P. coffeae, Radopholus similis, Helicotylenchus multicinctus, Meloidogyne spp.* which occur in variable abundance and species diversity from one geographical location to another (Reddy *et al*., 1999; Reddy *et al*., 2007). Cultural practices including corm paring, use of tissue cultured plantlets, hot water treatment; are the most widely used control options among these small-scale farmers.

Efforts to sustainable management of the plant-feeding nematodes have focused on integrated pest management where agricultural practices like breeding for resistant varieties, improved fallow, crop rotation, cover crops and soil fertility improvement are of a great importance. But due to land scarcity, the small-scale banana production systems in Kenya have been continuously exploited without any fallow period (Qaim, 1999). This continuous exploitation with low input incorporation can negatively influence the soil fertility but also impede the biological processes by reducing the soil fauna diversity and encouraging the banana pest build up (Kimenju *et al.*., 2009; Quénéhervé, 2009; Zhong *et al.*., 2016). Manure incorporation into the soil, which improves soil physico-chemical and biological properties, significantly reduces the abundance of herbivore nematodes both in soil and banana roots. This can be subsequent to increased population of bacteria and fungi as a result of biomass decomposition (Kivi, 2015). The application of nitrogen and carbon-rich amendments appears to be capable of inducing reduction of plant-parasitic nematodes in banana by creating favourable conditions for the build-up of antagonistic organisms (Pattison *et al.*., 2011) among others fungivore, bacterivore and omnivorous nematodes with a top-down effect on the herbivores (Kandji *et al*., 2001; Djigal *et al*., 2012). The increase in antagonistic organisms enhances the predation pressure on the plant-parasitic nematodes (Tabarant *et al*., 2011; Steel and Ferris, 2016). Besides, the decomposition of the organic matter can produce secondary metabolites that have a nematicidal effect (Oka, 2010; Thoden *et al.*., 2011) that depends on the quality of the organic matter as well as its decomposition status (Thoden *et al.*., 2011). In addition to influencing the density of herbivore nematodes in the soil, the incorporation of the organic amendment in the soil improves its fertility and hence boosts a vigorous growth of the banana plant, inducing its tolerance/resistance to nematode attacks (Thoden *et al.*., 2011).

On the other hand, predominance of plant-feeding nematode genera has been reported in banana sole stands, representing 53% of the nematode biomass (Gantait *et al.*., 2011). Moreover, maize production has been reported to be hampered by root-lesion nematodes (*Pratylenchus spp*) as well as root-knot nematodes (*Meloidogyne spp*) in an improved fallow production system of Western Kenya (Kandji *et al.*., 2003). Such a situation can be due to the floral homogeneity generated by improved fallows and the simplification of the agro-ecosystem through weed suppression. Consequently, this floral homogeneity favours the nematode species to which the chosen tree/shrub species are poor hosts and overwhelms other species that cannot identify alternative hosts (Kandji *et al.*., 2001). Hence, it becomes imperative to have a clear understanding about the effect of these agricultural practices on the population of soil nematode for their diffusion as potential parasitic nematode management options or soil fertility management strategies. The beneficial effects of agroforestry practices can turn to a disaster if the nematode host status of the tree component is not well known. In fact, these tree species may provide favourable conditions for parasitic nematode population build-up and induce drastic yield reduction in the subsequent/intercrop.

1.3 Justification

Increasing beneficial soil nematode diversity and species richness, which can promote soil health, requires commitment in the use of organic matter and time (Thoden *et al.*., 2011) under undisturbed ecosystem. Current banana production systems in Kenya are far from achieving this objective as most banana producers have challenges of accessing recommended quantities of organic matter (animal manure, green manure and compost) (Muthee *et al.*., 2019). Complex banana-tree systems may affect soil physio-chemical as well as biological properties due to permanent production of organic matter (litter fall or pruning, root decomposition) leading to an improved microclimate. Rigal *et al*. (2020) found that in a coffee-based agroforestry system, shade trees have a buffering effect on the seasonal

variability of the soil nematode communities. It maintained high counts of free-living nematodes, fungi, arbuscular mycorrhizal fungi and bacteria under the tree canopy in comparison to open areas. Using soil nematode communities as an indicator, this study aims at investigating the influence of agroforestry practices on the soil ecosystem health. Richness and diversity of the pant-feeding nematodes population and free-living nematodes in soil under banana-grevillea ecosystems will generate information on how agroforestry practices affect soil ecosystem services such as nutrient cycling and biological control of soil-borne pests.

1.4 Objectives

1.4.1 General objective

The general objective of this study was to establish the relationship between nematode communities and determinant soil factors in a banana- *Grevillea robusta* agroforestry ecosystems.

1.4.2 Specific objectives

1. To determine the changes in soil physico-chemical properties under sole crop and banana-*Grevillea robusta* agroforestry systems
2. To assess the effect of changed soil physical-chemical properties under banana-*Grevillea robusta* agroforestry systems on soil nematode populations and diversity.

1.5 Study hypothesis

1. Banana-*Grevillea robusta* agro-ecosystems do not influence the physico-chemical properties of the soil.
2. Soil physico-chemical properties in banana-grevillea agroforestry systems have no significant effect on the diversity and abundance of nematode populations.

CHAPTER TWO

LITERATURE REVIEW

2.1 Diversity and abundance of nematodes

Nematodes are organisms of small size (approximately 40 μm to 1.0 mm long) that cannot reshape soil and hence, obliged to live in existing pore spaces (majority of which occupy soil pores of 25–100 μm diameter), water cavities, or channels for propulsion within soil (Neher, 2010). Soil nematodes account among the most abundant invertebrates in the soil ecosystem, even though spatial variability among biomes due to latitudinal gradient can be evident (Procter, 1990) with highest soil nematode abundance and diversity found at medium-higher latitudes between 30 - 55° and the lowest abundance and diversity at 0 - 20° and 70 – 90° (Song *et al.*, 2017). Almost 25,000 species of nematodes are currently known, but soil nematodes represent 35% of them and approximately 10% are plant-parasites (Moura and Franzener, 2017). The most abundant nematodes population and diversity are found in temperate ecosystems and not in the tropics since the rapid decomposition and mineralization of organic inputs in these ecosystems due to high temperature and soil moisture does not favour the build-up of organic matter in the soil (Song *et al.*, 2017).

Despite their abundance in the soil ecosystems, nematodes account only for a small portion of the total soil animal biomass due to their small size but they may have significant functions in soil communities (Bernard, 1992). According to worldwide estimates in agricultural systems, losses to the plant-parasitic nematodes are, on average, estimated to 13% of total losses of different origins (Moura and Franzener, 2017). Apart from the pathogenic nematodes, other soil free-living nematodes provide ecosystems services that are vital for the functioning of agro-ecosystems. The most common soil functions involving nematodes include nutrient cycling/mineralisation and regulation of soil microbial populations. The magnitude of these functions and their relative importance depend on the above-ground biomass, the prevailing

climatic conditions particularly precipitation and temperature (Nisa *et al.*, 2021) and the soil physical and chemical properties such as soil bulk density, soil moisture content, inorganic nitrogen, soil organic carbon and cation exchange capacity (Nielsen *et al.*, 2014; Song *et al.*, 2017; van den Hoogen *et al.*, 2019).

The population of soil nematodes can vary with the agricultural practices that are being put into place (Dong *et al*., 2008; Zhao and Neher, 2013). The change in the nematode population structure can imply subsequent change in the provision of services and functions they were involved in and hence influences ecosystem productivity. In the next sections of this chapter, emphasis is put on nematodes as indicators of soil health, nematodes and soil-based ecosystem services, nematode as pathogenic agents and impacts of farming practices on nematode communities.

2.2 Nematodes as indicators of soil health

Soil health can be referred to as an integrative attribute that reflects the ability of soil to respond to agricultural management by preserving both the agricultural production and other ecosystem services (Barrios *et al..*, 2015). The monitoring and assessment of this soil characteristic is key. It requires the establishment of standards and a database of quantifiers which describe a good soil health status. The definition and measurement of soil quality/health is complicated. This is because it is not directly consumed by human beings or animals as compared to air and water which have well known standards (Doran and Parkin, 2015).

Based on its definition, soil health can be evaluated based on physico-chemical and biological properties (Lu *et al..*, 2020). On the list of various indicators of soil health and/or quality, the information from the biological processes can be evaluated in order to understand the effect of natural or anthropogenic perturbations in the soil ecosystems. In this context, living beings can inform about the increasing effects of environmental alterations (Moura and Franzener,

2017). Hence, soil micro-organisms are widely considered as soil health indicators since they are sensitive to fluctuations in management; they are well interconnected with valuable soil functions; they are important for elucidating ecosystem processes; and they are intelligible as well as useful to land managers (Neher, 2001; Lu *et al*., 2020).

Nematodes are usually thought of as meeting most of these criteria. In fact, the simplicity of extracting nematodes from soils and the possibility of their identification to significant taxa or 'functional groups' make them valuable indicators of biological diversity and for evaluating the effect of land use change on the soil properties (Yeates and Bongers, 1999). As an illustration, several studies tend to confirm that diversity and abundance of soil nematode community are, at some extent, dependent on the diversity of the above-ground vegetation community (Kimenju *et al*., 2009; Djigal *et al*., 2012; Diakhaté *et al*., 2013; Moura and Franzener, 2017) and can differ significantly depending on the management practices (Yeates and Bongers, 1999). Thus, disturbances in the aboveground vegetation can influence the soil nematode community structure if only they can influence the accessibility of potential hosts or prey in the soil (Matlack, 2001). The case of the Northern Queensland banana growing regions, where it was found that banana pure stand farming systems support a higher population of plant-feeding nematodes, with a declining diversity compared to less intensive plant systems such as pastures and forest (Pattison *et al*.., 2004) is a good illustration of the selective nature of nematodes when they are submitted to different levels of perturbation. Similarly, the introduction of a cover crop in banana plantation was reported to increase the population density in all the nematode feeding groups except herbivore nematodes, suggestive of a likely top-down regulation of plant-parasitic nematodes when higher trophic groups are promoted (Djigal *et al*.., 2012). In light of these evidences, it appears clear that soil biological processes can be apprehended by studying the structure of nematode populations in these soil ecosystems (Neher, 2010).

2.3 Nematodes and soil based ecosystem functions

Ecosystem functions involving soil nematodes proceed by abiotic or biotic mechanisms and include disintegration of organic matter and nutrient cycling, pests and disease biological control (Neher, 2010).

2.3.1 Organic matter decomposition

Among the detrital organisms, bacterial feeding nematodes are important in regulating the population structure of decomposer microflora, the rate of litter decay and the recycling of nutrients (Irshad *et al*., 2011). The number of trophic levels as well as the interactions among them are key in predicting the rates of decomposition of the litter (Neher, 2010). Besides, this decomposition rate is subjective to the quality of the organic residue (C:N ratio) but also the decomposing organisms involved (Ingham *et al*., 1985; De Mesel *et al*., 2006).

However, the decomposition rate can be reduced if bacterivore and fungivore nematode populations become increasingly dominant. When nematodes excessively feed on bacterial or fungal populations, the overall activity of the latter can be compromised (Irshad *et al*., 2011). Providentially, the hierarchy of the food chain in the soil is organised in such a way that, generalist predators feed on these bacterivore and fungivore nematodes (De Mesel *et al*., 2006). This enhances nutrient cycling and allows more nutrients to be availed for plant uptake. Important to mention is that some studies reveal that bacterivore nematodes can stimulate bacterial population growth and hence accruing their abundance (Jiang *et al*., 2017). In view of these contradicting conclusions, Ingham *et al.* (1985) ascertain that the mechanism by which bacterial-feeding nematodes increase the bacterial population in some studies and decrease it in others is intriguing and that the inconsistencies may be nematode species-specific.

2.3.2 Nutrient mineralization

Nutrient mineralization as facilitated by nematodes, results from nematode predation on bacterial, fungal, nematodes populations or other fauna (Mekonen *et al*., 2017). Absorbed C is important for both respiration and assimilation whereas consumed N, P and S are used for assimilation only. In general, nematodes have a greater C: nutrient ratio compared to their microbial (bacterial and fungal) prey (Yadav *et al*., 2018). As a consequence, nematodes ingest more nutrients than needed, and the excesses are excreted in the form of minerals or readily mineralizable compounds such as amino acids, NH_4^+ and PO_4^{-3} (Ferris *et al.*, 2012). However, the nutrient mineralization efficiency might vary depending on the nematode trophic group under consideration. As an illustration, it is hypothetically thought that N release via predation is due to the lower C:N ratio of bacteria (approximately 5:1) compared to bacterial feeding nematodes (with approximately 10:1) whereas fungi feeding nematodes tend to immobilize the nitrogen as most fungi species present a relatively high C:N ratio (approximately 11:1) (Ingham *et al*., 1985).

Nematodes affect nitrogen availability both directly and indirectly. Directly, nematodes excrete ammonium as a by-product since their prey usually has an inferior C:N ratio compared to the demand. Indirectly, they free microbial nitrogen immobilized through metabolism, excretion and dispersion of microbes to more appropriate substrates (Ingham *et al.*, 1985). In fact, Irshad *et al.* (2011) found out that the involvement of nematodes was essential so that a significant accumulation of ^{15}N (bacterial originating nitrogen) as well as the inorganic phosphorus in *Pinus pinaster* shoots can be observed in comparison to the sterile plants. But, even though the quantity of ^{15}N represented 0.7% of the total amount in the presence of bacteria, pine plants benefited from the nematode colonization in the rhizosphere. In this experimentation, the low accumulation of N in the shoots of plants grown alone (sterile plants) or with bacteria only compared to the combined treatment (Bacteria and Nematodes)

reveals that bacteria only, despite their ability to grow on nitrate, couldn't provide a source of N ready for uptake by plants (Irshad *et al.*, 2011). Similarly, Gebremikael *et al*. (2016) found significant increase of the net nitrogen and phosphorus by 25 % and 23 %, respectively, in the presence of nematodes compared to their absence. The increase in the net nitrogen and phosphorus, in this study, resulted in a 9 % improvement of *Lolium perenne* above ground biomass production (Gebremikael *et al*., 2016).

The mineralization rate as well as the concerned nutrients are more likely dependent on the dominant trophic group. In fact, bacterivore nematodes are more involved in nitrogen mineralization whereas fungivore nematodes facilitate the phosphorus mineralization (Ferris *et al.*, 2012). In conventional and integrated farming systems, bacterivore and predatory nematodes participate for 8% to 19% to nitrogen mineralization, respectively (Neher, 2010). However, fungi forest soils and bacterivore nematodes in low fertility deserts soils can cause nitrogen immobilization and hence moderating nitrogen mineralization (Neher, 2010).

2.3.3 Biological control of pests and diseases

While certain soil nematodes are pathogens to plants, others operate as predators, reducing the population of pathogenic bacteria and fungi and therefore preventing the spread of some illnesses vectored by these pests (Neher, 2010) such as the banana weevil (*Cosmopolites sordidus*) (Gold, 2001). In a greenhouse experiment, *Aphelenchus avenae* substantially suppressed *Ralstonia solani*-induced damping-off of cucumber (Ishibashi, 1991, 2005). In addition, both *Aphelenchus avenae* and *Steinernema carpocapsae* suppressed gall number (caused by the root-knot *Meloidegyne incognita*) on tomato roots (Ishibashi, 1991). Whereas mixed application of these nematodes was expected to cause significant decline in gall formation than single application, the contrary was true, insinuating an antagonistic interaction between *A. avenae* and *S. carpocapsae* (Ishibashi, 1991). This antagonistic

interaction between these nematodes seems to be eminent since many different nematode species concomitantly coexist in the soil.

2.4 Nematodes as plant pathogenic agents

Plant parasitic nematodes feed on the cytoplasm of plant cells by injuring the plant roots physically, inducing plant hormone responses that alter source-sink interactions and reduce primary productivity of their hosts. In their feeding process, the nematode may be internal or external to the root and either remain sedentary or migrate through plant tissue (Neher, 2010).

The damages caused to plants by plant-parasitic nematodes rarely occur distinctly from other soil-borne pathogen attacks. In fact, in nature plants are rarely, if ever, submitted to the influence a single potential pathogen. This is more recurrent as far as soil-borne pathogens are concerned, where there is a great possibility for interaction with other microorganisms occurring in the same ecological niche. The mechanisms facilitating these complex interactions include the exploitation of nematode-induced injuries by soil-borne pathogens, nematode- or pathogen-triggered physiological changes to the host plant, alteration of the rhizosphere ecosystem and the reduction of host resistance (Back *et al.*, 2002).

2.5 Impact of agricultural practices on soil nematode population

Different cropping and horticultural management practices induce a continuous perturbation of soil, soil wildlife and crops such that there is no equilibrium between these different components. Most of these disturbances are due to agricultural practices whose intensity and frequency influence both physico-chemical and biological soil parameters. In fact, manipulation of water and nutrients through agricultural practices (fertilization, irrigation, tillage, organic amendment, etc.) is more likely to modify the relative sizes of bacteria, fungi, algae, and plant roots, and thus the trophic structure of the nematode community (Bernard,

1992). In this section, mention is made of the most common agricultural practices implemented for the management of soil fertility and improvement of crop yield and that are likely to influence both directly or indirectly the soil nematofauna community. These practices include among others the crop cover, mulches, soil amendment, tillage practices, fallowing, crop rotation and agroforestry practices.

2.5.1 Cover crops and soil nematodes

Apart from improving soil fertility, crop cover is reputed as a practice that contributes to the maintenance of a high soil microbial activity. In a field experiment, Wang *et al.* (2006) found out that total abundance of bacterivores and fungivores was depressed by methyl bromide, solarisation, and solarisation + cover crop (cowpea, *Vigna onguiculata*) treatments compared to a natural fallow or cover crop (cowpea, *Vigna onguiculata*) treatments. However, this perturbation did not persist at the end of the subsequent intensive cultivation of pepper (*Capsicum annum*) in the plots previously subject to these treatment (Wang *et al.*, 2006). Similarly, DuPont *et al.* (2009) found a total nematode abundance 72% greater in cover crop treatments containing legumes compared to bare fallow, as a result of ample resources under cover crops treatment. In their experiment, Sánchez-Moreno *et al.* (2006) also observed a decreasing population density of bacterivore and fungivore nematode after continuous cultivation of cereals whereas omnivore and predators followed an opposite trend. Besides, the effectiveness of the cover crop in eradicating plant-parasitic nematodes depends on their host status as well as the cultivation season. Since different plants can have dissimilar effect on the population of plant-parasitic nematode, it is likely that plant species affects not only specific plant-feeding nematodes but also the impact of the microbial-feeding nematodes on the nematode fauna (Yeates and Bongers, 1999) insinuating that the effect of cover crop on the abundance of soil nematode is not only trophic group but also species dependent. During winter season, Wang *et al.* (2004) found that the cereal cover crops, except wheat, were more

efficient in reducing numbers of *Meloidogyne incognita* than the leguminous cover crops. This situation can partly be justified by the fact that organic matter with low C:N ratio tends to favour opportunistic bacterivore nematodes on the expense of high trophic groups of predatory and omnivorous nematodes that can reduce the plant-parasitic nematode population density (DuPont *et al.*, 2009).

2.5.2 Organic amendments, mulches, fallow, crop rotation and soil nematodes

Using compost, green and animal manure as organic amendments enhances or preserves soil health and soil quality. Moreover, organic amendments create favourable conditions for antagonistic soil organisms, stimulate the competitiveness of the non-pathogenic organisms and its decomposition can produce toxic compounds, all of which induce their direct effects on the dynamics of soil-borne pathogens, including plant-parasitic nematodes (Thoden *et al.*, 2011). Inconsistent results regarding the influence of organic amendment on the abundance of plant-feeding nematodes have been stated by several studies. Interestingly, these studies mostly find increasing crop yields as a consequence of organic amendment application. Such a situation can be ascribed to the role of the organic amendment in the stimulation of other free-living nematodes involved in nutrient mineralization as previously discussed. However, the quality and the quantity of organic inputs have a significant impact on nematodes and usually influence the overall structure of their population (Yeates and Bongers, 1999; Puissant *et al*., 2021).

Differently from the organic amendments that are incorporated in the soil, organic mulches are applied on the soil surface and can only decompose at a very low rate. Hence, the detection of their effect on soil nematode community structure can take long (Wang *et al.*, 2008). In a six year old raspberry orchard, Forge and Kempler (2009) found a 20 % and 34 % reduction of plant-parasitic nematode *Pratylenchus penetrans* on plots treated with broiler

dung with overlying mulch of shredded paper and layer dung + yard compost, respectively, compared to plots that received urea fertilizer. These data demonstrating differential effect on the plant-parasitic nematode *Pratylechus penetrans* by different kinds of organic mulches advocate that the effects are specific, not just associated with cumulative organic matter and the overall biological activity associated with it (Forge and Kempler, 2009).

