SHORT TERM SHIFTS IN SOIL NEMATODE FOOD WEB STRUCTURE AND NUTRIENT CYCLING FOLLOWING SUSTAINABLE SOIL MANAGEMENT IN A CALIFORNIA VINEYARD

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ABSTRACT

Short term shifts in soil nematode food web structure and nutrient cycling following sustainable soil management in a California vineyard

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Evaluating soil health using bioindicator organisms has been suggested as a method of analyzing the long-term sustainability of agricultural management practices. The main objective of this study was to determine the effects of vineyard management strategies on soil food web structure and function, using nematodes as bioindicators by calculating established nematode ecological indices. Three field trials were conducted in a commercial Pinot Noir vineyard in San Luis Obispo, California; the effects of (i) fertilizer type (organic and inorganic), (ii) weed management (herbicide and tillage), and (iii) cover crops (high or low water requirements) on nematode community structure, soil nutrient content, and crop quality and yield were analyzed. Overall, although nematode ecological indices indicated that all plots had disturbed soil food webs, the indices proved to be less useful for measuring subtle differences in soil management over the short-term than anticipated. They showed few differences treatments. In general, the most pronounced differences were seen by sample location (under the vine or in the tractor row) and sample date, rather than treatment. None of the evaluated strategies affected crop quality, although fertilizer had a slight effect on yield. However, several indices were correlated with soil chemical parameters, including pH, nitrogen, carbon, and, to a lesser extent, EC. These results indicate that while nematode indices can be useful for comparing the state of the soil food web under long-term soil conditions, they may not be a robust measure of how agricultural management practices change soil health over a single growing season.

Keywords: ecological indices, sustainability, vineyard, nematode, fertilizer, herbicide, tillage.

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1. INTRODUCTION

The term soil health refers to soil's ability to function as a living ecosystem (Doran and Zeiss, 2000; Kibblewhite et al., 2008). This ability is largely determined by the amount and type of soil organisms present; biological activity is the basis for many soil functions, such as decomposition of organic matter or nutrient cycling (Sánchez-Moreno and Ferris, 2007). The importance of soil biological drivers on these functions is increasingly being recognized by both researchers and the agricultural community (Wagg et al., 2014; Bardgett and van der Putten, 2014).

Organisms in the soil are organized into food webs, which are essentially more complex and interconnected versions of the familiar above-ground food chain. Energy and matter generally first enter the soil food web through photosynthates produced by plants. These chemicals are fed upon by soil organisms, and matter and energy then flow through the rest of the food web through various levels of predation or parasitism, termed trophic levels (Whalen and Sampedro, 2010). The basal trophic level includes bacterivores, and the apical trophic levels include predators. In the middle are fungivores, herbivores, and parasites (Whalen and Sampedro, 2010). Different species within a single trophic level can have varying life history strategies. For example, some species, termed r-strategists, may complete their life cycle quickly and produce large numbers of progeny, while others, termed k-strategists, may take more time to complete their lifecycle and produce smaller numbers of progeny (Ferris et al., 2001). However, when all of these organisms are present in an intact soil food web, the soil is more likely to be healthy and consequently support production agriculture (Wagg et al., 2014).

Production agriculture, however, often utilizes management practices that alter the soil food web and can consequently affect soil function (Birkhofer et al., 2008). Management has been shown to reduce soil biodiversity and shift the soil community composition (de Vries and Wallenstein, 2017), leading to diminished soil functions such as nutrient cycling and decomposition (Wagg et al., 2014). Agricultural soils have been described as existing on a "disturbance continuum" (Vonk et al., 2013), which potentially has long-term consequences for soil fertility and crop productivity. Therefore, it is important to assess effects of common management practices, such as fertilization or weed control, on the soil food web.

Unfortunately, direct measurement of all the taxa present within a soil food web is prohibitively difficult. It requires expert knowledge of all soil organisms, from microbes to macrofauna, and many of these organisms require different methods of analysis (i.e. earthworms can be directly counted, but bacteria may need to be identified using molecular techniques). In addition, some taxa are not temporally stable, meaning that single measurements in time may not provide an accurate picture of soil function as it relates to the soil food web. Bacteria, for example, can fluctuate diurnally, so soil