Continuous cultivation, as a result of pressure on land resources due to land scarcity, contributes to crop yield decrease in tropical farming systems. This is related to soil degradation as a result of soil biological activity reduction and organic matter depletion when nothing is done to compensate for the exported nutrients through crop harvest. Fallowing (natural or cultivated) is an agricultural practice that has long been implemented for the restoration of the soil fertility, erosion control, enhancement of biological activity and as a pest and/or disease management strategy (Odeyemi *et al.*, 2013). The soil nematode community structure is also affected by the duration of the fallow. In the Sahel, it was found that the average plant parasitic nematode population densities decreased linearly (r=0.68) and significantly with fallow age between 1 and 17 years. This decline would theoretically induce the plant-parasitic nematode community disappearance after 21 years (Cadet and Floret, 1995). In the 17-year-old fallow, these authors found greater populations of free-living nematodes in fenced plots than in disturbed ones and in woody than in herbaceous areas. Important to mention is that the influence of the fallow on the soil nematode community, particularly plant-feeding nematodes, depends on the host status of the vegetation cover and the nematode species under consideration. In the Nigerian agro-ecological conditions, Odeyemi *et al.* (2013) found that a 2-year-old *Chromolaena odorata* cultivated fallow and the combination of *Chromolaena odorata* with natural re-growth significantly reduced population densities of *Meloidogyne* spp. (77.2% and 51.17% reduction, respectively), *Pratylenchus* spp. (75% and 69% reduction, respectively) and *Helicotylenchus* spp (81.3% and 67% reduction,

respectively) compared to natural fallow. However, the increase in population density of *Rotylenchulus* under *Chromolaena odorata* by 16%, opposing with the decrease by 54.1% in the population density in the natural regeneration fallow management revealed the potential host status of *C. odorata* to this particular nematode species (Odeyemi *et al.*, 2013).

Crop rotation is often resorted to as an integrated management strategy of plant-feeding nematodes. Their suppression through crop rotation is a result of either active or passive processes. The active processes consist of alternating plant species that produce allelochemicals that inhibit the multiplication of the nematodes or reduce their physiological activities whereas the passive processes refer to the alternative cultivation of host and non-host plant species that interrupt the reproduction cycles of the nematodes (Halbrendt, 1996). This implies that the effectiveness of crop rotation in the management of plant-feeding nematodes depends on the host status of plant species in the sequence (Kratochvil *et al.*, 2004; Matute and Anders, 2012). As an illustration, a study conducted in the Western Bengal, India, found that a crop sequence of cabbage, mustard and rice had a suppressive effect on *Meloidogyne incognita* whereas okra, brinjal, cowpea and tomato supported nematode growth in the field (Chandra and Khan, 2011). Hence, crop rotation sequences that diminish the abundance of plant-feeding nematodes and increase that of free living nematodes are the most wanted (Matute and Anders, 2012).

2.5.3 Tillage, inorganic fertilization and soil nematodes

Tillage practices varying from conventional tillage to conservation tillage (no-tillage and reduced tillage) influence soil physio-chemical and biological parameters either directly or indirectly by inducing change in the soil environment (soil pH, soil water content, bulk density) (Zhang *et al.*, 2019). Soil organisms respond differently to tillage disturbance. This response vary among species with high tolerance among micro-organisms compared to

macro-organisms or those belonging to high trophic levels (Zhang *et al.*, 2019). Soil nematode community structure is strongly influenced by the disturbance imposed by different tillage regimes and is mostly used as a reflection of stability of the soil ecosystem (Yeates and Bongers, 1999). Comparing the effect of the tillage practices (conventional versus no-tillage) on the soil nematode structure, Okada and Hadara (2007) found insignificant tillage effects on nematode density whereas the effects on diversity and community indices were visibly substantial. The conventional tillage tends to favour opportunistic bacterial nematode feeders whereas high trophic level groups (omnivores and predators) are sensibly depressed since they are susceptible to physical as well as chemical disturbances (Sánchez-Moreno *et al*., 2006; Neher, 2010). Hence, no-tillage supports a diverse community of soil nematodes since it allows organic matter build-up in soil, and hence providing microhabitats with suitable moisture and food (microbes and protozoa) for the nematodes (Okada and Harada, 2007). This was confirmed by high nematode indices (Maturity Index, Structure Index and Chanel Index) in no-tillage compared to standard tillage.

Studies assessing the effect of mineral fertilizers on the community of plant-feeding nematodes have reported inconsistent conclusions. Those reporting increasing counts of plant-feeding nematodes in mineral fertilized treatments attribute this trend to an increase in the root biomass that provide more feeding sites to the herbivore nematodes (Benkovic-Lacic *et al.*, 2013; Okae-Anti *et al.*, 2013). However, the observed perturbation of the free-living nematode community structure in the mineral fertilized field is due to change in subsequent soil agrochemical properties (soil pH and CEC) that become hostile to high trophic groups (omnivores and predators) nematodes (Gruzdeva *et al*., 2007; Benkovic-Lacic *et al*., 2013). Inorganic fertilizers consistently suppress the population density of soil free-living nematodes in croplands (Zhao and Neher, 2013) as well as in secondary tropical forest soils where phosphorus addition has a greater effect compared to nitrogen addition (Zhao *et al*., 2014).

However, the application of NPK at 60 kg ha^{-1} and 180 kg ha^{-1} on soils with a background incorporation of organic manure did not influence the structure of nematode population in a 9-year experiment in Russian agro-ecological conditions whereas the application of these rates of mineral fertilizer on plot without manure background resulted in a significant dominance of phytophages over other trophic groups (Gruzdeva *et al.*, 2007).

2.5.4 Agroforestry practices and nematode population dynamic

Studies of soil nematode dynamics have largely focused on the agricultural practices susceptible to induce change in the above-ground vegetation and soil perturbations (physical or chemical) induced by different farming systems. Only fragmented knowledge exists about the effects of agroforestry practices on abundance and diversity of soil nematode populations either due to temporal sequences or spatial arrangement of the woody component of the system. More important is the fact that the scarce studies on the influence of agroforestry practices on the soil fauna do not cover the majority of agro-ecological zones as well as the diverse agroforestry systems in the tropics and hence, result generalization is still limited (Barrios *et al.*, 2012). Besides, the commonly adopted homegarden agroforestry systems are a complex mixture of different tree species with annual crops whose influence on the soil physico-chemical as well as biological properties results from complex interactions among the different elements that constitute the system. Therefore, most of the existing results on nematode community structure in agroforestry systems can shed light on our understanding of soil ecosystem functioning under agroforestry systems without being a practical tool for decision making.

As an illustration, Falkowski *et al.* (2019) found that *Lonchocarpus guatemalensis* negatively affected the counts and diversity of plant parasitic nematodes and resulted in a 25.4% increase of plant-parasitic nematode per meter from this particular tree's stems in the Lacandon Maya,

Mexico, agroforests. Whereas this trend was not observed for other tree species and other nematode feeding groups (Falkowski *et al.*, 2019), the occurrence of many tree species on the same farm might have induced a dilution effect on the nematode populations (Viketoft *et al.*, 2009). In these agro-ecosystems, the nematode population regenerated faster after fire disturbance. The nematode community displayed tendencies that seemed to depend more on successional stages and management practices than time from fire disruption (Diemont and Martin, 2005).

Besides, the effect of individual trees on the nematode population structure can be affected by the tree size and age. Studies in Lacandon agroforests didn't find any trend with respect to nematode and soil chemical properties in *milpa* and *acahual* (early successional stages of the Lacandon agroforest, 5-12 years after fire-induced perturbation) along an increasing distance from the *Ochroma pyramidale*. Yet, in later stage of the succession (secondary forest) nematodes exhibited trends contrasting that of leaf litter depth, with total nematode increasing from 8 per 20 g soil at the trunk to over 60 at a distance of 14 m. This trend is inconsistent with expectations and precludes the existence of inhibitory effect of the leaf litter of this particular tree species (Diemont *et al.*, 2006).

CHAPTER THREE

MATERIALS AND METHODS

3.1 Description of the study site

This study was conducted in Kirinyaga County, which is located 120 km North West of Nairobi (Noah *et al.*, 2019). This County is situated between latitudes 0°1' and 0°40' South and longitudes 37° and 38° East and covers an area of 1,478.1 km^2 (Oginosako *et al*., 2006). It lies between 1,158 m asl in the South and 5,380 m asl at the Peak of Mount Kenya (Castro, 1983). The area has a bimodal rainfall pattern, with long rains from March to May and short rains from October to November (Jaeztold *et al*., 2006). The study area was subdivided into three agro-ecological zones (Figure 1 and Table 1) based on their probability of meeting the temperature and water requirements of the crops as established by Jaeztold *et al*. (2006).

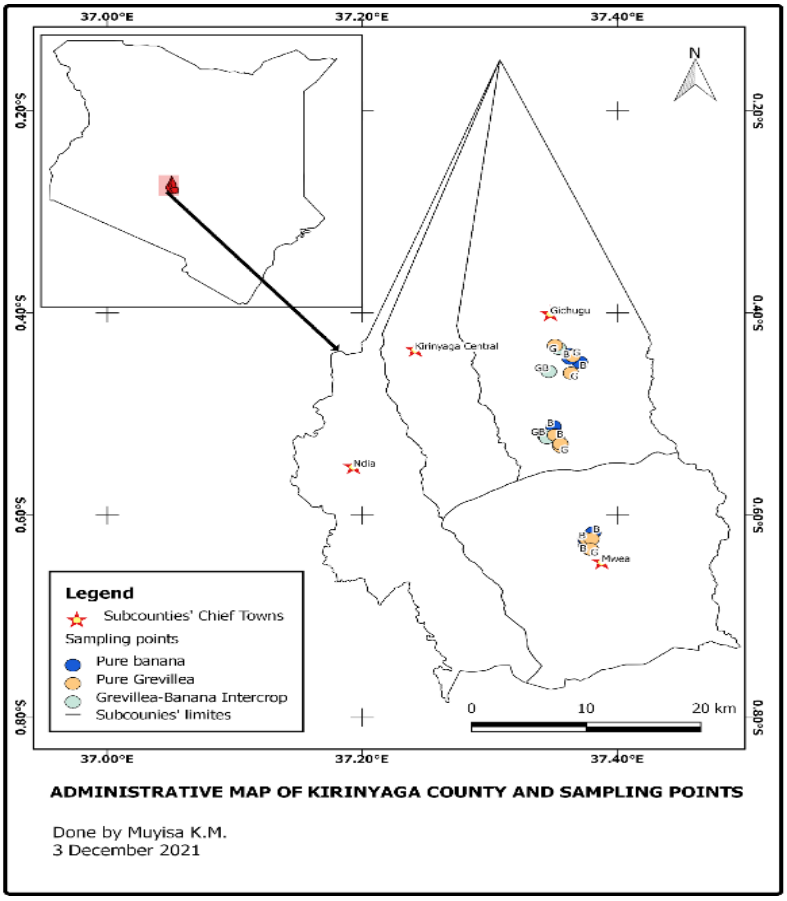

Figure 1: Administrative units in Kirinyaga County and sample collection points

Table 1: Characterization of the study site based on Jaeztold *et al*. (2006)

	AEZ	Altitude range (1)	Average annual rainfall (1)	Soil Type (2)	Soil Characteristics (1,2)	Acreage (1)		Land use and tree plantation
						In ha per household	In ha per person	
1	Highland Zone (LH1= Tea-dairy zone)	1760-2130 m asl	1 700-2 150 mm	Nitisols, Andosols	Well drained, extremely deep, dark reddish brown to dark brown, friable and slightly smeary clay, with an acid humic topsoil and high fertility	0.62	0.16	• Highly intensive mixed farming: crop, livestock and tree production (3). • Tea plants occupy more space on farm such that other trees are not allowed inside a tea farm and only some exotic tree species are planted on the farm edge (4).
2	Midland Zone (UM1=Coffee-tea zone and UM2=main coffee zone)	1400-1820 m asl	1 200-1 820 mm	Ferralsols, Cambisols, Acrisols, Phaeozems,	Well drained, moderately deep to deep, dark red to yellowish red, friable, sandy clay loam to clay	0.85	0.21	Numerous trees are planted, even if species number is not so high, with the predominance of exotic trees (3).
3	Lowland Zone (LM3=cotton zone and LM4=marginal cotton zone)	1090-1280 m asl	800-1 200 mm	Vertisols, Ferralsols and Acrisols,	Poorly drained, very deep, dark grey to black, firm to very firm, bouldery and stony cracking clay; in places with a calcareous, slightly saline deeper subsoil	1.6	0.40	• Less land fragmentation and prevalence of food crop cultivation (5). • Dominance of indigenous tree species such as *Melia volkensii*, *Acacia* spp. and *Commiphora* spp., frequently preserved under natural vegetation without perturbation or retained on agricultural lands from the natural vegetation (4).

(1) (Jaeztold *et al*., 2006) ; (2) (Pauw and Sombroek, 1980); (3) (Oginosako *et al*., 2006), (4) (Kehlenbeck *et al*., 2011) ; (5) (Office of the Governor, Kirinyaga County, 2017)

Abbreviations: m asl= meter above sea level, AEZ=Agro ecological zone, LH= Low Highland, UM=Upper midland, LM=Low midland

3.2 Selection of the farms for soil sampling and household survey

For each cropping system, three representative farms were randomly selected in each AEZ for soil and litter sampling. The selection of farms within the same AEZ was based on similarity in tillage practices, pesticide/chemical application, irrigation, topography and at least three kilometres apart. In total, 27 farms were identified within the three AEZ. A data entry tool was used to capture information on the farming operations as well as *Grevillea robusta* tree management practices undertaken in the farming systems belonging to different AEZ (Appendix 7).

3.3 Collection of soil samples

The protocol used in soil sampling is presented in Figure 2. Under the banana-grevillea intercrop, soil sampling was done at fixed points around the tree (Anderson and Ingram, 1996) as an adaptation of the method described by Kamau *et al.* (2017). The area around the selected trees was delineated into four concentric zones, A, B, C and D. Approximately, the sampling point A, B, C and D around the single grevillea tree were always taken at 0.25; 1; 2 and 5 m from the tree stem, respectively, since the average canopy diameter of these trees was 5 m under the current management scheme in the Central Kenya (Owate, 2018).

In banana and grevillea pure stands, two sampling points were marked following a random zigzag method (Estefan *et al*., 2013). From each sampling point, five samples were collected, bulked and mixed thoroughly to make one composite sample from which one kilogramme was taken for both nematode extraction and soil physico-chemical determination. From one sampling point to another, sampling implements were sterilized by spraying with 70% alcohol to avoid cross contamination. Samples were transferred into ziplock polythene bags and kept in a cool box before delivery to the laboratory.

Soil sampling took place during the dry and rainy season which occurred in April and July 2021, respectively. A total of 108 soil samples was collected in each of the seasons as illustrated in table 2 below.

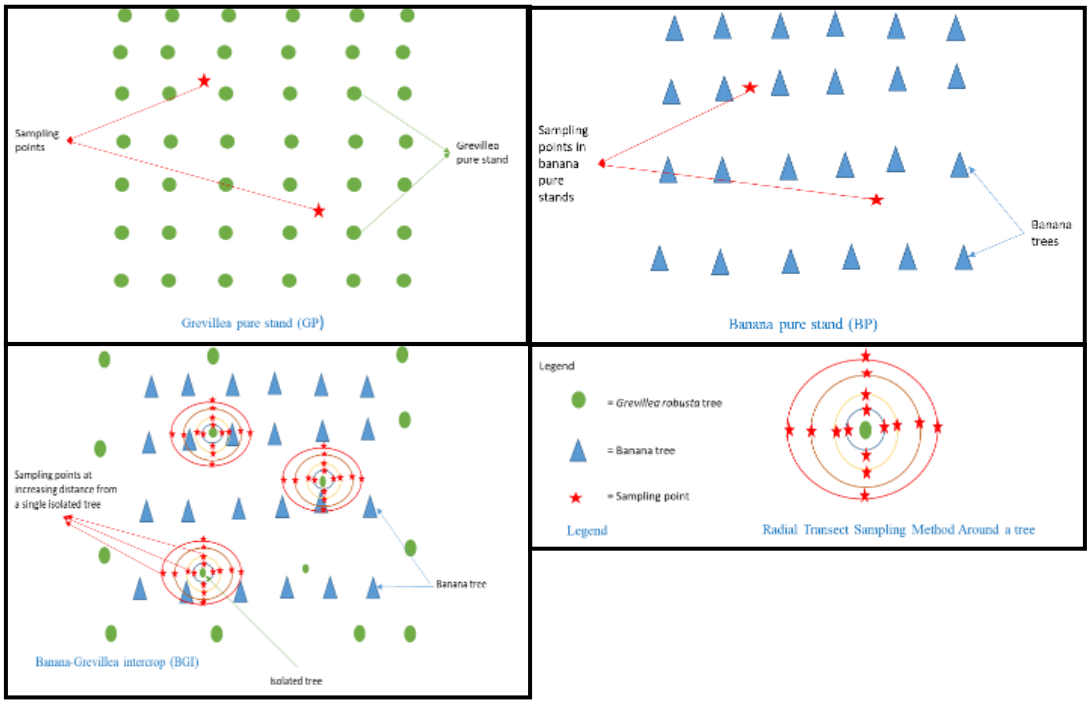

Figure 2: Soil sampling method used to collect samples from fields under sole Grevillea, sole banana and banana-grevillea agroforestry system

Table 2: Sampling methods and sample size in the three cropping systems

Type of Cropping Systems	Sampling method	Number of Composite Samples per Farm	Number of farms per AEZ	Total number of samples
Grevillea Pure Stand Inside Farm (GIP)	Zig Zag	2	3	6
Banana Pure Stand Soil (BPS)	Zig Zag	2	3	6
Banana-Grevillea Intercrop Inside the Farm (BGI)	Zig Zag and Radial Transect	8	3	24
Total Number of Soil Samples /AEZ/ season				36
Total Number of Samples / Season			36 x 3	108
Total Number of Samples			108x 2	216

3.4 Procedures for extraction of nematode, identification and classification

Nematodes extraction from composite soil samples was done using Baermann tray technique, a modification of the Baerman Funnel techniques as described by Kleynhans *et al.* (1999). A 200 cm^3 composite soil sub-sample was spread onto a double-layer of paper towels which was supported by a coarse-meshed screen standing in a shallow plastic dish. Water was added into the dish until the soil looked wet. The meshed screens were covered with a plastic dish to reduce the evaporation rate. Nematodes were allowed 48 hours to move from the soil through the paper towels, into the water in the dish. The nematode suspension was concentrated before a known volume was drawn and nematode examined and enumerated under a compound microscope.

Nematodes extracted from soil samples were fixed by suspending the extractant in a hot water bath at 50-70°C (Hooper, 1970; van Bezooijen, 2006) and fixed in 4 % formalin solution (Zhong *et al.*, 2016). After settling, nematodes were counted by microscopic observation at x40 magnification (van Bezooijen, 2006) and the total nematode counts were recorded. From the slide mount of each soil sample, all the encountered nematodes were identified to genus level based on the morphological and morphometric features of the nematodes by the use of a compound microscope at x400 magnification (Thuo *et al.*, 2020a). Identification tools consisted of nematode standard identification keys among others “The Pictorial Key to Genera of Plant Parasitic Nematodes”, “C.I.H. Description of Plant Parasitic Nematodes and the Interactive Diagnostic Key to Plant-parasitic and free-living nematodes” (Tarjan *et al*., 1977).

All the enumerated nematodes were grouped into five trophic groups of herbivores, bacterivores, fungivores, predators and omnivores (Bongers and Bongers, 1998). Thereafter, all nematode genera were assigned to functional guilds based on the combination of feeding

type and life history characteristics expressed as colonizer–persister (c-p) scores which range from 1 (extremely r-strategist) to 5 (K-strategist) as described by Ferris *et al*. (2001).

3.5 Calculations of the nematode ecological indices

These indices include: Shannon-Wiener's diversity index, Taxonomic evenness, Maturity Index (MI), plant parasitic index (PPI), Channel Index (CI), Structure Index (SI) and Enrichment Index (EI).

Shannon-Wiener's diversity index was used to assess the diversity of nematode community and calculated as:

$$Diversity\ H' = -\sum_{i=1}^{s} pi\ log_e\ pi \qquad \text{(Equation 1) (Yeates and Bongers, 1999b)}$$

Where p_i is the proportion of individuals in the *i*th taxon, *s* is the total number of taxa identified in a sample. The taxonomic evenness is a useful index to assess the distribution of individuals among the different taxa identified in a sample and was calculated as

$$Evenness = \frac{H'}{H'max} \qquad \text{(Equation 2)}$$

Where *H'*= Shannon-Wienner's diversity index and *H'max*=$\log_e S$; S being the total number of taxa identified in the sample.

The maturity index (MI) is based on non-plant feeding taxa and considered as a measure of environmental disturbance (Ferris and Bongers, 2009). It is calculated as

$$MI = \sum_{i=1}^{f} \frac{vi * ni}{n} \qquad \text{(Equation 3)}$$

Where v_i = colonizer-persister (c-p) value assigned to the taxon *i*, n*i* = number of nematodes in each of the *f* taxa (except plant parasitic nematodes) and n = total number of nematodes in the sample (except Plant Parasitic Nematodes) (Ferris and Bongers, 2009). The same equation was used for the calculation of the Plant Parasitic nematode Index (PPI) where n*i* is the

number of plant parasitic nematodes in each taxon of plant parasitic nematodes and n the total number of the plant parasitic nematodes in the sample.

The distribution of nematodes in functional groups based on their trophic group and life strategy (c-p group) allowed the calculation of: the Enrichment Index (EI), Structure Index (SI) and Channel Index (CI). According to Ferris *et al* (2001), the EI provides location of the food web along the enrichment trajectory (enriched or depleted) and is calculated as

$$EI = 100 * \frac{e}{e+b} \qquad \text{(Equation 4)}$$

In a similar way, the SI provides location of the food web along the structure trajectory for nematodes of c-p values greater than or equal to 3 and is calculated as

$$SI = 100 * \frac{s}{s+b} \qquad \text{(Equation 5)}$$

In equation 4 and 5, b, e and s represent the basal, enrichment and the structural components of the nematode fauna and calculated as (Ferris and Bongers, 2009):

$b = (Ba_2+Fu_2)*W_2$; where $W_2 = 0.8$

$e = (Ba_1*W_1) + (Fu_2*W_2)$; where $W_1 = 3.2$ and $W_2 = 0.8$

$s = (Ba_n*W_n + Ca_n*W_n + Fu_n*W_n + Om_n*W_n)$

where n = 3-5; $W_3 = 1.8$; $W_4 = 3.2$; $W_5 = 5.0$

The Channel Index which provides the partition flow of resources through fungal and bacterial decomposition pathways (Ferris and Bongers, 2009) informs about the primary decomposition channel and reflects the proportion of opportunistic fungal-feeding nematodes among all opportunistic fungal and bacterial-feeding nematodes (Cesarz *et al*., 2015). This index is calculated as

$$CI = 0.8 * \frac{Fu2}{3.2*Ba1 + 0.8*Fu2} \qquad \text{(Equation 6) (Ferris } et\ al\text{., 2001)}$$

3.6 Soil chemical characterization

For the soil chemical analyses, the following parameters were analysed: Soil Organic Carbon, Soil Total Nitrogen, Soil ammonium and nitrate nitrogen (NH_4^+-N and NO_3^--N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), pH, texture, bulk density and soil moisture content.

Soil organic carbon was determined following Walkley-Black method (Poudel, 2020; Sullivan *et al.*, 2019), total nitrogen was determined by Kjedahl method. Available nitrogen namely Ammonium-N and nitrate-N were extracted using 2M potassium chloride (KCl) method (Gami and Ketterings, 2017) and determined by the steam-distillation methods of analysis on a single 2M KCl soil extracts (Okalebo *et al*., 2002). Available K, Ca and Mg were analysed using the Mehlich double acid method followed by atomic absorption spectrophotometer analysis for their quantification whereas phosphorus was quantified by the ascorbic acid colorimetric method as described by Okalebo *et al*. (2002). Soil pH was measured with an electrical pH-meter in a 1 to 2.5 soil to water solution.

3.7 Determination of soil physical characteristics

Soil moisture content was determined by oven-drying a known soil mass (W_1) at 105 °C to a constant weight (W_2). Moisture content was then calculated following equation (7) below.

Soil moisture content (%) = $\frac{W1-W2}{W2-C} * 100$ (Equation 7) (Estefan *et al*., 2013).

Where W_1 = Weight of fresh soil + container

W_2= Weight of the dry soil + container and C= weight of the container

The soil bulk density was measured by the core ring method which consists of using a thin-sheet metal tube of well-known weight (W_1) and volume (V) to pick an undisturbed surface soil sample. After cutting the soil beneath the tube bottom, excess soil from the tube ends was

carefully removed using a knife. The tube containing this soil sample was oven-dried at 105°C for 2 days, and weighed (W_2). Soil bulk density was calculated following equation (8).

Soil bulk density (g/cm^3) = $\frac{W1-W2}{V}$ (Equation 8) (Okalebo *et al*., 2002)

Soil texture was determined by the hydrometer method. It consists of saturating 50 g of air-dried soil sample which has been passed through a 2 mm sieve with water and 50 ml of 10% Calgon (Sodium Hexametaphosphate) solution to ensure dispersion of individual soil particles. It is recommended to keep on adding hydrogen peroxide until effervescence stops which ascertains a complete digestion of the organic matter (Anderson and Ingram, 1996). When this reaction stopped, the sample was transferred in a shaking bottle and shaken on a reciprocal shaker for 6 hours. The suspension was transferred from the shaking battle to a measuring cylinder filled to the 1000 ml mark with water. Before taking the first reading, the suspension was thoroughly mixed by inverting the cylinder carefully ten (10) times. At 40 seconds, the first hydrometer reading (H_1) and the suspension temperature (T_1) were taken (Okalebo *et al*., 2002). After two hours, the second hydrometer reading (H_2) and temperature (T_2) was taken without disturbing the suspension. Necessary corrections were made on the hydrometer readings before calculation of the different particle size percentages (Okalebo *et al*., 2002) following equations 9, 10 and 11 below.

Sand (%) = $\frac{50-H1\prime}{50} * 100$ (Equation 9)

Clay (%) = $\frac{H2\prime}{50} * 100$ (Equation 10)

Silt (%) = [100 - sand (%) – clay (%)] (Equation 11)

Where H_1' and H_2' are the corrected hydrometer reading 1 and reading 2, respectively.

3.8 Characterization of *G. robusta* litter

Litter traps measuring one meter (m^2) were installed in each field for litter collection and left in place for 50 days, from 4 July 2021 to 22 August 2021. Where trees are scattered in the field (banana-grevillea intercrop), the litter traps were installed in the zone under the tree canopy and in grevillea sole stands they were kept in the middle of the zone delineated by the four closest trees in fields.

The litter was weighed and then processed for chemical analyses where carbon, organic matter, total nitrogen, potassium, calcium, magnesium, phosphorus, lignin and polyphenols content were measured. Complete oxidation of samples was accomplished using Kjeldahl procedures followed by atomic absorption spectrophotometry for potassium, calcium and magnesium analyses. Phosphorus content in the litter was quantified by the Ascorbic Acid colorimetric method (Okalebo *et al*., 2002). Lignin content was quantified following the Van Soest fiber analysis (Goering and Van Soest, 1970). Polyphenols were extracted with methanol as described by Che Sulaiman *et al*. (2017) and total soluble polyphenols were analysed by the Folin-Denis method (Okalebo *et al*., 2002).

3.9 Data Analysis

Data were analysed following a factorial design (3 x 3 x 2) where the independent factors were Agroecological Zones (Highland zones, Midland zones and Lowland zones), cropping systems and seasons (dry and rain).

To assess the effects of agro-ecological zone, cropping system and season on nematode abundance, generalised linear mixed models (GLMM) were used using the package lme4 in R (Bates *et al*., 2015) because soil nematode data deviated from normality (Shapiro-Wilk test) and lacked homogeneity of variance (Levene's test). Further, negative binomial regression was chosen as an extension of the Poisson distribution, using (1|replicates) as a random term

(Kamau *et al.,* 2017) due to a high proportion of zero counts in this dataset. When significant effects were obtained from analysis of variance (ANOVA), Tukey's HSD test was carried out for means separation at $p < 0.05$. To assess the relationship between soil physico-chemical properties and nematode community parameters, Pearson correlation test was conducted. Multivariate analyses were carried out to discriminate the influence of soil factors on the composition of the soil nematode community. The abundance of the different soil nematode genera were used as response variables, and the soil factors served as explanatory variables in a multivariate structure of the Canonical Correspondence Analysis (CCA) thanks to vegan package of R statistical software (Borcard *et al*., 2011).

Data on nematode feeding groups were subjected to tests for generic richness, abundance, Shannon-Wiener's and Maturity indices. These indices were subjected to correlation analysis with the soil properties to reveal how soil health across the banana-grevillea complexes varies. Analysis of the socio-economic data was done using the Fisher's Exact Test for Count Data for independence of factors (The Pennsylvania State University, 2021; The University of Texas at Austin, 2015).

CHAPTER FOUR

RESULTS

4.1 Household survey results and description

The surveyed households cultivate either dessert banana only (55.56 %) or a mixture of dessert and cooking banana (44.44 %). Farmers obtained planting materials from their own banana plantations, neighbours, institution selling tissue cultured seedlings or any combination of these sources of planting materials (Figure 3). The age of the banana plantations fluctuated between 1 year and more than 5 years. Majority of farmers (44.4 %) had more than 5 year-old banana plantations whereas 33.3 % hold a 1 to 3 year-old plantation and only 22.3 % cultivate a 3 to 5 year-old plantation. The planting density was significantly higher in banana sole stands than in grevillea-banana intercrops (Table 3). The dominant banana planting density extended to more than 600 stools/ha (61.1 %) whereas 39.9 % of banana farms were planted at 300 to 600 stools/ha of planting density.

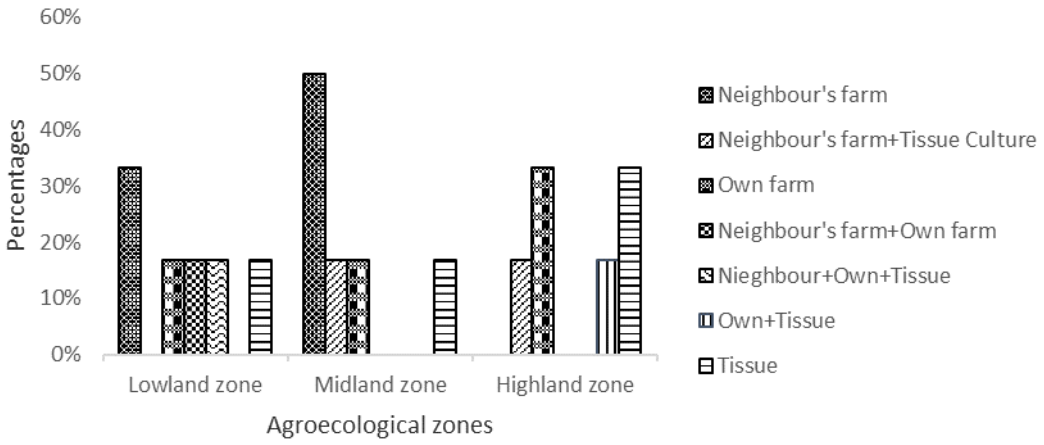

Figure 3: Source of banana planting material

In grevillea-banana systems, 44.4 % of farmers grew other crops including cereals, legumes and vegetables whereas the remaining (55.6 %) did not. Where banana is intercropped with other annual crops, land preparation consisted of ploughing, harrowing and in most cases the combination of the two (Table 3). In addition to manure, which is mostly used, inorganic

fertilizers like CAN, DAP and NPK (17-17-17; 23-23-23 and 25-25-25) are used to supplement the nutrient deficiencies of the annual intercrops (Figure 4).

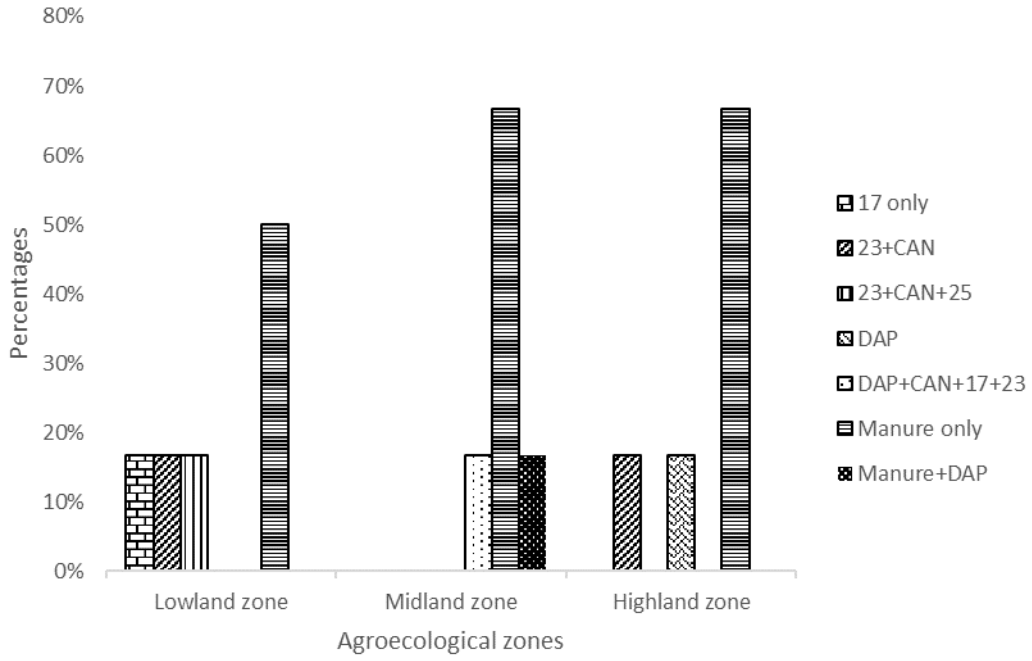

Figure 4: Fertilizer applied on the intercrops

On the banana disease symptoms occurrence, only 27.8 % of farmers have never observed any symptom on their banana plants. Common symptoms of banana diseases reported by farmers included leaf yellowing evolving in leaf wilting, banana toppling, banana stunted growth followed by banana toppling and fruit rot (Figure 5). Management of banana diseases included uprooting the diseased plants, use of pesticides or no action. The management of the diseased plants was highly dependent on the observed symptoms (p-value=<0.001). In this regard, it was found out that all the farmers who experienced banana toppling did not apply any disease management strategy whereas those who experienced banana toppling coupled with stunted growth and fruit rot, only uprooted the diseased banana. However, among those who observed leaf yellowing followed by plant wilting, 40 % uprooted the diseased plants, 30 % used pesticides and the remaining 30 % did not take action.

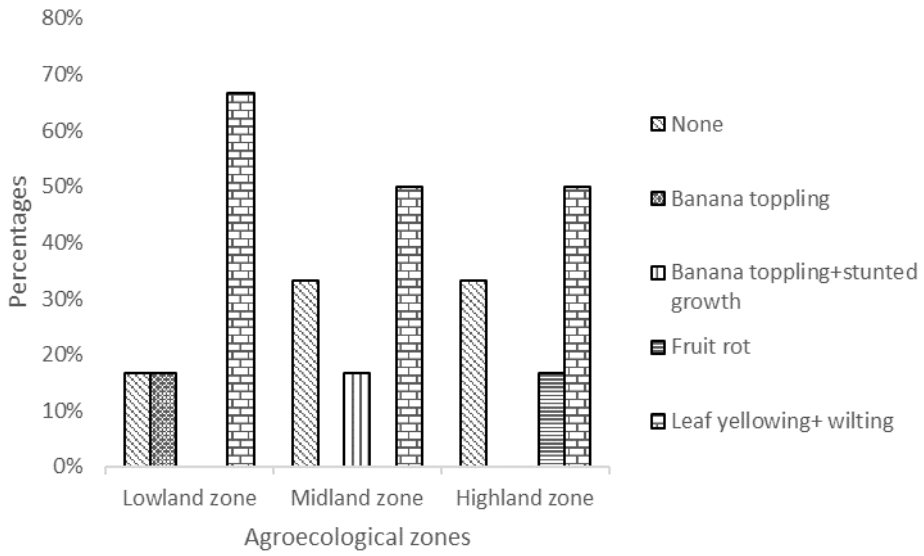

Figure 5: Common symptoms of banana diseases

In farms involving *G. robusta* tree cultivation, the age of the trees ranged from 3 to more than 20 years. Before tree plantation, these farms were either under annual crops, bush fallow, planted fallow or coffee. The tree planting density was significantly higher (p-value = 0.0295) in grevillea pure stands than in grevillea-banana intercrops. Pruning was the only tree management practice done by farmers once in a year (55.56 %), twice in a year (27.78 %), once every two years (5.56 %) and no pruning at all (11.11 %). Pruned litter was used as mulch (50 %), burned (37.5%) or incorporated into the soil after mixing with animal manure (12.5 %). The twigs and big branches were used as fuelwood.

4.2 Chemical characterization of *Grevillea robusta* litter

The mean litter fall was higher in grevillea sole stands (9.89 t/ha) compared to grevillea-banana intercrops (8.48 t/ha). Similarly, highland zone produced more litter fall (12.44 t/ha) than the lowland and the midland zones which yielded 8.81 and 6.30 t/ha, respectively. The total organic carbon, organic matter, phosphorus, calcium and phenols in *G. robusta* litter decreased as the altitude increases (Table 4). Conversely, N and lignin content in litter increased from the lowland at 6.93 g/kg and 35.71 % to the highland at 7.50 g/kg and 39.62

%, respectively. This induced a decreasing C/N ratio trend from the lowland (65.17) to the highland (45.17) zones.

The quality of *Grevillea robusta* litter did not significantly differ between cropping systems. *Grevillea robusta* litter fall, total nitrogen, phosphorus, lignin and polyphenols were slightly higher in grevillea pure stands compared to grevillea-banana intercrops (Table 4). Conversely, total organic carbon, organic matter, C/N ratio, potassium, magnesium and calcium contents were slightly higher in litter collected from the grevillea-banana intercrops than the one collected in grevillea sole stands (Table 4). However, K and Mg content differed between AEZs (Table 4). In the lowland zone, K content was significantly higher at 3.75 g/kg compared to the highland (1.99 g/kg) and the midland (1.77 g/kg) zones. The Mg content in litter was significantly lower at 1.78 g/kg in the highland zone compared to 4.19g/kg in the lowland.

Table 3: Characteristics of the surveyed households

	Variables	Levels	Frequencies (%)							
			Agro Ecological Zones				Cropping systems			
			Lowland	Midland	Highland	*p*-value Fisher's exact test	Banana	Grevillea	Grevillea-Banana	P-value Fisher's exact test
1	Banana variety	Cooking+Dessert	16.70	33.30	83.30	0.1104	33.30	--	55.60	0.1104
		Dessert	83.30	66.70	16.70		66.70	--	44.40	
2	Age of banana plantation	1 to 3 years	66.70	16.70	16.70	0.4197	33.30	--	33.30	1
		3 to 5 years	0.00	33.30	33.30		22.20	--	22.20	
		>5 years	33.30	50.00	50.00		44.40	--	44.40	
3	Banana density	300 to 600 tools/ha	16.70	33.30	66.70	0.3495	11.10	--	66.70	**0.04977**
		> 600 tools/ha	83.30	66.70	33.30		88.90	--	33.30	
4	Banana+other intercrops	No intercrop	66.70	50.00	50.00	0.4088	66.70	--	44.40	0.223
		Cereals + Legumes	0.00	0.00	33.30		0.00	--	22.20	
		Cereals+Legumes+Vegetables	0.00	16.70	16.70		0.00	--	22.20	
		Vegetables	33.30	33.30	0.00		33.30	--	11.10	
5	Land preparation for intercrops	None	66.70	50.00	50.00	0.4068	66.70	--	44.40	0.5162
		Harrowing	16.70	0.00	0.00		11.10	--	0.00	
		Harrowing+Ploughing	16.70	16.70	50.00		11.10	--	44.40	
		Ploughing	0.00	33.30	0.00		11.10	--	11.10	
6	Disease management	No disease experienced	16.70	33.30	33.30	0.8564	22.20	--	33.30	0.8519
		No treatment	16.70	33.30	16.70		22.20	--	22.20	
		Pesticides	33.30	16.70	0.00		11.10	--	22.20	
		Uprooting diseased plants	33.30	16.70	50.00		44.40	--	22.20	
7	Previous crops before tree planting	Annual crops	66.70	50.00	66.70	1	--	55.60	66.70	0.7719
		Bush fallow	33.30	16.70	16.70		--	33.30	11.10	
		Coffee	0.00	16.70	0.00		--	0.00	11.10	
		Planted fallow	0.00	16.70	16.70		--	11.10	11.10	
8	Age of trees	>20years	0.00	33.30	33.30	0.1404	--	33.30	11.10	0.5465
		10 to 20 years	83.30	16.70	16.70		--	22.20	55.60	
		3 to 10 years	16.70	50.00	50.00		--	44.40	33.30	
9	Tree density	< 100 trees/ha	0.00	0.00	16.70	0.3684	--	11.10	0.00	**0.02954**
		100 to 300 trees/ha	16.70	0.00	50.00		--	0.00	44.40	
		300 to 600 trees/ha	0.00	33.30	0.00		--	0.00	22.20	
		600 to 900 trees/ha	33.30	33.30	16.70		--	33.30	22.20	
		> 900 trees/ha	50.00	33.30	16.70		--	55.60	11.10	

Table 4: Chemical composition of *Grevillea robusta* litter from different agro-ecological zones and cropping systems in Kirinyaga County

	Agroecological zones						p-value		
	Lowland		Midland		Highland				
	Cropping systems								
	Grevillea	Grevillea-Banana	Grevillea	Grevillea-Banana	Grevillea	Grevillea-Banana	AEZ	CS	AEZ:CS
Litterfall (t/ha)	10.55^{a}	7.07^{a}	7.05^{a}	5.55^{a}	12.07^{a}	12.81^{a}	0.0529	0.4536	0.6438
C (g/kg)	425.40^{a}	435.97^{a}	367.07^{a}	425.37^{a}	376.37^{a}	403.55^{a}	0.1482	0.0622	0.4465
OM (g/kg)	731.69^{a}	749.86^{a}	631.35^{a}	731.63^{a}	647.35^{a}	694.11^{a}	0.1482	0.0622	0.4465
TN (g/kg)	7.17^{a}	6.70^{a}	7.30^{a}	5.57^{a}	7.43^{a}	7.57^{a}	0.4139	0.2739	0.4376
C/N ratio	62.33^{a}	68.00^{a}	52.33^{a}	78.00^{a}	54.67^{a}	53.50^{a}	0.4687	0.1618	0.295
K (g/kg)	3.81^{a}	3.70^{a}	1.93^{b}	1.61^{b}	1.72^{b}	2.26^{ab}	0.0053**	0.9361	0.74
P (mg/kg)	427.78^{a}	419.44^{a}	413.89^{a}	338.89^{a}	355.56^{a}	344.45^{a}	0.3611	0.4441	0.7487
Mg (g/kg)	3.81^{ab}	4.58^{a}	2.61^{ab}	3.01^{ab}	1.80^{b}	1.77^{b}	<0.001***	0.1425	0.3944
Ca (g/kg)	9.91^{a}	10.86^{a}	8.02^{a}	10.57^{a}	8.70^{a}	11.91^{a}	0.8255	0.149	0.8164
Lignin (%)	36.4^{a}	35.03^{a}	39.66^{a}	35.86^{a}	40.31^{a}	38.93^{a}	0.1112	0.1144	0.688
Phenol (%)	5.63^{a}	6.04^{a}	4.83^{a}	4.5^{a}	5.40^{a}	3.29^{a}	0.2125	0.3239	0.2714

Abbreviations: TOC=total organic carbon, OM= organic matter, TN=total nitrogen, C=carbon, N=nitrogen, K=potassium, P=phosphorus, Mg=magnesium, Ca=calcium, AEZ= Agroecological zone, CS= Cropping system. Mean separation by Tukey's Honest Significant Difference test. In the row, figures followed by similar letter are not significantly different. *p*-values significance: '***' *p*-value < 0.001;'**' *p*-value < 0.01; '*' *p*-value < 0.05. *n*=3

4.3 Characterization of soils under grevillea-banana agrosystems

Soil physio-chemical properties significantly differed between AEZs, cropping systems and seasons ($p < 0.05$) (Table 5).

Soil moisture content was significantly different among the three AEZs, with higher value recorded in the highland zone at 38.63 % followed by the midland zone at 31.95 % and the lowland zone at 26.46 % (Table 5). A significant interactive effect was depicted between AEZ and cropping system on soil moisture content. Hence, in the highland zone, grevillea and grevillea-banana agrosystems had significantly higher soil moisture content compared to banana sole stands. In the midland zone however, a significantly higher soil moisture was observed in banana and grevillea sole stands compared to grevillea-banana intercrop. In the lowland zone, no significant difference was noticed between cropping system with regards to their soil moisture content (Table 5). Besides, the soil moisture content was significantly higher during the dry season (37.12 %) compared to the wet season (27.57 %). Grevillea sole stands had a significantly lower soil bulk density than banana sole stands and grevillea-banana intercrops. No significant difference was noticed in mean soil bulk densities between AEZs but mean values of soil bulk density were significantly higher in dry season than wet season.

Significantly higher soil pH was found in the lowland zone at 5.75 compared to the midland and highland zones, whose respective pH was 5.06 and 5.11 and did not differ. A significant interaction effect between AEZ and cropping system on soil pH was noticed and soil pH under grevillea sole stands in the midland zone was the lowest whereas pH under grevillea in the lowland zone was the highest (Table 5). The mean values of total soil organic carbon decreased significantly from the highland zone at 28.46 g/kg to the lowland zone at 24.29 g/kg. Soil organic carbon in grevillea and banana sole stands did not significantly differ (28.38 g/kg and 27.92 g/kg, respectively) but was higher than the one found in grevillea-banana intercrops (25.34 g/kg). Total organic carbon in the dry season amounted 26.95 g/kg

and was significantly higher compared to the one recovered in the rainy season (25.61 g/kg). The C/N ratio was only influenced by the season with a significantly higher mean value in the dry season at 10.81 compared to the one obtained in the rainy season (8.16).

The total soil nitrogen was significantly higher in the wet season at 3.44 g/kg than in the dry season at 2.78 g/ kg whereas no significant difference was observed neither between cropping systems nor AEZs. A slight increase in total soil nitrogen content was observed from the lowland (2.91 g/kg) to the highland (3.22 g/kg) zones, through the midland zone (3.20 g/kg). Soil from the banana sole stands had a higher nitrogen content at 3.23 g/kg compared to grevillea-banana intercrops (3.10 g/kg) and grevillea sole stands (3.04 g/kg).

Soil NH_4-N significantly differed only between seasons. Significantly higher amounts of NH_4^- N were recovered from these soils during the dry than the wet season. When assessed in the cropping systems, no significant difference in NH_4-N was found though grevillea-banana intercrops yielded higher amounts of NH_4-N (158.86 mg/kg) compared to grevillea and banana sole stands (153.34 mg/kg and 150.26 mg/kg, respectively). In the AEZs, the highest but not significantly different soil NH_4-N content was found in the highland zone followed by the lowland and the midland (136.38 mg/kg) zones (Table 5). The variability in the NO_3-N content was not significant neither between AEZs, cropping systems nor seasons.

Soil phosphorus content was significantly different between cropping systems and AEZs. Besides, a significant interaction effect between AEZs and cropping system was noticed. In lowland and midland zones, grevillea sole stands as well as grevillea-banana intercrops contained 0.03 gP/kg which was significantly lower than the mean value recorded in banana sole stands (Table 5). However, phosphorus content of the three cropping systems did not significantly differ in the highland zone. All soil exchangeable bases (K, Mg and Ca) were significantly dependent on the AEZs. Soil potassium content was significantly higher in the lowland zone (175.22 mgK/kg) than in the highland zone which was also significantly higher

than the one found in the midland zone (Table 5). Soil magnesium content on its behalf increased significantly in the highland than in both the lowland and midland zones, whose soil magnesium contents did not differ significantly. Soil calcium content was not significantly different in highland and midland zones. However, the soil calcium content in these two zones was significantly lower than the one observed in the lowland zone (Table 5). Comparing the cropping systems, the highest soil magnesium and calcium contents were found in banana sole stands followed by grevillea-banana intercrops and grevillea sole stands (Table 5). Soil potassium content on its behalf was the highest in banana sole stands followed by grevillea sole stands and grevillea-banana intercrops. Soil potassium and magnesium contents were higher in the dry season compared to the rainy season. On the contrary, soil calcium content was higher in the rainy season compared to the dry season (Table 5).

Table 5: Physio-chemical properties of soil as influenced by AEZs and cropping systems during the dry and rainy seasons

	AgroEcological Zones								
	Lowland			Midland			Highland		
	Cropping systems								
	Banana	Grevillea	Grevillea-Banana	Banana	Grevillea	Grevillea-Banana	Banana	Grevillea	Grevillea-Banana
	Dry season								
Bulkdensity (g/cm^3)	0.76^{bc}	0.69^{cd}	0.77^{bc}	0.76^{bc}	0.76^{bc}	0.75^{c}	0.91^{a}	0.62^{d}	0.81^{b}
Moisture content (%)	28.53^{c}	28.87^{c}	29.84^{c}	41.98^{ab}	40.53^{ab}	37.77^{b}	42.37^{ab}	44.00^{a}	42.87^{a}
pH	5.76^{ab}	6.50^{a}	5.75^{ab}	5.53^{abc}	4.47^{c}	5.10^{bc}	5.82^{ab}	5.19^{bc}	4.95^{bc}
TOC (g/kg)	26.6^{b}	30.07^{a}	23.9^{b}	26.98^{ab}	27.93^{ab}	27.41^{ab}	29.75^{a}	28.93^{a}	27.39^{ab}
TN (g/kg)	2.42^{a}	3.08^{a}	2.60^{a}	2.35^{a}	2.42^{a}	3.42^{a}	2.93^{a}	2.67^{a}	2.52^{a}
C/N ratio	11.25^{a}	9.86^{a}	9.9^{a}	11.90^{a}	12.54^{a}	9.25^{a}	10.61^{a}	11.82^{a}	12.55^{a}
NH_4-N (mg/kg)	211.42^{a}	223.60^{a}	243.92^{a}	176.08^{a}	195.55^{a}	145.73^{a}	214.41^{a}	186.24^{a}	255.95^{a}
NO_3-N (mg/kg)	134.91^{a}	85.29^{a}	159.38^{a}	67.69^{a}	187.03^{a}	118.68^{a}	86.78^{a}	189.9^{a}	99.95^{a}
P (g/kg)	0.06^{a}	0.02^{c}	0.03^{c}	0.05^{ab}	0.02^{c}	0.02^{c}	0.04^{abc}	0.03^{bc}	0.03^{bc}
K (mg/kg)	170.17^{ab}	178.10^{a}	174.31^{a}	166.01^{ab}	132.66^{bc}	125.74^{c}	154.96^{abc}	159.32^{ab}	155.01^{ab}
Mg (mg/kg)	1092.22^{ab}	787.32^{ab}	499.75^{b}	701.04^{ab}	165.18^{b}	506.56^{b}	1807.14^{a}	242.00^{b}	309.36^{b}
Ca (mg/kg)	803^{a}	739.33^{a}	549.29^{ab}	480.33^{ab}	169.50^{b}	507.75^{ab}	558.83^{ab}	488.33^{ab}	508.58^{ab}
	Rainy season								
Bulkdensity (g/cm^3)	0.96^{a}	0.61^{b}	0.7^{b}	0.67^{b}	0.59^{b}	0.73^{b}	0.80^{ab}	0.71^{b}	0.64^{b}
Moisture content (%)	27.71^{bcd}	22.16^{d}	22.74^{d}	27.21^{bcd}	24.01^{cd}	24.64^{cd}	31.78^{abc}	41.17^{a}	33.19^{ab}
pH	5.61^{ab}	5.72^{a}	5.60^{ab}	5.19^{abc}	4.76^{c}	5.10^{bc}	5.23^{abc}	4.93^{bc}	5.08^{bc}
TOC (g/kg)	27.28^{ab}	27.28^{ab}	21.16^{b}	28.16^{a}	26.52^{ab}	23.45^{ab}	28.74^{a}	29.53^{a}	28.75^{a}
TN (g/kg)	3.76^{ab}	2.96^{b}	3.09^{b}	3.64^{ab}	3.01^{b}	3.34^{ab}	4.27^{a}	4.13^{a}	3.63^{a}
C/N ratio	8.04^{a}	9.65^{a}	7.39^{a}	8.51^{a}	10.86^{a}	7.70^{a}	7.03^{a}	7.23^{a}	8.52^{a}
NH4-N (mg/kg)	119.56^{a}	94.55^{a}	113.60^{a}	107.47^{a}	127.98^{a}	115.16^{a}	114.42^{a}	126.48^{a}	105.90^{a}
NO3-N (mg/kg)	135.47^{a}	186.99^{a}	190.81^{a}	100.47^{a}	162.01^{a}	201.47^{a}	188.82^{a}	121.27^{a}	120.67^{a}
P (g/kg)	0.05^{a}	0.04^{ab}	0.03^{ab}	0.05^{a}	0.01^{b}	0.02^{b}	0.03^{ab}	0.03^{ab}	0.03^{b}
K (mg/kg)	173.62^{ab}	183.3^{a}	175.06^{a}	161.07^{ab}	97.69^{c}	105.85^{c}	135.52^{bc}	160.29^{ab}	135.83^{b}
Mg (mg/kg)	289.62^{ab}	230.94^{ab}	169.6^{b}	374.20^{ab}	158.58^{b}	318.67^{ab}	474.34^{a}	338.98^{ab}	428.58^{a}
Ca (mg/kg)	1345.17^{a}	1251.67^{ab}	799.46^{abc}	563.00^{bcd}	73.33^{d}	523^{cd}	447.83^{cd}	439.83^{cd}	429.75^{d}

Abbreviations: TOC=total organic carbon, TN=total nitrogen, C=carbon, N=nitrogen, K=potassium, P=phosphorus, Mg=magnesium, Ca=calcium. Mean separation by Tukey's Honest Significant Difference test. Means followed by the same letter are not significantly different, along the rows. *n*=6 in banana and grevillea pure stands; *n*=24 in grevillea-banana intercrops

4.4 Characterization of nematode community under grevillea-banana agrosystems

4.4.1 Trophic groups of the soil nematode community

In total, 28 nematode genera distributed in five trophic groups were recovered from soil in grevillea-banana cropping systems of Kirinyaga. Bacterial feeding nematodes were the most frequently occurring feeding group and comprised 45 % of the encountered genera. They were followed by plant parasitic nematodes, fungivore nematodes, omnivorous and predator nematodes in a descending order of the frequency of occurrence of their respective genera (Figure 6).

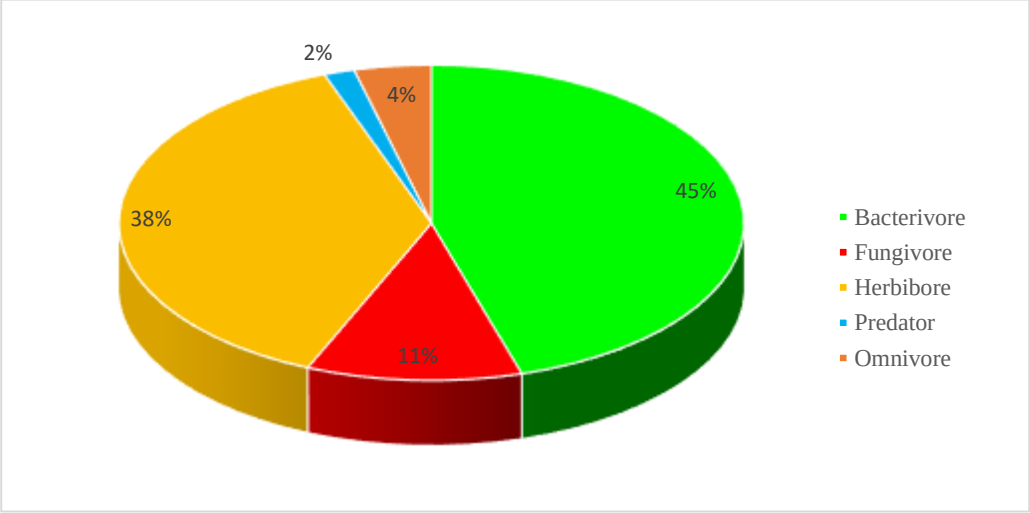

Figure 6: Frequency of occurrence of nematode from different trophic groups

The total abundance (total individual counts) of different trophic groups did not follow a similar trend to that of their frequency of occurrence. Though bacterivore nematodes were the most frequently encountered, plant parasitic nematodes were the most abundant (51 % of the population) followed by bacterivore, omnivore, fungivore and predator nematodes (Figure 7).

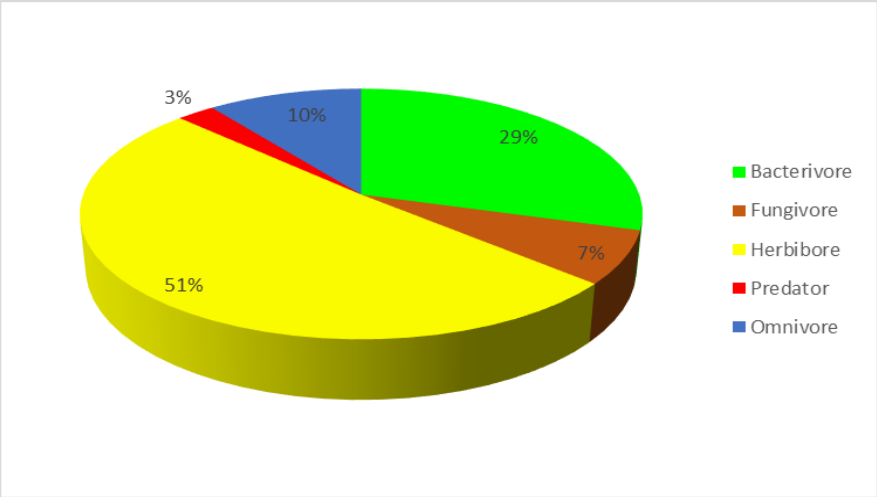

Figure 7: Proportion of abundance of nematodes from different trophic groups

In each trophic group, the recorded nematode genera contributed differently to the total abundance of that particular trophic group. In the plant parasitic trophic group for instance, four genera namely *Meloidogyne*, *Helicotylenchus*, *Pratylenchus* and *Scutellonema* accounted for more than 90 % of all the plant parasitic nematodes recovered. Among bacterivore nematode, *Rhabditis* alone represented more than 50 % of the recorded population and *Aphelenchus* accounted for more than 60 % of all the fungivore nematodes (Figure 8).

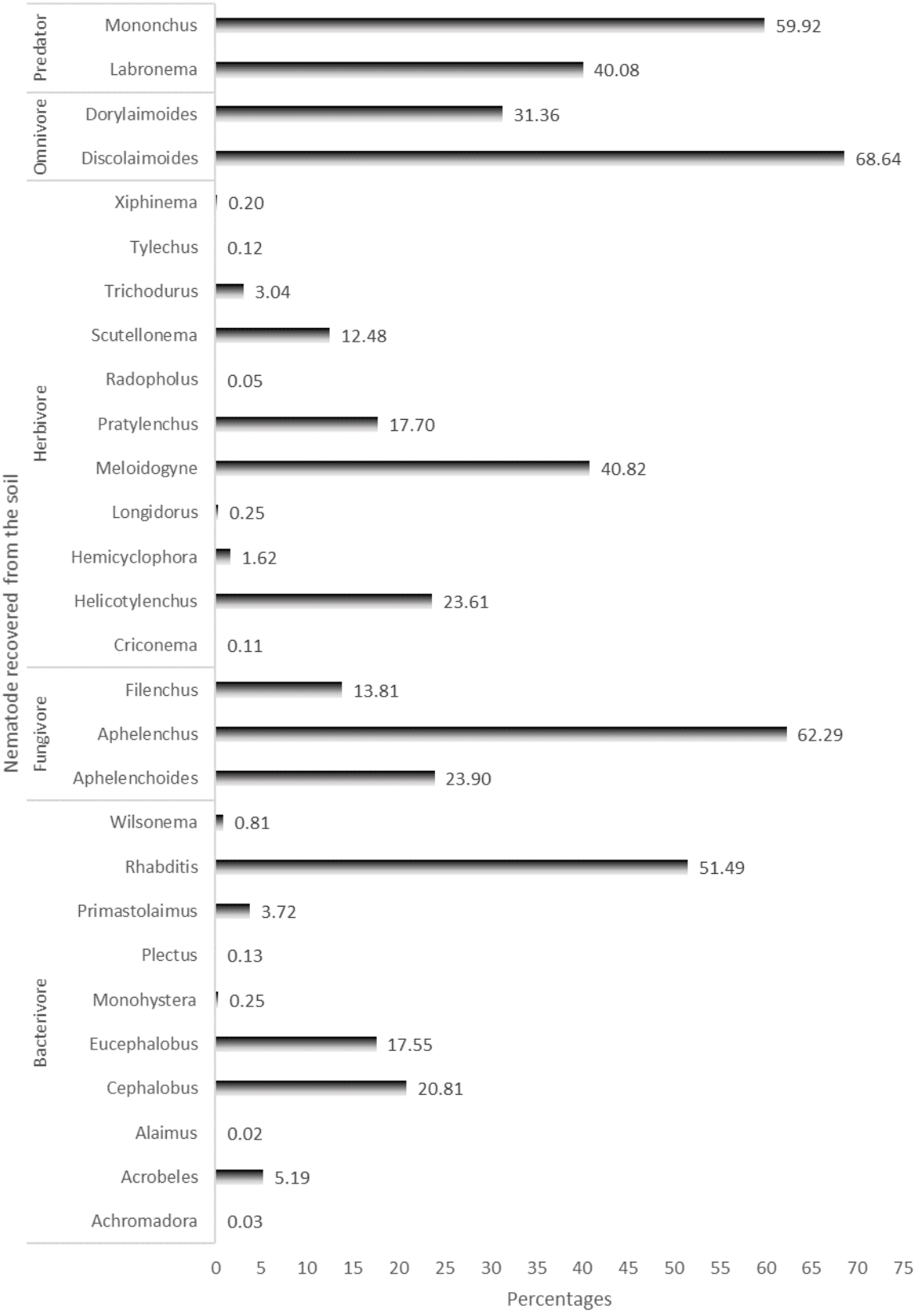

Figure 8: Contribution of nematodes from different genera to the total abundance of the respective nematode trophic group

The population density of all the trophic groups was significantly influenced by the season as well as the interaction between AEZs and cropping system. All the nematode trophic groups had significantly higher population densities in the wet season compared to the dry season. For instance, the population of bacterivore nematodes was 82 % higher in the rainy season than in the dry season while the respective number of fungivore and plant parasitic nematodes were 77 and 86 % higher. The population of predators and omnivore nematodes was nearly double in the rainy season compared to the dry season (95 and 99 %, respectively). Significantly higher counts of bacterivore nematodes were recorded in banana sole stands of the highland zone (170.17 individuals/200 cc soil) compared to all the other zones whereas the lowest population in this trophic group was found in grevillea-banana intercrops of the midland zone (35.33 individuals/200 cc soil). Population of fungivore nematodes was significantly higher in banana sole stands and grevillea-banana intercrops in the lowland. In the midland, this trophic group was significantly higher in grevillea sole stands whereas it was higher in grevillea sole stands and grevillea-banana intercrops in the highland zone (Table 6). The abundance of populations of predator as well as omnivore nematodes was significantly higher in banana sole stands of the lowland zone (20.66 and 56.66 individuals/200 cc soil, respectively) only compared to all the other farming systems in all the zones. Banana sole stands of the lowland zone yielded the highest population density of plant parasitic nematodes (371.67 individuals/200 cc soil). The second highest counts of these nematodes were found in banana sole stands of the midland (205.33 individuals/200 cc soil) and highland zone (122.92 individuals/200 cc soil) whereas grevillea sole stands and grevillea-banana intercrops of all the zones recorded the lowest counts of plant parasitic nematodes (Table 6).

Table 6: Effect of cropping system, AEZ and season on abundance of soil nematodes (individuals/200 cc soil) in different trophic groups

	AgroEcological Zones								
	Lowland			Midland			Highland		
	Cropping Systems								
	Banana	Grevillea	Grevillea-Banana	Banana	Grevillea	Grevillea-Banana	Banana	Grevillea	Grevillea-Banana
	Dry season								
Bacterivore	31.33^{ab}	48.5^{ab}	46.92^{ab}	54.67^{ab}	39.2^{ab}	26.88^{b}	114.17^{a}	47.5^{ab}	50.75^{ab}
Fungivore	20.83^{a}	2^{b}	12.17^{a}	5.5^{b}	11.4^{a}	8.67^{ab}	8.67^{ab}	14.5^{a}	12.88^{a}
Predator	13^{a}	3^{ab}	2.42^{b}	0.5^{b}	0.8^{b}	4^{ab}	4.67^{ab}	5.33^{ab}	3.75^{ab}
Omnivore	38.33^{a}	20.83^{ab}	10.21^{b}	3.67^{b}	21.8^{ab}	14.12^{b}	7.17^{b}	20.67^{ab}	16.25^{b}
Herbivore	247.67^{a}	39^{b}	54.12^{b}	146.67^{ab}	8.6^{b}	76.62^{b}	73.83^{b}	60.67^{b}	75.5^{b}
	Rainy season								
Bacterivore	61.33^{ab}	87.33^{ab}	86.33^{ab}	90^{ab}	73^{ab}	43.79^{b}	226.17^{a}	93.83^{ab}	90.25^{ab}
Fungivore	36.17^{a}	3.5^{b}	20.67^{ab}	9^{b}	21.2^{ab}	15.5^{ab}	22^{ab}	23^{ab}	22.5^{ab}
Predator	28.33^{a}	5.17^{b}	4.67^{b}	0.83^{b}	1.2^{b}	6.83^{b}	11.83^{ab}	10.67^{ab}	7.08^{b}
Omnivore	75^{a}	43.67^{ab}	22.67^{b}	5.83^{b}	43.2^{ab}	26.71^{b}	16.33^{b}	44.33^{ab}	30.46^{ab}
Herbivore	495.67^{a}	65^{b}	107.88^{b}	264^{ab}	16.4^{b}	154^{b}	172^{ab}	112.17^{b}	108.46^{b}

Mean separation by Tukey's Honest Significant Difference test. Means followed by the same letter are not significantly different, along the rows. *n*=6 in banana and grevillea pure stands; *n*=24 in grevillea-banana intercrops

4.4.2 Generic diversity and abundance of the soil nematode community

The occurrence of the nematode genera was significantly dependent the cropping systems as well as between nematode genera and AEZs. Nematodes in the *Alaimus* and *Radopholus* genera were only detected in grevillea-banana intercrops. Similarly, the genera *Achromadora, Criconema, Longidorus, Monohystera* and *Tylenchus* were not found in banana sole stands whereas all the 28 genera were found in grevillea-banana intercrops. Among the AEZs, the genera *Alaimus* was recovered only from the midland zone and the genera *Criconema* from the highland only. Besides, there was no record of *Xiphinema* in the lowland zone nor that of *Achromadora* in the highland. Genera *Hemicliophora, Monohystera, Plectus, Radopholus, Tylenchus* and *Xiphinema* were not found in the midland zone (Table 7).

A part from *Achromadora* and *Plectus*, the abundance of all the other nematode genera was higher in the rainy season than the dry season. The abundance of *Acrobeles* and that of *Monohystera* was significantly higher in the lowland compared to midland and highland zones. The population of *Eucephalobus* was significantly higher in the highland zone than the lowland zone which in turn had a higher population compared to the midland zone. The population density of *Helicotylenchus* was significantly higher in the midland zone compared to the lowland and highland zones, whose population density did not significantly differ. The abundance of *Longidorus*, *Plectus*, *Pratylenchus*, *Rhabditis*, *Tylenchus* and *Xiphinema* was always higher in the highland zone than the lowland and the midland zones. The lowland and midland zones significantly differed only in the abundance of *Pratylenchus* and *Rhabditis* (Table 7). Among the nematode genera whose population density significantly differed between cropping systems, *Dorylaimoides*, *Tylenchus* and *Xiphinema* always had significantly higher populations in grevillea sole stands followed by grevillea-banana intercrops and the least recorded in banana sole stands. Significantly higher population of *Longidorus* was recovered from grevillea-banana intercrops compared to grevillea sole stands. Significantly

higher populations of *Helicotylenchus*, *Meloidogyne*, *Rhabditis*, *Trichodorus* and *Wilsonema* were recorded in banana sole stands compared to grevillea-banana intercrops and grevillea sole stands, which did not significantly differ (Table 7).

Table 7: Abundance of soil nematode genera (individuals/200 cc soil) as influenced by AEZs, cropping system and Season

Nematode genera	AgroEcological Zones								
	Lowland			Midland			Highland		
	Cropping systems								
	Banana	Grevillea	Grevillea-Banana	Banana	Grevillea	Grevillea-Banana	Banana	Grevillea	Grevillea-Banana
	Dry season								
Achromadora	0^{a}	0.5^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}
Acrobeles	2^{ab}	4^{ab}	4.62^{a}	2.5^{ab}	0.8^{ab}	3.46^{ab}	0.33^{b}	2.83^{ab}	0.46^{b}
Alaimus	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0.04^{a}	0^{a}	0^{a}	0^{a}
Aphelenchoides	2.33^{ab}	0.17^{b}	3.67^{a}	3^{ab}	1.8^{b}	2.08^{ab}	2^{ab}	4.33^{a}	2.79^{ab}
Aphelenchus	13.83^{a}	1.67^{b}	7.92^{ab}	0.33^{b}	9.4^{ab}	5.54^{ab}	6.33^{ab}	6.17^{ab}	7.54^{ab}
Cephalobus	2.17^{b}	9.67^{ab}	10^{a}	9.33^{ab}	13.6^{a}	7.58^{ab}	12.33^{a}	10.83^{a}	11.29^{a}
Criconema	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	1^{a}	0.21^{ab}
Discolaimoides	30.83^{a}	13.17^{ab}	7.42^{b}	3.67^{b}	7.4^{b}	11.29^{b}	5.17^{b}	14^{ab}	10.04^{b}
Dorylaimodes	7.5^{ab}	7.67^{ab}	2.79^{b}	0^{b}	14.4^{a}	2.83^{b}	2^{b}	6.67^{ab}	6.21^{ab}
Eucephalobus	6^{b}	11.33^{a}	7.29^{ab}	6^{b}	6.4^{ab}	4.92^{b}	11.83^{a}	11.5^{a}	10.96^{ab}
Filenchus	4.67^{a}	0.17^{b}	0.58^{b}	2.17^{ab}	0.2^{b}	1.04^{b}	0.33^{b}	4^{a}	2.54^{ab}
Helicotylenchus	58.33^{ab}	0^{b}	10.04^{b}	72^{a}	5.4^{b}	26.17^{ab}	10^{b}	12.83^{ab}	9.62^{b}
Hemicycliophora	0^{b}	1.5^{a}	3.54^{a}	0^{b}	0^{b}	0^{b}	0^{b}	1.5^{ab}	0.58^{ab}
Labronema	5.5^{a}	0.17^{b}	1.62^{ab}	0^{b}	0.8^{b}	1.92^{ab}	0.83^{b}	1.67^{ab}	1.54^{ab}
Longidorus	0^{b}	0^{b}	0.04^{b}	0^{b}	0^{b}	0.29^{ab}	0^{b}	0.33^{ab}	0.54^{a}
Meloidogyne	157^{a}	29.5^{b}	15.5^{b}	46^{ab}	3^{b}	18.62^{b}	38.33^{ab}	30.83^{b}	34.79^{b}
Monohystera	0^{b}	0.5^{a}	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	0.17^{ab}	0.04^{b}
Mononchus	7.5^{a}	2.83^{ab}	0.79^{b}	0.5^{b}	0^{b}	2.08^{ab}	3.83^{ab}	3.67^{ab}	2.21^{ab}
Plectus	0^{a}	0^{a}	0.25^{a}	0^{a}	0^{a}	0^{a}	0.17^{a}	0.5^{a}	0.04^{a}
Pratylenchus	0^{b}	3.17^{ab}	20.21^{a}	10^{ab}	0.2^{b}	7.96^{ab}	21.17^{a}	7.67^{ab}	21.83^{a}
Primastolaimus	1.5^{ab}	0.33^{b}	1.33^{ab}	0.17^{b}	5.4^{a}	2.29^{ab}	1.17^{ab}	2.5^{ab}	1.92^{ab}
Radopholus	0^{a}	0^{a}	0.08^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0.12^{a}
Rhabditis	17.17^{b}	21.83^{b}	23.12^{b}	36^{ab}	13^{b}	8.42^{b}	88^{a}	19.17^{b}	25.75^{ab}
Scutellonema	23.67^{a}	1.83^{ab}	3.83^{ab}	10.67^{ab}	0^{b}	22.46^{a}	0.33^{b}	3^{ab}	3.75^{ab}
Trichodorus	8.67^{a}	2.17^{ab}	0.75^{b}	8^{ab}	0^{b}	1.12^{ab}	4^{ab}	1.33^{ab}	3.42^{ab}
Tylenchus	0^{b}	0.83^{a}	0.12^{b}	0^{b}	0^{b}	0^{b}	0^{b}	0.17^{b}	0.29^{ab}
Wilsonema	2.5^{a}	0.33^{ab}	0.29^{b}	0.67^{ab}	0^{b}	0.17^{b}	0.33^{ab}	0^{b}	0.29^{b}
Xiphinema	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	2^{a}	0.33^{ab}

				Rainy season					
Achromadora	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0.04^{a}	0^{a}	0^{a}	0^{a}
Acrobeles	3.67^{ab}	2.67^{ab}	9.67^{a}	3.83^{ab}	1.17^{ab}	4.25^{ab}	0.83^{ab}	4.5^{ab}	0.5^{b}
Alaimus	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0.08^{a}	0^{a}	0^{a}	0^{a}
Aphelenchoides	3.17^{b}	0.33^{b}	6.92^{a}	5^{ab}	2.33^{b}	3.83^{ab}	5^{ab}	7.17^{a}	4^{ab}
Aphelenchus	26.17^{a}	3^{b}	12^{ab}	0.33^{b}	15.17^{ab}	10^{ab}	16.17^{ab}	10^{ab}	14.62^{ab}
Cephalobus	4.33^{b}	19.17^{ab}	16.88^{ab}	16^{ab}	21.17^{ab}	11.71^{b}	30.67^{a}	22.33^{ab}	21.33^{ab}
Criconema	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	1.5^{a}	0.29^{ab}
Discolaimoides	60.17^{a}	25.17^{ab}	16.17^{b}	5.83^{b}	11.5^{b}	21.83^{b}	11.33^{b}	31.17^{ab}	18^{b}
Dorylaimodes	14.83^{ab}	18.5^{a}	6.5^{b}	0^{b}	24.5^{a}	4.88^{b}	5^{b}	13.17^{ab}	12.46^{ab}
Eucephalobus	11.33^{ab}	19.5^{a}	12.54^{ab}	10.5^{b}	10^{b}	9.5^{b}	28.83^{a}	21.5^{a}	18.5^{ab}
Filenchus	6.83^{a}	0.17^{b}	1.75^{b}	3.67^{ab}	0.17^{b}	1.67^{b}	0.83^{b}	5.83^{a}	3.88^{ab}
Helicotylenchus	124.83^{a}	0^{b}	17.96^{b}	134.3^{a}	7.83^{b}	43.25^{ab}	23.5^{ab}	22.17^{ab}	11.75^{b}
Hemicycliophora	0^{b}	3.83^{a}	8.54^{a}	0^{b}	0^{b}	0^{b}	0^{b}	3.33^{ab}	1^{ab}
Labronema	10.33^{a}	0.33^{b}	2.96^{ab}	0^{b}	1^{b}	3^{ab}	2^{ab}	1.83^{ab}	2.92^{ab}
Longidorus	0^{b}	0^{b}	0.04^{ab}	0^{a}	0^{b}	0.46^{ab}	0^{b}	0.83^{a}	0.83^{a}
Meloidogyne	301.83^{a}	49.17^{b}	29.12^{b}	79.67^{ab}	5.67^{b}	38.38^{b}	90^{ab}	51.17^{b}	51.71^{b}
Monohystera	0^{b}	4^{a}	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	0.17^{b}	0.21^{b}
Mononchus	18^{a}	4.83^{ab}	1.71^{b}	0.83^{b}	0^{b}	3.83^{ab}	9.83^{ab}	8.83^{ab}	4.17^{ab}
Plectus	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	0.33^{ab}	0.67^{a}	0.04^{b}
Pratylenchus	0^{b}	4.67^{b}	42.62^{a}	17^{ab}	0.17^{b}	18.75^{ab}	49.17^{a}	22.83^{ab}	31.83^{ab}
Primastolaimus	2.67^{ab}	1.33^{ab}	2.08^{ab}	0.17^{b}	8.33^{a}	4.08^{ab}	2.33^{ab}	7.33^{a}	1.88^{ab}
Radopholus	0^{a}	0^{a}	0.08^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0^{a}	0.17^{a}
Rhabditis	34.17^{b}	40.67^{b}	44.67^{b}	58.33^{ab}	20.17^{b}	13.88^{b}	162.33^{a}	37.33^{b}	47.33^{b}
Scutellonema	50.83^{a}	4^{ab}	7.83^{ab}	18^{ab}	0^{b}	51.25^{a}	0.83^{b}	5.33^{ab}	6.17^{ab}
Trichodorus	18.17^{a}	3.33^{b}	1.58^{b}	15^{ab}	0^{b}	1.92^{b}	8.5^{ab}	2.33^{b}	3.75^{b}
Tylenchus	0^{b}	0^{b}	0.08^{ab}	0^{b}	0^{b}	0^{b}	0^{b}	0.33^{a}	0.42^{a}
Wilsonema	5.17^{a}	0^{b}	0.5^{b}	1.17^{ab}	0^{b}	0.25^{b}	0.83^{ab}	0^{b}	0.46^{b}
Xiphinema	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	0^{b}	2.33^{a}	0.54^{ab}

Mean separation by Tukey's Honest Significant Difference test. Means followed by the same letter are not significantly different, along the rows. n=6 in banana and grevillea pure stands; n=24 in grevillea-banana intercrops

4.4.3 Community and ecological indices of the soil nematode community

The overall nematode abundance was significantly influenced by the seasons as well as the cropping systems. Nematode population was 86 % higher in the rainy season compared to the dry season. The nematode population in banana sole stands was significantly higher at 380.86 compared to 193.84 and 167.29 individuals/200 cc soil in grevillea-banana intercrops and grevillea sole stands, respectively.

The taxonomic richness was significantly different between AEZs with significant interaction effects between AEZs and cropping systems. Hence, the highest significant taxonomic richness was recorded in grevillea sole stands and grevillea-banana intercrops of the highland zone, followed by the banana sole stands of the lowland zone. All the other cropping systems in the different AEZs did not significantly differ among themselves (Table 8). The slightly higher taxonomic richness observed in the dry season at 10.22 was not significantly different from 9.94 genera recovered during the rainy season. The evenness of the distribution of individual nematodes among the genera significantly differed among cropping systems. The mean evenness index value in grevillea-banana intercrops at 0.83 and grevillea sole stands at 0.82 was significantly higher than the one observed in banana sole stands at 0.74. Though not significantly different, the evenness index was higher in the highland zone (0.83) followed by the lowland zone and the midland zones whose evenness index scored 0.81 and 0.80, respectively. The evenness index was slightly higher in the dry season (0.82) compared to the rainy season (0.81). The Shannon's diversity index calculated based on these nematode genera significantly differed between AEZs and cropping systems. A significantly higher Shannon's diversity index was recorded in the highland zone at 1.99 compared to 1.79 and 1.72 obtained in the lowland and the midland, respectively. Grevillea-banana intercrops and grevillea sole stands scored a significantly higher Shannon's diversity index at 1.89 and 1.84, respectively, compared to 1.6 recorded in banana sole sands. The Shannon's diversity index

was slightly higher in the dry season (1.86) compared to the rainy season (1.81), but no significant difference was noticed.

The Channel Index significantly differed between AEZs. Lowland and highland zones did not significantly differ for their Channel Index (15.41 and 15.32, respectively). However, these two AEZs had a significantly lower Channel Index compared to the midland zone whose mean Channel Index scored 37.34. The Channel Index in the different cropping systems did not significantly differ, though slightly higher in grevillea-banana intercrops (24.06) compared to banana (21.53) and grevillea (17.45) sole stands. Seasonal variation of the Channel Index was not significant, with close values in dry and rainy seasons (22.37 and 22.8, respectively). The Enrichment Index was significantly higher in the lowland and highland zones at 71.07 and 69.51, respectively, compared to the midland zone. No significant difference was found in Enrichment Index between cropping systems and seasons, but banana and grevillea sole stands scored a close and slightly higher Enrichment Index (67.2 and 67.1, respectively) compared to grevillea-banana intercrops (65.5).

The AEZs and cropping systems had significant interaction effects on Plant Parasitic Index, Maturity Index, Basal Index as well as the Structure Index. The Plant Parasitic Index was significantly higher at 3.52 under banana sole stands of the midland zone compared to 2.50 under grevillea sole stands in the lowland zone. Three significantly different groups of AEZ-cropping system were depicted with regard to Maturity Index. Significantly higher Maturity Index was recorded under banana sole sands in the lowland and grevillea-banana intercrops in the midland zones followed by grevillea sole stands in all the AEZs which in turn happened to score a significantly higher Maturity Index compared to banana sole stands in the midland and the highland zones (Table 8). The Basal Index was significantly higher under banana sole stands in the midland only at 41.25 compared to all the other farming systems of the three AEZs. Structure Index revealed three different groups of combination AEZs-cropping system

(Table 8). The two extremes comprise banana sole stands in the lowland which scored the highest Structure Index at 81.43 whereas banana sole stands in the midland scored the lowest value of the Structure Index at 12.88. Grevillea-banana intercrops of the midland zone significantly differed from the two extreme combinations but did not significantly differ from the remaining combinations, which are intermediate to these two extremes (Table 8). None of these four indices (PPI, MI, BI and SI) was significantly influenced by the season ($p > 0.05$) (Table 8).

Table 8: Soil nematode community and ecological indices as influenced by AEZs, cropping systems and Season

Nematode community and ecological indeces	AgroEcological Zone								
	Lowland			Midland			Highland		
	Cropping systems								
	Banana	Grevillea	Grevillea-Banana	Banana	Grevillea	Grevillea-Banana	Banana	Grevillea	Grevillea-Banana
	Dry season								
Total bundance	351.17^{a}	113.33^{b}	125.83^{b}	211^{ab}	81.8^{b}	130.29^{b}	208.5^{ab}	148.67^{b}	159.12^{b}
Number of genera	10.33^{abc}	8.83^{bc}	9.83^{abc}	7.33^{c}	8^{bc}	9.46^{bc}	9.67^{abc}	13.83^{a}	12.08^{ab}
Evenness	0.75^{b}	0.82^{a}	0.82^{a}	0.71^{a}	0.83^{a}	0.83^{a}	0.77^{b}	0.83^{a}	0.85^{a}
DI	1.76^{ab}	1.77^{ab}	1.83^{ab}	1.4^{b}	1.7^{ab}	1.84^{ab}	1.64^{ab}	2.13^{a}	2.07^{a}
PPI	2.67^{a}	2.53^{a}	3.09^{a}	3.03^{a}	2.4^{a}	3.05^{a}	3.04^{a}	3.13^{a}	3.07^{a}
MI	2.62^{a}	2.34^{ab}	2.16^{ab}	1.76^{ab}	2.39^{ab}	2.57^{a}	1.79^{ab}	2.7^{a}	2.3^{ab}
PPI.MI	1.03^{ab}	1.28^{ab}	1.49^{ab}	1.75^{a}	1.01^{b}	1.25^{ab}	1.87^{a}	1.26^{ab}	1.37^{ab}
BI	11.79^{b}	12.9^{b}	21.01^{b}	41.26^{a}	16.58^{b}	19.4^{b}	12.67^{b}	17.12^{b}	17.79^{b}
EI	71.95^{a}	70.32^{a}	71.03^{a}	57.45^{b}	58.71^{b}	57.72^{b}	72.22^{a}	69.49^{a}	69.93^{a}
SI	81.37^{a}	58.3^{ab}	46.82^{ab}	13.1^{b}	71.37^{a}	67.93^{a}	54.03^{ab}	71.34^{a}	67.01^{a}
CI	27.89^{ab}	2.96^{b}	15.26^{ab}	29.08^{a}	33.15^{a}	37.45^{a}	6.2^{b}	20.08^{ab}	17.97^{ab}
	Rainy season								
Total abundance	696.5^{a}	204.67^{b}	242.21^{b}	369.67^{ab}	155^{b}	246.83^{b}	448.33^{ab}	284^{ab}	258.75^{b}
Number of genera	10.33^{ab}	7.5^{b}	9.62^{ab}	7.33^{b}	8^{ab}	9.29^{ab}	9.67^{ab}	13.67^{a}	11.6 2^{ab}
Evenness	0.74^{b}	0.83^{a}	0.82^{a}	0.7^{b}	0.8^{a}	0.81^{a}	0.78^{b}	0.82^{a}	0.84^{a}
DI	1.75^{ab}	1.66^{ab}	1.79^{ab}	1.38^{ab}	1.65^{ab}	1.78^{ab}	1.67^{ab}	2.09^{a}	2.01^{a}
PPI	2.55^{ab}	2.07^{b}	2.85^{ab}	4.01^{a}	2.4^{ab}	2.9^{ab}	2.54^{ab}	3.05^{ab}	3.04^{ab}
MI	2.75^{a}	2.3^{ab}	2.09^{ab}	1.76^{b}	2.38^{ab}	2.57^{a}	1.72^{b}	2.41^{ab}	2.24^{ab}
PPI/MI	0.94^{b}	1.15^{b}	1.41^{b}	2.35^{a}	1.01^{b}	1.17^{b}	1.6^{ab}	1.28^{b}	1.38^{b}
BI	11.74^{b}	12.11^{b}	19.88^{b}	41.24^{a}	16.09^{b}	20.23^{b}	12.96^{b}	16.12^{b}	21.96^{b}
EI	71.93^{a}	73.13^{a}	70.34^{ab}	57.65^{b}	57.98^{b}	56.38^{b}	71.92^{a}	70.06^{ab}	67.69^{ab}
SI	81.49^{a}	58.74^{ab}	51.62^{ab}	12.66^{b}	71.05^{a}	66.33^{a}	53.84^{ab}	73.65^{a}	63.19^{a}
CI	28.37^{ab}	2.73^{b}	15.47^{b}	28.86^{ab}	33.16^{ab}	42.48^{a}	6.14^{b}	17.87^{ab}	14.7^{b}

Abbreviation: DI= Shannon's Diversity Index, PPI=Plant Parasitic Index, MI= Maturity Index, BI= Basal Index, EI = Enrichment Index, SI= Structural Index, CI= Channel Index. Mean separation by Tukey's Honest Significant Difference test. Means followed by the same letter are not significantly different, along the rows. *n*=6 in banana and grevillea pure stands; *n*=24 in grevillea-banana intercrops

4.5 Nematode community structure as influenced by soil physico-chemical properties

The Pearson correlation matrix between the assessed soil physio-chemical properties and nematode community and ecological indices (Table 9) revealed a significantly positive correlation between soil bulk density and the overall nematode abundance as well as that of Plant Parasitic Nematodes. Soil moisture content was significantly and positively correlated with genera richness, Shannon's diversity index and Plant Parasitic Index whereas it was negatively and significantly correlated with the population density of fungivore nematodes. Soil temperature was negatively correlated with taxonomic richness and Shannon's diversity index. Overall nematode abundance, the abundance of Plant Parasitic Nematodes and the Enrichment Index were negatively correlated with soil silt content whereas they were positively correlated to soil clay content. Channel Index was positively correlated with soil silt but negatively correlated with soil clay content. Soil clay content was in turn positively correlated to the evenness of the nematode population. Plant Parasitic Index and the Channel Index were significantly decreasing as the soil pH increases whereas the EI followed an opposite trend. The total organic carbon was positively and significantly associated with the overall nematode abundance, abundance of Plant Parasitic Nematodes and Structure Index. However, a significant but negative association was observed between soil total organic carbon and the Channel Index. The Maturity Index was negatively correlated with the soil phosphorus content whereas soil potassium and calcium content were positively associated with the Enrichment Index. Soil potassium content was negatively correlated with Maturity Index and Channel Index. The same trend was observed between soil calcium content and Channel Index, on one hand, and between soil magnesium content and the Plant Parasitic Index, on the other.

The population density of some nematode genera was significantly correlated with soil physio-chemical properties (Table 10). For instance, the abundance of *Helicotylenchus* was positively correlated with soil bulk density whereas a negative correlation was found between the

population density of *Monohystera* and the same parameter. Soil moisture content was negatively correlated with the abundance of *Acrobeles* but *Xiphinema* population density was positively correlated. Soil temperature and the population density of *Acrobeles* were positively correlated whereas it was negatively correlated with the population density of *Cephalobus, Criconema, Eucephalobus, Filenchus* and *Xiphinema*. Soil sand content was positively correlated with the population density of *Hemicycliophora* but negatively correlated with that of *Helicotylenchus*. The population density of *Acrobeles, Cephalobus* and *Primastolaimus* was positively correlated with soil silt content whereas *Alaimus, Meloidogyne, Pratylenchus, Radopholus, Scutellonema, Trichodorus* and *Tylenhus* were negatively associated with this soil factor. A significantly positive correlation was depicted between soil clay content and the population density of *Alaimus, Criconema, Helicotylenchus, Scutellonema* and *Trichodorus* whereas the *Acrobeles* was negatively correlated with this soil factor. There was a negative correlation between soil pH and *Prismatolaimus* abundance but a positive one with that of *Wilsonema*. Similarly, total organic carbon was negatively associated with the abundance of *Acrobeles* but positively with *Dorylaimodes* and *Meloidogyne.* There was a negative correlation between carbon to Nitrogen ratio and the abundance of *Aphelenchus*, a positive one between NO_3-Nitrogen and the population density of *Acrobeles*, *Alaimus* and *Scutellonema* whereas soil phosphorus was positively associated with *Filenchus* and *Trichodorus*. Soil potassium was negatively correlated with *Longidorus* but positively associated with *Hemicycliophora*, *Primastolaimus* and *Wilsonema* whereas soil calcium content was positively correlated with *Filenchus* and *Primastolaimus* population density.

Due to seasonal variability in the nematode population density, the results of the canonical correspondence analysis (CCA) revealed that the distribution of nematode population in the dry season is governed by different soil factors compared to the wet season. In the dry season, all the analysed soil factors explained 40.62 % of the variance of the distribution of the five trophic

groups. Among these soil factors, only soil temperature, soil silt content, soil carbon content, phosphorus, potassium and magnesium were significantly determinant of the distribution of the five nematode trophic groups. Soil temperature, total organic carbon and phosphorus were positively associated with herbivore nematodes as well as predator nematodes whereas soil silt content and potassium were negatively associated with these nematode trophic groups. The distribution of bacterivore, fungivore and omnivorous nematodes was positively associated with silt, potassium and magnesium (Figure 10 A). In the rainy season however, the same soil factors explained only 30.55 % of the distribution of these nematode trophic groups. Soil temperature, silt content, bulk density, total organic carbon, ammonium nitrogen and potassium were the significant determinant factors of the distribution of the population of the five nematode feeding groups. Soil temperature, bulk density and total organic carbon were positively associated with the distribution of Plant Parasitic Nematodes only whereas they were negatively associated with all the other nematode trophic groups. On the contrary, silt, potassium and ammonium nitrogen content were negatively associated with the distribution of herbivore nematodes but positively associated with the distribution of all the other nematode trophic groups (Figure 10 B).

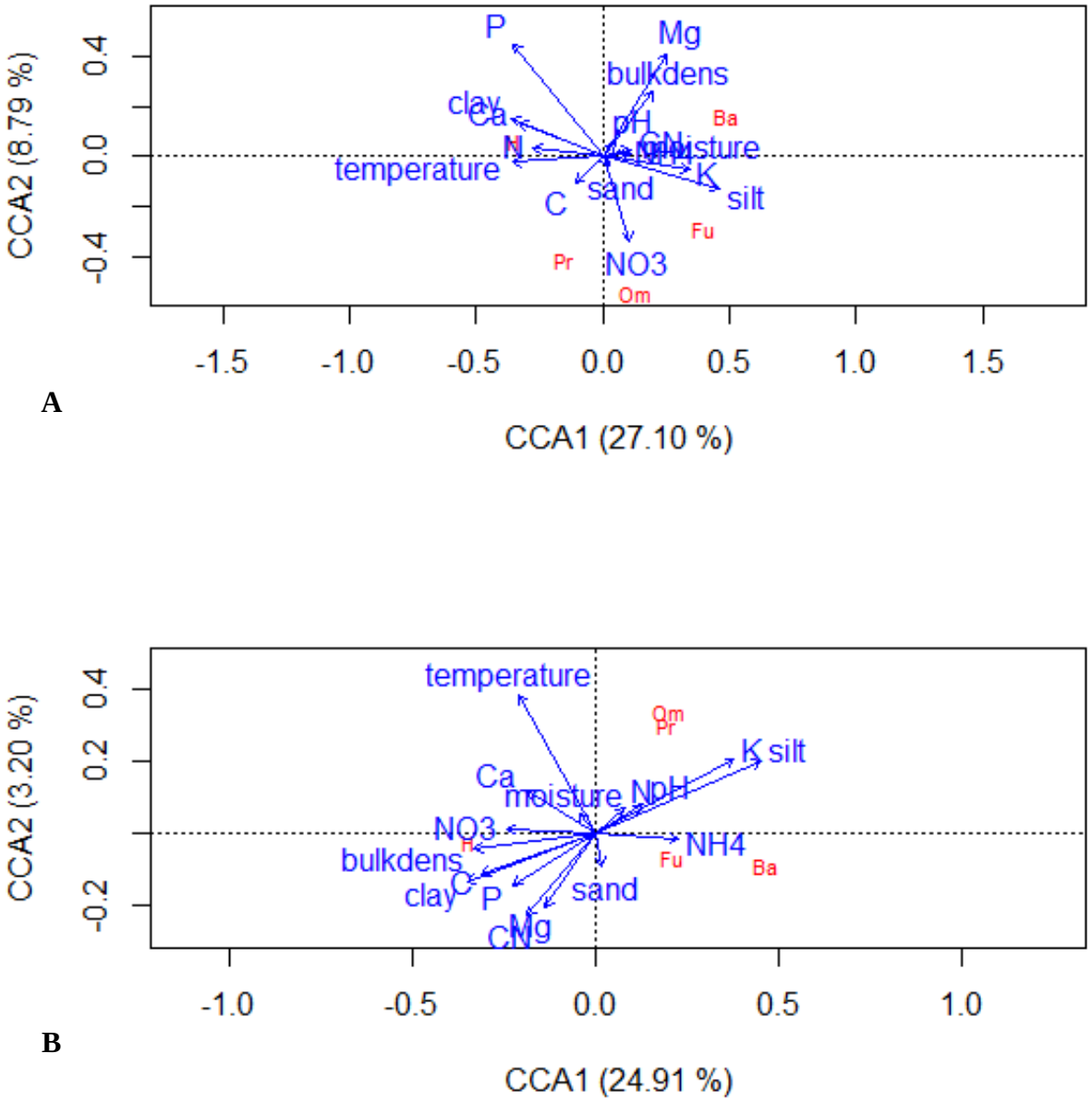

Figure 9: Biplot projecting the nematode trophic groups and soil factors on the first two canonical correspondence axes (A) Dry season (B) Rainy season. Ba= Bacterivore nematodes, Fu= Fungivore nematodes, H= Plant parasitic nematodes, Om= Omnivores, Pr= Predator

Table 9: Pearson correlation matrix (*r*) between soil physico-chemical properties, abundance and soil nematode trophic group abundance and ecological indices of nematodes in different trophic groups

	Bulk dens.	Moisture	Soil Temp.	Sand	Silt	Clay	pH	TOC	TN	C/N ratio	NH_4-N	NO_3-N	P	K	Ca	Mg
Total abundance	**0.15***	-0.09	-0.01	0.00	**-0.21****	**0.19***	0.06	**0.13***	0.09	-0.01	-0.1	0.11	0.05	-0.09	0.1	-0.02
Genera richness	0.05	**0.18****	**-0.14***	0.00	0.08	0.06	-0.09	0.11	-0.04	0.08	0.02	0.02	-0.05	0.01	0.04	-0.07
Eveness	-0.11	0.03	-0.13	0.07	0.13	**-0.17***	0.02	-0.11	0	-0.02	0.06	0.08	-0.13	0.08	-0.01	-0.06
Bactericore	0.05	-0.07	-0.12	0.00	0.000	0.01	-0.01	0.01	0.02	0	-0.05	-0.01	-0.05	0.09	0	0.05
Fungivore	0.01	**-0.17***	0.03	0.04	-0.10	0.06	-0.04	-0.07	0.11	-0.14	-0.03	0.1	0.02	-0.03	0.04	-0.01
Predator	0.07	0.01	-0.01	-0.05	-0.05	0.08	0.01	0.07	0.07	-0.05	-0.03	0.08	-0.12	-0.03	0.12	0.01
Omnivore	0.03	-0.1	0.02	-0.02	-0.02	0.03	-0.02	0.08	0.08	-0.07	-0.11	0.11	-0.06	0.06	0.08	-0.09
Herbivore	**0.16***	-0.05	0.05	0.00	**-0.25****	**0.22****	-0.07	**0.16***	0.08	0.02	-0.09	0.12	0.11	-0.16	0.11	-0.04
DI	0.01	**0.14***	**-0.14***	0.02	0.05	-0.07	-0.04	0.02	-0.02	0.04	0.05	0.07	-0.1	0.05	0.04	-0.1
PPI	0.03	**0.2****	0.00	0.05	-0.05	0.00	**-0.14***	0.1	0.05	0.01	0.03	0.04	-0.08	-0.05	-0.11	**-0.15***
MI	0.02	0.05	0.05	-0.12	0.10	-0.03	-0.07	0.11	-0.03	0.07	-0.03	0.14	**-0.17***	**-0.14***	0.05	-0.08
PPI/MI	0.04	0.11	-0.02	0.07	-0.08	0.03	-0.01	0.03	0.06	-0.04	0.03	-0.05	0.08	0.08	-0.07	0
BI	-0.12	-0.05	-0.08	0.03	0.02	-0.03	-0.04	**-0.15***	-0.02	-0.05	0.01	-0.04	0.02	-0.03	**-0.14***	-0.02
EI	0.1	0.03	0.09	0.02	**-0.25****	**0.21****	**0.15***	0.12	-0.01	0.1	0.04	-0.03	0.13	**0.21****	**0.17***	0.08
SI	0.1	0.09	-0.02	-0.04	0.02	-0.01	-0.02	**0.2****	0.01	0.06	-0.05	0.11	-0.07	-0.1	0.11	-0.06
CI	0.05	-0.08	-0.02	0.02	**0.23*****	**-0.23*****	**-0.21****	**-0.15***	0.03	-0.13	-0.05	0.07	-0.13	**-0.3*****	**-0.18****	-0.01

Abbreviation: DI= Shannon's Diversity Index, PPI=Plant Parasitic Index, MI= Maturity Index, BI= Basal Index, EI = Enrichment Index, SI= Structural Index, CI= Channel Index, TOC=total organic carbon, TN=total nitrogen, NH_4-N= Ammonium nitrogen, NO_3-N= Nitrate nitrogen, K=potassium, P=phosphorus, Mg=magnesium, Ca=calcium. *r* values marked in bold and followed by * indicate a significant correlation.

Table 10: Pearson correlation matrix (r) between soil physico-chemical properties and abundance of soil nematode genera

	Bulk density	Moisture	Soil Temp.	Sand	Silt	Clay	pH	TOC	TN	C/N ratio	NH4-N	NO3-N	P	K	Ca	Mg
Achromadora	-0.03	-0.06	0.08	-0.04	0.04	0.00	0.08	0.02	-0.01	0	-0.01	-0.07	-0.02	0.01	-0.04	-0.02
Acrobeles	-0.04	**-0.21****	**0.15***	-0.02	**0.19****	**-0.14***	0.07	**-0.2****	0.02	-0.09	0.02	**0.15***	-0.03	**0.18****	0.1	-0.1
Alaimus	-0.03	-0.02	0.01	-0.13	**-0.14***	**0.21****	-0.08	-0.08	0.04	-0.06	0.03	**0.21****	-0.07	-0.03	-0.06	-0.02
Aphelenchoides	0.13	-0.11	0.01	0.03	0.03	-0.04	0.09	0.02	0.03	-0.02	-0.03	0.11	0.01	0.02	0.12	0.02
Aphelenchus	0.07	-0.13	0.01	0.04	-0.10	0.06	-0.04	-0.09	0.12	**-0.16***	-0.01	0.08	-0.06	-0.03	-0.05	-0.04
Cephalobus	-0.09	-0.09	**-0.15***	-0.05	**0.15***	-0.08	-0.09	-0.12	0.03	-0.12	-0.04	-0.05	-0.13	-0.03	-0.11	-0.03
Criconema	0.07	-0.1	**-0.15***	-0.08	-0.13	**0.17***	-0.03	0.02	0.08	-0.07	-0.11	0.13	-0.03	0.02	0.12	-0.08
Discolaimoides	0.07	-0.1	0.06	-0.03	-0.05	0.05	-0.03	0.02	0.08	-0.07	-0.11	0.13	-0.03	0.02	0.12	-0.08
Dorylaimodes	-0.05	-0.06	-0.05	0.01	0.03	-0.03	0.01	**0.15***	0.07	-0.05	-0.07	0	-0.07	0.12	-0.01	-0.07
Eucephalobus	-0.04	-0.1	**-0.17***	0.05	0.04	-0.07	-0.12	-0.1	0.05	-0.11	-0.07	-0.02	-0.12	-0.03	-0.13	-0.1
Filenchus	0	-0.04	**-0.15***	-0.02	-0.06	0.07	-0.1	0.02	0.03	-0.01	-0.02	0	**0.26*****	-0.02	**0.16***	0.07
Helicotylenchus	**0.14***	-0.03	0.05	**-0.16***	-0.11	**0.21****	-0.04	0.11	0.05	-0.02	-0.03	-0.02	0.11	0.11	0.03	-0.02
Hemicycliophora	0.08	-0.13	0.13	**0.14***	0.01	-0.10	0.05	-0.07	0.04	-0.05	-0.04	-0.03	-0.08	**0.16***	0.12	-0.05
Labronema	0.1	-0.05	0.05	0.09	-0.08	-0.01	0.02	0.02	0.03	-0.04	-0.03	0.07	-0.05	-0.02	0.08	-0.02
Longidorus	-0.09	0.09	-0.10	-0.06	-0.01	0.06	-0.04	0.11	-0.01	0.02	-0.06	-0.04	-0.06	**-0.15***	0.03	-0.03
Meloidogyne	0.07	-0.01	0.03	0.09	**-0.17***	0.09	-0.07	**0.14***	-0.01	0.07	-0.05	0.02	0.04	-0.09	0.11	-0.03
Monohystera	**-0.15***	-0.09	-0.04	-0.07	0.05	0.02	0.05	0.06	0.02	-0.02	0.01	0.01	-0.04	0.03	0.11	0.01
Mononchus	0.03	0.04	-0.04	-0.10	-0.02	0.09	0	0.07	0.07	-0.04	-0.02	0.06	-0.11	-0.02	0.1	0.02
Plectus	-0.01	0.05	-0.09	0.00	-0.13	0.11	-0.08	-0.05	-0.03	-0.01	0.03	0.01	0.01	0.03	-0.03	-0.03
Pratylenchus	0.11	0.05	-0.01	0.00	**-0.15***	0.13	0.01	0.02	0.08	-0.05	-0.07	0.1	0.08	-0.04	0.02	-0.03
Primastolaimus	-0.06	-0.03	-0.02	-0.10	**0.17***	-0.08	**-0.18****	-0.06	0.08	-0.13	-0.07	0.06	-0.13	**0.15***	**0.16***	-0.06
Radopholus	-0.07	-0.01	0.00	0.06	**-0.17***	0.11	-0.06	-0.12	-0.04	-0.05	-0.02	0.05	0.05	-0.03	-0.08	-0.04
Rhabditis	0.11	-0.01	-0.10	0.02	-0.08	0.07	0.05	0.09	0	0.06	-0.04	-0.02	0.01	0.12	0.06	0.12
Scutellonema	0.08	-0.05	0.03	-0.03	**-0.14***	**0.15***	-0.02	0.06	0.13	-0.03	-0.05	**0.21****	0.05	-0.13	0.07	0.02
Trichodorus	0.12	0.01	0.00	-0.08	**-0.17***	**0.21****	-0.06	0.12	0.1	-0.02	-0.03	0.09	**0.14***	-0.02	0.05	-0.04
Tylenchus	-0.05	0.02	0.00	0.01	**-0.15***	0.13	-0.02	0.03	-0.03	0	-0.05	-0.09	0.04	-0.04	-0.03	-0.03
Wilsonema	0.1	-0.02	0.07	0.03	-0.09	0.06	**0.15***	0.08	0.09	0.03	-0.03	0.02	0.04	**0.23*****	0.06	0.02
Xiphinema	-0.11	**0.41*****	**-0.22*****	0.10	-0.07	0.00	-0.13	0.12	-0.04	0.11	0.03	-0.06	0.01	0.02	-0.07	-0.06

Abbreviation: TOC=total organic carbon, TN=total nitrogen, NH_4-N= Ammonium nitrogen, NO_3-N= Nitrate nitrogen, K=potassium, P=phosphorus, Mg=magnesium, Ca=calcium. *r* values marked in bold and followed by * indicate a significant correlation.

CHAPTER FIVE

DISCUSSION, CONCLUSION ET RECOMMANDATION

5.1 Discussion

5.1.1 Effects of AEZs on quality of *Grevillea robusta* litter

The high amount of *G. robusta* litterfall observed in the highland zone compared to the midland and the lowland zones could be explained by the age of the plantations, the planting density and the pruning regimes. In this zone, some *G. robusta* sole stands were more than 20 years old, with high plantation density and trees that had not been pruned since establishment leading to high litter accumulation. In the present study, the age of trees, tree planting density and tree management practices outweighed the influence of climatic factors on the amount of litter deposition. As a result, the highland zone had good soil moisture content during the study period, it receives regular precipitation throughout the year and has a cooler temperature compared to lowland areas (Jaeztold *et al*., 2006) which could favour leaf retention on the expense of litter deposition (Talemos *et al*., 2018). Other environmental factors like wind and the intensity of rainfall (Wang *et al*., 2013; Giweta, 2020) might have accentuated the effect of the age and planting density on the amount of litterfall observed in the highland zone. The mean annual litterfall of 9.18 t/ha found in the present study corroborates with values reported by Becker *et al*. (2015) which ranged from 4.6 to 10.7 t/ha in sites around Mt. Kilimanjaro and those reported by Lu and Liu (2012) in evergreen hardwood forests of Central Taiwan which ranged from 6.58 to 9.17 t/ha.

The concentration of macronutrients in *G. robusta* litter decreased with increasing elevation, except N which was higher in the highland zone than the midland and lowland zones. The nutrient retranslocation trend observed in the present study corroborates with results reported by Lu and Liu (2012) in evergreen hardwood forests of Central Taiwan where the litter

nutrient fluxes of C, N, P, K, Ca and Mg tended to be higher in forests at low altitude (782 m asl) compared to the mid and the high altitudes (up to 2,098 m asl). Besides, the prevailing drought and high temperature in the lowland zone are likely to hamper the nutrient retranslocation from the senescent leaves (Drenovsky *et al*., 2019). The retranslocation proficiency of P at 0.042 % in the lowland zone denotes an incomplete and low P retranslocation (Lu and Liu, 2012) compared to the 0.037 and 0.035 % found in the midland and highland zones, respectively. Nitrogen, on the other hand, showed a complete retranslocation in the lowland and midland zones compared to highland zone. These results are consistent with Drenovsky *et al* (2019) who found that complete P retranslocation in hardwood species was less frequently observed in vertisols, which is the predominant soil type in the lowland zones of Kirinyaga County (Pauw and Sombroek, 1980; Jaeztold *et al*., 2006), across a range of climatic conditions whereas N retranslocation was complete in the same conditions. Results of nutrient retranslocation in the present study reflect an adaptive behaviour of *G. robusta* to soil fertility, where low soil fertility induces an efficient nutrients retranslocation from senescent leaves to active and/or storage organs (Drenovsky *et al*., 2019) as it is the case of most tropical ecosystems with low fertility (Vergutz *et al*., 2012), confirming that *G. robusta* can strive in oligotrophic ecosystems (Richards and Schmidt, 2010).

5.1.2 Effect of cropping systems on soil physico-chemical properties

The observed significant differences in organic carbon, bulk density, exchangeable bases and P between banana sole stands, grevillea sole stands and grevillea-banana intercrops can be due to differences in farm management practices such organic matter inputs, inorganic fertilization and tillage practices. Grevillea sole stands produced more litter, as a result of high tree planting density and sporadic or no pruning at all, which is left to decompose on the soil surface resulting in a retarded decomposition (Karanja *et al*., 2006). However, in grevillea-

banana intercrops, grevillea litter was integrated into the soil during site preparation and the branches were used as firewood, fodder, or combined with animal manure, potentially reducing soil C inputs. On the other hand, banana sole stands were intensively managed and received more care in terms of manure application than grevillea-banana intercrop. As a result, banana sole stands and grevillea-banana intercrops had a higher bulk density compared to grevillea sole stands which was due to the high organic carbon in soils from the grevillea sole stands (Ruehlmann and Körschens, 2009; Hossain *et al*., 2015; Jourgholami *et al*., 2018; Li *et al*., 2019). Moreover, the roots of *G. robusta* may contribute to SOM resulting in increased pore space and low bulk density (Jin *et al*., 2017). This is because *G. robusta* develops a large network of roots with a length density of 1.1 to 1.7 cm cm^{-3} and 50 % of which can be found at less than 30 cm of the soil profile (Smith *et al*., 1999).

Exchangeable bases (K, Mg and Ca) and P were always significantly higher in banana sole stands compared to grevillea-banana intercrops and grevillea sole stands. In addition to a potential competition for soil nutrients between banana and grevillea, differences in soil fertility management might have contributed to the significant difference in exchangeable bases and P between the cropping systems. Such a trend was reported by Nesper *et al* (2019) in coffee-based agroforestry systems where C, Mg, B and available S kept on decreasing with the increase in the density of *G. robusta* on the expense of other native shading trees in India. Apart from the regular and substantial amounts of manure applied to banana sole stands compared to *G. robusta* sole stands, banana sole stands would benefit from the inorganic fertilizers applied on vegetable or cereal intercrops. Besides, banana sole stands were located in the vicinity of the homestead, where they could increasingly receive organic inputs in form of kitchen waste and crop residues, whereas *G. robusta* pure stands were owned by schools or located far from homestead. These results agree with Okumu *et al*. (2011) and Muthamia *et al*. (2011) who found a soil fertility gradient with increasing distance from the homestead in

banana production areas of Central Highlands of Kenya. Similar results have been reported from Central Uganda where soil fertility management was more intense near the homestead than at distant points in banana farms (Alou *et al*., 2014).

5.1.3 Effect of AEZ, cropping system and season on abundance of soil nematodes

The present study depicted a significantly higher nematode population density during the wet season compared to the dry season and in banana sole stands compared to grevillea sole stands or their intercrops. The same seasonal trend was observed in all the trophic groups and agrees with the previous studies (Thuo *et al*., 2020b; Huo *et al*., 2021). In managed ecosystems, it has been observed that the rainy season coincides with active root growth, nitrogen mineralization and intense decomposition of applied manure and organic matter and microbial activity, influencing nematode feeding, motility and their multiplication (Da Silva *et al.*, 2020). Besides, the amount of rainfall can affect other soil abiotic parameters (soil organic carbon, soil pH, soil moisture and soil water holding capacity) which in turn directly affect the nematode trophic group composition and abundance (Levi *et al.*, 2012). As a matter of fact, Liu *et al*. (2020) reported a depressive effect of excessive rainfall on the nematode population of a temperate forest as a result of soil acidification and inhibited soil fungal growth.

Significant interactive effects of AEZs and cropping systems were depicted with regard to the population density of all the trophic groups due to the shift in the dominant trophic group in banana sole stands from plant parasitic nematodes in the lowland and midland zones to bacterivore nematodes in the highland zone. This trend is congruent with the findings of Nielsen *et al*. (2014) and Xiao *et al*. (2021) who reported that on a global scale, plant parasitic nematodes dominate warm sites because there is more plant biomass for parasites to exploit whereas bacterial feeding nematodes dominate colder sites. The interactive effects of AEZs and cropping systems on the nematode community structure is indicative of the importance of

the combined effects of climatic factors and the land use/land cover in shaping the distribution of above and belowground inhabiting organisms (Da Silva *et al*., 2020). The findings of the present study indicate that overall nematode abundance in different cropping systems does not reflect assemblage composition, hence no general trend can be depicted without independently analysing the different taxa and/or functional groups.

The sharp increase of bacterivore nematodes in banana sole stands in the highland zone is concomitant with the increase of the dominant genus *Rhabditis*, a resilient and highly prolific genus in response to soil nutrient enrichment and moisture conditions (Bongers and Bongers, 1998). Besides, the highest growth rate, the shortest reproductive period and the maximum total reproductive output in the genus *Rhabditis* was reported at temperatures between 10 and 15°C (Woombs and Laybourn-Parry, 1984), conditions that are characteristic of the highland zone.

Significantly higher population density of plant parasitic nematodes was recovered from banana sole stands compared to grevillea sole stands or their intercrops. This situation might be consecutive to homogeneity of the plant community structure in banana sole stands which can disrupt the biological control of the pests including parasitic nematodes due to simplified soil food web (Eisenhauer *et al*., 2011). In this case, there is a high possibility of a build-up of populations of host specific herbivore nematodes (Kimenju *et al*., 2009) as was the case in banana plantations compared to cacao agroforestry systems or the undisturbed natural forests of Belize, Mayan Mountain region (McQueen and Treonis, 2020). The increase of population density in this trophic group was consecutive to the dominance of *Meloidogyne, Helicotylenchus* and *Pratylenchus* genera, which are known to count pathogenic species of East African Highland Banana varieties (Reddy *et al*., 1999; Reddy *et al*., 2007). This agrees with previous studies which found that these genera are highly prevalent in most of the Kenyan banana growing areas (Reddy *et al*., 2007; Nyang'au *et al*., 2021).

Population density of fungivore, omnivore and predator nematodes followed a similar trend, being more abundant in banana sole stands of the lowland zone only. Such a pattern is in contradiction with previous studies which found that omnivore and predator nematodes are usually regarded as sensitive to disturbances (tillage, fertilization, crop rotation, pollution) and hence less prevalent in intensively managed agrosystems (Yeates and Bongers, 1999; Dong *et al*., 2008; Zhao and Neher, 2013; Zhong *et al*., 2016). The trend in the distribution of omnivore nematodes described in the present study has been strongly influenced by the dominant omnivore nematode genera *Discolaimoides,* which accounted for more than 65 % of all the nematode in this trophic group. The genera *Dorylaimoides* was always more abundant in grevillea sole stands followed by grevillea-banana intercrops and least in banana sole stands, reflecting a depressive effect of physical and chemical perturbations on this genera in accordance with its life history characteristics (Ferris *et al*., 2001; Ferris and Bongers, 2009). The observed higher omnivore and predator population density in banana sole stands in the lowland zone could be a positive response to organic fertilization that offset the disruptive effect of soil tillage in this zone (Treonis *et al*., 2010). The influence of organic fertilization on high trophic level nematodes has been found highly significant when increasing amounts of C-rich amendment are added to soil (Puissant *et al*., 2021) or a diverse cover crop maintained on soil surface (Pan *et al*., 2016); influencing the population density of other nematode trophic groups which constitute food resources to omnivore and predator nematodes (Renčo *et al*., 2010). The distribution pattern of fungal-feeding nematodes was highly influenced by the dominant genera *Aphelenchus* which is empirically believed to feed on Arbuscular Mycorrhizal Fungi (AMF) (Jiang *et al.*, 2020) and particularly the genus *Glomus* which is abundant in banana fields of Mwea zone (Muiruri *et al*., 2022). This idea should be treated with care and further research is required, as it has been established that the palatability of mycorrhizal fungi by hyphae-feeding nematodes varies depending on whether

they are produced symbiotically or saprotrophically in the absence of the symbionts (Brussaard *et al*., 2002).

5.1.4 Effect of AEZ, cropping system and season and the diversity of nematode community and its ecological indices

In the light of taxonomic richness, evenness and Shannon's diversity indices, soil nematode diversity differed between the agro-ecological zones as well as the cropping systems. Altitude is a significant factor influencing the diversity of soil fauna at every elevation, representing different environmental and soil physico-chemical properties that can affect the diversity of above and below-ground biota (Kashyap *et al*., 2022). Taxonomic richness and Shannon's diversity indices were significantly higher in the highland zone compared to the midland and the lowland zone. In contrast to previous studies that found a decreasing nematode diversity with increasing altitude (Afzal *et al*., 2021; Zhang *et al*., 2021; Kashyap *et al*., 2022), the reported trend in the present study can be due to relatively higher soil organic carbon, moisture content and cooler temperature at high elevation compared to the zone of low altitudes. Similar findings were reported in a study in Kashmir valley where the maximum diversity was recorded in zones of temperatures between 11 and 20°C (Nisa *et al*., 2021), a range close to that prevailing in the highland zone. In addition to moisture and temperature conditions, Kergunteuil *et al*. (2016) found that high elevation soils harbour low numbers of nematophagous organisms such as fungi and hence provide a viable environment for nematodes to thrive. However, majority of studies that have reported a decreasing nematode diversity at high elevation were carried out either at elevations above 3,000 m asl (Kashyap *et al*., 2022) or cold deserts (Afzal *et al*., 2021; Zhang *et al*., 2021) where persistent low temperatures might have negatively affected some nematode genera. The reduced diversity of soil nematodes in banana sole stands compared to grevillea sole stands and grevillea-banana intercrops might be caused by high perturbation in banana pure stands through tillage and

application of inorganic fertilizers. Such an observation demonstrates that soil nematode community structure is affected by management practices mediated through soil properties (Pan *et al*., 2016). It has been found that these periodic disturbances can impede the natural succession in croplands and promote the proliferation of only few species that can successfully strive in these fluctuating conditions (Bongers and Bongers, 1998). Moreover, the predominance of few species of plant parasitic nematodes in the banana sole stands induced an imbalanced distribution of the nematode population among the recorded genera. Five nematode genera namely *Achromadora, Criconema, Longidorus, Monohystera* and *Tylenchus* are indirectly affected by tillage (Fiscus and Neher, 2002), and were not recovered in banana sole stands. The trend of nematode diversity in this study is in agreement with the one described in agroecosystems and natural forests of Embu and Taita-Teva, Kenya, (Kimenju *et al*., 2009). Likewise, Thuo *et al*. (2020a) reported a high nematode diversity and genus richness in untilled compared to tilled soils of Murang'a, Machakos and Makueni Counties, Kenya, indicating that change in the nematode community structure could conceal a wide variability of physical, chemical and biological properties of soils in reaction to disturbances.

The nematode community was significantly mature and structured in grevillea sole stands and grevillea-banana intercrops compared to banana sole stands. The low value of Maturity Index in banana sole stands is indicative of a disturbed ecosystem mainly driven by intensive tillage regime (Bongers and Bongers, 1998; Bongers and Ferris, 1999). However, the significant interactions between agroecological zones and cropping systems set aside the lowland zone which had its highest Maturity Index in banana sole stands. The high Maturity Index in these banana sole stands supports results of abundant omnivore and predator nematodes in the lowland zone, indicating a recovering process after a disturbance (Bongers and Ferris, 1999; Ferris and Bongers, 2009). The Structure Index followed the same trend as the Maturity Index

and hence emphasizes the hypothesis of a recovery from stress and a higher food web connectivity inducing a functional resilience to disturbance (Ferris *et al*., 2001) in banana sole stands of the lowland zone. These findings disagree with Puissant *et al*. (2021) who found a low maturity and structure of nematode community, a less stable food web dominated by opportunistic taxa in tilled farms compared to a conservation cropping system. Enrichment Index as well as the Channel Index were not significantly different between the cropping systems. However, the PPI/MI ratio was significantly higher in banana sole stands compared to grevillea sole stands and grevillea-banana intercrops. This finding implies that banana sole stands are nutrient-rich compared to other cropping systems and agrees with other studies where the PPI/MI ratio was found to be a sensitive indicator of enrichment in agro-ecosystems (Bongers, 1990; Bongers *et al*., 1997; Ferris and Bongers, 2009).

5.1.5 Influence of soil physico-chemical properties on nematode community structure

The structure of soil nematode community can be affected by soil properties or interaction with other soil microorganisms and/or above-ground vegetation. The overall abundance of soil nematodes was positively associated with bulk density, total organic carbon and clay content but negatively correlated with silt content, indicating the importance of soil texture and structure in shaping the soil nematode community (Yeates, 1999). Nematodes have been found to populate soils of low bulk density and coarse texture compared to compacted and finely structured ones (Quist *et al*., 2019). The decrease in soil bulk density was due to increased soil organic matter, soil moisture levels and porosity; which are vital for soil microorganisms (Da Silva *et al*., 2020). The fact that the abundance of plant parasitic nematodes was significantly correlated with the same soil factors as the overall nematode community abundance namely bulk density, total organic carbon, clay and silt content insinuates that this dominant trophic group could influence the response of the whole community to changes in some soil abiotic factors. The positive association between the

overall nematode abundance and soil organic carbon is consistent with several other studies which found an increase in the nematode population density after incorporation of organic matter with subsequent increase in soil organic carbon (Okada and Harada, 2007; Hu and Qi, 2010; Ito *et al*., 2015; Keith *et al*., 2009; Renčo *et al*., 2010; Treonis *et al*., 2010; Puissant *et al*., 2021). However, Oka (2010) reported that the influence of soil organic matter on the dynamic of nematode populations depends on its decomposition status with a possibility of being detrimental at the early stage of the decomposition process due to the release of organic acids and build-up of antagonistic microbiota secreting some nematicidal compounds. Moreover, Li *et al*. (2021) found that root carbon inputs induced a greater change in soil nematode community compared to litter carbon inputs, suggesting that not only the amount of soil organic matter affects soil organisms but also its inherent characteristics (Margenot and Hodson, 2016).

Whereas all the other trophic group did not show any preferential relationship with the measured soil properties, the abundance of fungivore nematode only decreased as soil moisture increases. Since nematodes are dependent on the continuity of the soil water films for movement (Yeates and Bongers, 1999), a positive relationship was expected between nematode abundance and soil moisture content. This contrasting result is consistent with Sylvain *et al*. (2014) and Franco *et al*. (2019) who found that the abundance of soil animals is positively and non-linearly influenced by incremental water availability at lower soil moisture only and tends to be depressed when soil moisture rises above 15 %, which was the case in the present study. The effect of soil moisture on the abundance of soil nematode varies depending on whether the observations are made on a local (landscape) or global (regional) scale suggesting that soil moisture is critically important in controlling the activity of soil nematodes (Kumar *et al*., 2014) but needs to be considered in conjunction with other factors

like precipitation regime, soil cover and soil substrate (Sylvain *et al*., 2014; Olatunji *et al*., 2019; Franco *et al*., 2019).

Soil moisture was positively associated with nematode diversity which decreases with temperature rise. These results agree with Bakonyi *et al*. (2007) who found that increasing soil temperature associated with soil drying depresses soil nematode density. However, nematode genera responded differently to changes in soil moisture and temperature, affecting the diversity of their community (Bakonyi *et al*., 2007). Similar observations were made in an abandoned-field grassland in China where enhanced water availability under water addition treatment increased the plant species diversity and root biomass providing a favourable microenvironment for a diverse nematode community inducing a bottom-up control (Song *et al*., 2016). In a study on the effect of soil moisture and temperature on bacterial functional diversity and bacterial feeding nematodes, Papatheodorou *et al*. (2004) found a higher density of bacterial feeding nematode in humid-warm plots whereas the higher generic richness was recorded in warm plots only. This observation partially agrees with findings of the present study in that increasing warm conditions were detrimental to the diversity of the nematode community which was favoured by increasing soil moisture.

Results of the CCA showed a change in the driving forces of the nematode community composition and structure between the dry and the rainy season. This might have been strongly influenced by the seasonal change in most of the measured soil physico-chemical properties which altered the soil abiotic environment and subsequently affected the distribution of the biotic component (Jiang *et al*., 2013). Only 40.6 % and 30.5 % of the observed variance of the distribution of nematode community was attributed to the measured soil properties in the dry and wet season, respectively. This variation in nematode distribution is consistent with ecological studies and suggests that stochastic variation or other soil factors that were not included in this analysis are important for soil fauna distribution (Sánchez-

Moreno *et al*., 2006; Viketoft, 2013; Kamau *et al*., 2017). In the dry season, soil temperature, total organic carbon and phosphorus positively influenced the distribution of plant parasitic nematodes whereas silt and potassium content had a negative influence on the nematodes of this particular trophic group. These results agree with Thuo *et al*. (2020a) who found that the population of predator nematodes increases with soil organic matter and carbon, fungivores and herbivores reduced when potassium increased in vertisols, cambisols and arenosols. Moreover, these authors found that predators and omnivores occupied similar niches while bacterivores and fungivores were found in similar conditions (Thuo *et al*., 2020a). During the wet season, plant parasitic nematodes were positively associated with increasing soil temperature, bulk density and organic carbon. The high abundance of free-living nematodes with rise in ammonium nitrogen supports the importance of free-living nematodes in nitrogen mineralisation (Sánchez-Moreno *et al*., 2006; Jiang *et al*., 2013) and its detrimental effect on plant parasitic nematodes (Oka, 2010).

Among the soil macronutrients, only potassium was consistently related to the distribution of soil nematode trophic groups. Population density of bacterivores, fungivores and omnivores were positively associated with increasing amounts of this nutrient whereas it depressed herbivores' population density. Repellent effects of potassium ions were reported on *Meloidogyne incognita* while *Rotylenchus reniformis* was attracted by the same ions in an *in vitro* experiment (Quénéhervé and Le Saux, 2002), suggesting that the response of plant parasitic nematodes to the increasing concentrations of potassium is species dependent. Increasing soil potassium was reported in a *Chromolaena odorata* fallow with a depressive effect on the population of *Meloidogyne spp* and *Pratylenchus spp* (Odeyemi *et al*., 2013). Significantly lower population density of *Pratylenchus spp* was recovered from sugarcane roots (Noronha *et al*., 2020) and those of soybean (Freitas *et al*., 2017; Leiva *et al*., 2020) in sites with high potassium content. Similarly, application of moderate amounts of potassium

fertilizer (60 kg/ha) in a field trial exhibited a strong ability to inhibit the biological activity of *Heterodora glycines*, a soybean cyst nematode (Gao *et al*., 2018). The potential mechanisms inducing the likely resistance to root invasion by nematodes include the effect of balanced K nutrition on the stabilization of cell structure, thickening of cell wall and prevention of the expansion of intracellular space (Freitas *et al*., 2017; Noronha *et al*., 2020).

5.2 Conclusions

In Kirinyaga County, soil characteristics of farms of the lowland zone differ from those of the midland and highland zones; nutrient rich under banana sole stands compared to grevillea sole stands and grevillea-banana intercrops.

1. Intercropping *G. robusta* with banana significantly reduced selected soil nutrients except N compared to soils under banana sole stands. Intercropping banana and grevillea trees increases the competition for these nutrients and contradicts our first hypothesis that ruled out any significant influence of these cropping systems on the soil physico-chemical properties.

2. Abundance of nematode population (bacterivore, fungivore, omnivore and predator trophic groups) were differently influenced by the interactive effects of agro-ecological zones and cropping systems. Plant parasitic nematodes decreased with altitude and their numbers were high in banana sole stands and substantially depressed in grevillea sole stands and grevillea-banana intercrops.

3. Soil nematode community was more diverse and taxonomically richer in the highland zone compared to the midland and lowland zones, in grevillea-banana intercrops and grevillea sole stands compared to banana sole stands which partially agrees with our second hypothesis in that they failed to depict a consistent pattern of nematode trophic group abundance, except herbivore nematodes, in the cropping systems.

4. The nematode ecological indices (SI, MI and EI) suggest that grevillea sole stands and grevillea-banana intercrops are more stable, with a complex and interconnected food web. Intercropping grevillea-banana can be a sustainable option compared to banana monoculture since the former maintains a healthy soil whereas the latter favours the build-up of plant parasitic nematode population.

5.3 Recommendations

Based on the results of this study the following recommendations are formulated

1. Studies to determine the grevillea tree spacing and pruning regime and maximum age that minimize the above and below-ground competition in banana-grevillea intercrops are required to address on-farm tree management practices and optimum land allocation.
2. Studies assessing the severity of nematode attack on banana, the nutritional status of banana in grevillea-banana intercrops and the productivity of the entire system in terms of banana yield and tree biomass are required for the improvement of our knowledge as far as the economic implications of such a promising technology are concerned
3. Other studies using nematodes as an indicator to assess the soil health conditions of grevillea-based agroforestry with other annual crops like beans, maize, sweet potatoes in diverse ecological conditions are required before the generalization of conclusions of the present study.

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APPENDICES

Appendix 1: *p*-values associated with the soil physico-chemical properties as influenced by AEZ, cropping system and season

Soil parameters	*p*-value						
	AEZ	CS	Season	AEZ:CS	AEZ:Season	CS:Season	AEZ:CS:Season
Bulkdensity (g/cm^3)	0.6622	<**0.001*****	<**0.001*****	**0.009****	**0.0188***	0.0589	<**0.001*****
Moisture content (%)	<**0.001*****	0.3399	<**0.001*****	**0.0395***	<**0.001*****	0.6753	**0.0446***
pH	<**0.001*****	0.0523	0.1806	**0.0011****	0.3601	0.1458	0.1683
TOC (g/kg)	<**0.001*****	<**0.001*****	**0.0367***	0.1016	**0.044***	0.4712	0.4023
TN (g/kg)	0.1826	0.7637	<**0.001*****	0.1238	**0.0185***	0.098	0.4565
C/N ratio	0.2144	0.2876	<**0.001*****	**0.0345***	0.1275	0.7439	0.8027
NH4-N (mg/kg)	0.4704	0.975	<**0.001*****	0.9742	0.225	0.9436	0.8982
NO3-N (mg/kg)	0.2313	0.4765	0.0738	0.4377	0.8146	0.7212	0.515
P (g/kg)	**0.0042****	<**0.001*****	0.62	<**0.001*****	0.1703	0.2927	0.3164
K (mg/kg)	<**0.001*****	**0.0241***	**0.0038****	<**0.001*****	**0.0319***	0.8219	0.5359
Mg (mg/kg)	**0.0403***	<**0.001*****	<**0.001*****	**0.0182***	0.1074	<**0.001*****	**0.0203***
Ca (mg/kg)	<**0.001*****	0.0553	0.0553	<**0.001*****	<**0.001*****	0.6069	0.5949

Abbreviations: AEZ= AgroEcological Zone; CS= Cropping system, TOC=total organic carbon, TN=total nitrogen, C=carbon, N=nitrogen, K=potassium, P=phosphorus, Mg=magnesium, Ca=calcium. *p*-values marked in bold are significant: '***' *p*-value < 0.001; '**' *p*-value < 0.01; '*' *p*-value < 0.05

Appendix 2: *p*-values associated with abundance of soil nematode trophic groups as influenced by AEZ, CS, Season and their interactions

Soil nematode trophic groups	*p*-values						
	AEZ	CS	Season	AEZ:CS	AEZ:Season	CS:Season	AEZ:CS:Season
Bacterivore	<0.001***	0.0294*	<0.001***	0.0137*	0.8845	0.9575	0.9994
Fungivore	0.1269	0.6111	<0.001***	<0.001***	0.9836	0.9627	0.9897
Predator	0.3542	0.2308	0.0332*	0.0035**	0.9634	0.9775	0.9999
Omnivore	0.4339	0.1401	<0.001***	<0.001***	0.93	0.9916	0.9971
Herbivore	0.4478	<0.001***	<0.001***	<0.001***	0.8352	0.9354	0.9651

Abbreviations: AEZ= AgroEcological Zone; CS= Cropping system. *p*-values marked in bold are significant: '***' *p*-value < 0.001; '**' *p*-value < 0.01; '*'*p*-value < 0.05

Appendix 3: *p*-values associated with abundance of soil nematode genera as influenced by AEZ, cropping systems, Season and their interactions

Nematode genera	*p*-values						
	AEZ	CS	Season	AEZ:CS	AEZ:Season	CS:Season	AEZ:CS:Season
Achromadora	0.3739	0.2944		0.6077			
Acrobeles	<0.001***	0.2799	0.1422	0.0056**	0.9039	0.8788	0.917
Alaimus	0.4668	0.1765		1			
Aphelenchoides	0.7112	0.7113	1	<0.001***	0.9886	0.9945	0.9912
Aphelenchus	0.3171	0.8739	0.0087**	<0.001***	0.9161	0.9845	0.9849
Cephalobus	0.0786	0.4543	<0.001***	0.0162*	0.8173	0.9066	0.9997
Criconema	1	<0.001***	0.4051	1	0.9998	0.9045	1
Discolaimoides	0.3315	0.6515	<0.001***	<0.001***	0.9443	0.995	0.9935
Dorylaimodes	0.4679	0.0019**	0.0035	<0.001***	0.8757	0.9996	0.9992
Eucephalobus	0.0047**	0.7085	0.0014**	0.865	0.9938	0.9604	0.9957
Filenchus	0.1898	0.0993	0.1229	0.0048**	0.8569	0.8965	0.9791
Helicotylenchus	0.0012**	<0.001***	0.0368*	<0.001***	0.9043	0.868	0.9942
Hemicyclophora	<0.001***	1	<0.001***	<0.001***	0.9835	0.997	1
Labronema	0.5337	0.2886	0.1548	0.0014**	0.9681	0.9507	0.9991
Longidorus	<0.001***	0.0064**	0.0627	0.3444	0.7778	0.8431	1
Meloidogyne	0.1159	<0.001***	0.0078**	0.0028**	0.9453	0.9779	0.9937
Monohystera	0.0369*	1	<0.001***	0.2936	1	<0.001***	1
Mononchus	0.4849	0.3208	0.1515	0.0142*	0.9893	0.9954	0.9998
Plectus	0.0458*	0.7485	1	1	<0.001***	0.9737	1
Pratylenchus	0.0025**	0.0827	0.0224*	<0.001***	0.9498	0.9889	0.9288
Primastolaimus	0.1102	0.1292	0.0722	0.0059**	0.876	0.6833	0.9189
Radopholus	1	0.5699	0.7519	1	0.9706	1	1
Rhabditis	<0.001***	<0.001***	<0.001***	0.0233*	0.8781	0.9983	0.9999
Scutellonema	0.009	0.1412	0.0759	<0.001***	0.9656	0.9991	0.9991
Trichodorus	0.8902	<0.001***	0.2193	0.0177*	0.8844	0.9633	0.9961
Tylenchus	0.0016**	0.0454*	0.9945	0.6916	0.8713	0.811	1
Wilsonema	0.2801	0.125*	0.6299	0.5734	0.9468	0.4349	1
Xiphinema	<0.001***	<0.001***	0.3045	1	1	0.8623	1

Abbreviations: AEZ= AgroEcological Zone; CS= Cropping system. *p*-values marked in bold are significant: '***' *p*-value < 0.001; '**' *p*-value < 0.01; '*' *p*-value < 0.05

Appendix 4: *p*-values associated with nematode community and ecological indices as influenced by AEZs, cropping systems and Season and their interactions

Community and ecological indices	*p*-values						
	AEZ	CS	Season	AEZ:CS	AEZ:Season	CS:Season	AEZ:CS:Season
Total abundance	0.3117	<0.001***	<0.001***	0.0866	0.9203	0.9583	0.9785
Number of genera	<0.001***	0.3449	0.5323	0.0098**	0.975	0.9428	0.9822
Evenness	0.3197	<0.001***	0.6495	0.8145	0.8108	0.9864	0.9994
DI	<0.001***	<0.001***	0.3495	0.0943	0.9907	0.915	0.9989
PPI	0.259	0.0811	0.358	0.0197*	0.5035	0.661	0.2984
MI	0.1326	0.0162*	0.5406	<0.001***	0.8497	0.8562	0.9613
PPI.MI	0.5471	0.0064**	0.7409	<0.001***	0.7239	0.7913	0.3294
BI	0.0748	0.1551	0.7147	<0.001***	0.7512	0.9175	0.9909
EI	<0.001***	0.8647	0.7838	0.9988	0.9787	0.9518	0.9999
SI	0.185	0.0319*	0.995	<0.001***	0.7817	0.9937	0.9902
CI	<0.001***	0.3518	0.9203	0.0596	0.7384	0.9895	0.9955

Abbreviation: DI= Shannon's Diversity Index, PPI=Plant Parasitic Index, MI= Maturity Index, BI= Basal Index, EI = Enrichment Index, SI= Structural Index, CI= Channel Index, AEZ= AgroEcological Zone; CS= Cropping system. *p*-values significance: '***' *p*-value < 0.001; '**' *p*-value < 0.01; '*'*p*-value < 0.05

Appendix 5: *p*-values associated with the correlation between soil physico-chemical factors and nematode trophic groups, community and ecological indices

	Bulk density	Moisture	Soil Temp.	Sand	Silt	Clay	pH	TOC	TN	C/N ratio	NH4-N	NO3-N	P	K	Ca	Mg
Total abundance	0.0259	0.1875	0.9069	0.9689	0.0025	0.0259	0.3944	0.0499	0.1853	0.9059	0.159	0.1224	0.4347	0.2118	0.1334	0.7294
Genera richness	0.4488	0.0083	0.0485	0.9916	0.2329	0.3631	0.1725	0.1025	0.3101	0.2263	0.7671	0.766	0.507	0.8785	0.6085	0.3044
Eveness	0.1123	0.6626	0.0564	0.3251	0.0501	0.0133	0.7234	0.1006	0.9852	0.7713	0.452	0.291	0.0677	0.2402	0.8771	0.3557
Bacterivore	0.7956	0.3264	0.0739	0.9656	0.9841	0.8527	0.964	0.8584	0.9711	0.976	0.4552	0.9323	0.4816	0.1966	0.9515	0.4474
Fungivore	0.1355	0.0134	0.6656	0.5518	0.1617	0.3812	0.5673	0.2894	0.104	0.0475	0.7133	0.1545	0.801	0.6409	0.5649	0.8276
Predator	0.3259	0.8994	0.8508	0.4887	0.4612	0.2699	0.8983	0.3277	0.3037	0.4906	0.6812	0.2533	0.0879	0.6539	0.0711	0.9075
Omnivore	0.6813	0.1363	0.7429	0.8103	0.735	0.7014	0.7625	0.25	0.2164	0.3034	0.1331	0.1511	0.3868	0.3819	0.2452	0.1685
Herbivore	0.022	0.4275	0.5014	0.9629	0.0002	0.0012	0.3355	0.0207	0.2389	0.8038	0.2409	0.1113	0.1214	0.23	0.1056	0.5664
DI	0.8525	0.0373	0.0459	0.7616	0.4913	0.3221	0.5494	0.7839	0.816	0.5904	0.4784	0.3431	0.1342	0.4407	0.5389	0.149
PPI	0.6206	0.0034	0.9821	0.4303	0.4697	0.9848	0.0383	0.1559	0.4696	0.9061	0.6385	0.5959	0.2686	0.499	0.1042	0.0317
MI	0.8189	0.4295	0.4961	0.0923	0.1615	0.6263	0.2827	0.0967	0.6945	0.3184	0.7015	0.0505	0.0133	0.0348	0.4692	0.2271
PPI/MI	0.5147	0.1011	0.8237	0.2752	0.2226	0.6211	0.8974	0.6353	0.4043	0.6084	0.6709	0.4562	0.2208	0.246	0.3138	0.9794
BI	0.0809	0.4479	0.2377	0.6813	0.8155	0.6621	0.5273	0.0264	0.768	0.4336	0.8573	0.6076	0.8111	0.6764	0.0377	0.8103
EI	0.1296	0.6317	0.1783	0.7533	0.0002	0.0017	0.0313	0.0684	0.8353	0.1283	0.5621	0.6932	0.0527	0.0025	0.0105	0.2216
SI	0.1506	0.1757	0.7934	0.5554	0.8007	0.8829	0.7513	0.0037	0.8452	0.401	0.4582	0.1265	0.3284	0.1425	0.123	0.3478
CI	0.4313	0.227	0.7858	0.8073	0.0009	0.001	0.0022	0.0347	0.6877	0.0628	0.4843	0.3694	0.0562	0	0.0097	0.8454

Appendix 6: *p*-values associated with correlation between soil physico-chemical properties and abundance of soil nematode genera

	Bulk density	Moisture content	Soil Temp.	Sand	Silt	Clay	pH	TOC	TN	C/N ratio	NH_4-N	NO_3-N	P	K	Ca	Mg
Achromadora	0.6824	0.3904	0.2206	0.537	0.5187	0.9472	0.2247	0.7621	0.8349	0.9878	0.861	0.3561	0.7851	0.8928	0.5868	0.7935
Acrobeles	0.595	0.0024	0.0266	0.7497	0.0063	0.0388	0.2896	0.0032	0.7815	0.174	0.7742	0.0357	0.6491	0.0085	0.1336	0.1353
Alaimus	0.6787	0.7834	0.8538	0.0591	0.0355	0.0019	0.2279	0.2525	0.5382	0.4186	0.6492	0.0043	0.3194	0.6125	0.3845	0.7982
Aphelenchoides	0.0552	0.0978	0.9402	0.6669	0.7107	0.5511	0.2045	0.8015	0.7116	0.8078	0.7193	0.1473	0.8718	0.7271	0.0679	0.7458
Aphelenchus	0.3072	0.0546	0.8507	0.5297	0.142	0.3674	0.5544	0.1711	0.0877	0.0225	0.8524	0.286	0.3556	0.6858	0.4752	0.5252
Cephalobus	0.1702	0.1688	0.0312	0.4582	0.0263	0.2379	0.1869	0.0718	0.6369	0.0921	0.5586	0.5324	0.0657	0.7135	0.1041	0.6105
Criconema	0.3236	0.1021	0.0239	0.2178	0.0581	0.012	0.0809	0.3323	0.8689	0.7843	0.8532	0.3881	0.8217	0.8798	0.127	0.3546
Discolaimoides	0.3214	0.1584	0.4054	0.6868	0.4771	0.4585	0.658	0.7616	0.2684	0.3001	0.1457	0.0648	0.6692	0.752	0.0903	0.2431
Dorylaimodes	0.4907	0.4172	0.5033	0.8863	0.6586	0.6947	0.8365	0.0309	0.2817	0.4468	0.3635	0.9483	0.2855	0.0885	0.9349	0.3086
Eucephalobus	0.5573	0.1445	0.0131	0.4724	0.5346	0.3437	0.0762	0.1572	0.4952	0.0973	0.3144	0.7974	0.085	0.6733	0.0628	0.1621
Filenchus	0.9969	0.5157	0.0258	0.7425	0.3632	0.29	0.1328	0.7757	0.6922	0.9314	0.7423	0.9792	0.0001	0.7617	0.0161	0.3405
Helicotylenchus	0.0355	0.6385	0.4375	0.0176	0.1013	0.0025	0.5574	0.1005	0.4398	0.7801	0.6348	0.8304	0.0969	0.114	0.6328	0.7799
Hemicyclophora	0.2312	0.0588	0.0638	0.0346	0.8669	0.149	0.4283	0.3202	0.5574	0.4658	0.547	0.6979	0.221	0.0158	0.0889	0.4284
Labronema	0.1579	0.4504	0.4359	0.192	0.2198	0.8401	0.8025	0.7462	0.6333	0.6061	0.7036	0.3065	0.4788	0.7822	0.2261	0.8177
Longidorus	0.2137	0.2078	0.1333	0.3745	0.884	0.4022	0.5213	0.1119	0.9358	0.7303	0.4425	0.6041	0.36	0.0261	0.7139	0.6251
Meloidogyne	0.2819	0.8596	0.6557	0.2079	0.012	0.1937	0.3213	0.0348	0.871	0.3103	0.4828	0.7781	0.5118	0.1786	0.1236	0.6124
Monohystera	0.0331	0.1997	0.5278	0.2881	0.5018	0.8251	0.4521	0.4101	0.7478	0.8134	0.9397	0.1838	0.5133	0.7079	0.1147	0.9266
Mononchus	0.6589	0.5739	0.5457	0.1483	0.8168	0.1723	0.9503	0.324	0.3207	0.552	0.7781	0.4332	0.1207	0.781	0.1315	0.7826
Plectus	0.8943	0.501	0.2067	0.9494	0.0595	0.1082	0.2145	0.4855	0.6936	0.8487	0.7255	0.8866	0.8869	0.6464	0.678	0.6632
Pratylenchus	0.1149	0.495	0.9309	0.9556	0.0311	0.0562	0.8437	0.7196	0.2478	0.4403	0.3205	0.1549	0.2362	0.578	0.7539	0.6305
Primastolaimus	0.3676	0.6854	0.7296	0.1587	0.0107	0.2435	0.0069	0.4165	0.2248	0.0553	0.3299	0.4458	0.0502	0.0245	0.021	0.3606
Radopholus	0.3103	0.867	0.9805	0.4127	0.013	0.1129	0.3544	0.092	0.5311	0.4871	0.7371	0.5233	0.4463	0.6166	0.2673	0.6032
Rhabditis	0.1225	0.8679	0.1516	0.8231	0.2621	0.3253	0.4916	0.1747	0.9845	0.3685	0.5744	0.833	0.8478	0.07813	0.4212	0.0849
Scutellonema	0.2631	0.4416	0.7117	0.6456	0.0344	0.0306	0.7391	0.4073	0.054	0.7006	0.509	0.0038	0.4511	0.0555	0.3262	0.8124
Trichodorus	0.0821	0.847	0.9728	0.2188	0.0116	0.0018	0.4086	0.0845	0.1577	0.7238	0.6663	0.1957	0.0393	0.7214	0.4923	0.5677
Tylenchus	0.4853	0.7923	0.9581	0.9316	0.0237	0.0509	0.7935	0.683	0.6988	0.9819	0.5162	0.2328	0.5763	0.5184	0.6342	0.66
Wilsonema	0.1583	0.7989	0.2968	0.626	0.1817	0.3603	0.0303	0.2733	0.1929	0.6129	0.7129	0.7544	0.5252	0.0006	0.3804	0.7628
Xiphinema	0.1183	0	0.0009	0.1516	0.2919	0.9913	0.0584	0.0776	0.5461	0.1186	0.7136	0.4128	0.8641	0.8138	0.3303	0.3881

Appendix 7: Questionnaire for farm biodata collection

I. FARM IDENTIFICATION

AEZ	
Cropping system	
Farm N°	
Farm Code	

II. ABOUT BANANA FARMING

1. Banana variety under cultivation
   a. Cooking banana b. Dessert banana c. Others

2. Origin of the suckers/seedlings
   a. Own farm b. Neighbours' farms c. Tissue cultured seedlings d. Others

3. Age of the plantation
   a. < 1 year b. 1 to 3 years c. 3 to 5 years d. > 5 years
4. Planting density
   a. <100 banana stools/ha b. 100 to 300 banana stools/ha c. 300 to 600 banana stools/ha d. >600 banana stools/ha
5. Do you intercrop Banana with other crops?
   a. Yes b. No
6. If yes, which ones?
   a. Cereals b. Legumes c. Tubers d. Vegetables e. Others

7. Do you plant cover crops?
   a. Yes b. No
8. If Yes, which ones?
9. What are the different farming operations that you undertake for land preparation before plantation of intercrops?

10. Do you use inorganic fertilizers and/or manure on those crop? Banana?
    a. Yes b. No
11. If Yes, which ones?
12. Do you experience some banana diseases?
    a. Yes b. No
13. If Yes, what are the most common symptoms that you usually observe?
    a. Leaf wilting b. Banana stunting c. Fruit rot d. Banana toppling d. Others

14. How do you treat these diseases?
    a. Uprooting the diseased plants b. Use of pesticides c. No treatment d. Others

15. Do you practice irrigation?
    a. Yes b. No

III.ABOUT GREVILLEA PLANTATION

1. Before tree plantation, what was this land affected to?
   a. Annual crops b. Coffee c. Tea d. Planted fallow e. Bush fallow f. Others

2. Approximate age of the Grevillea trees
   a. < 3 years b. 3 to 10 years c. 10 to 20 years d. 20 to 30 years e. > 30 years
3. Planting density
   a. < 100 trees/ha b. 100 to 300 trees/ha c. 300 to 600 trees/ha d. 600 to 900 trees/ha e. > 900 trees/ha
4. Do you prune the trees?
   a. Yes b. No
5. If Yes, how often?
   a. Once a year b. Two times a year c. Three times a year d. Other

6. How do you manage the litter after pruning
   a. Incorporation to the soil b. Applied as mulch c. Used as fodder d. Other

7. What other management operations do you apply on the Grevillea trees?
   a. Coppicing b. Pollarding c. Other

8. Do you intercrop Grevillea with other crops?
   a. Yes b. No
9. If Yes, which ones?
   a. Cereals b. Legumes c. Tubers d. Vegetables e. Others

10. Do you use inorganic fertilizers and/or manure on those crops?
    a. Yes b. No
11. If Yes, which ones.

12. Do you practice irrigation
    a. Yes b. No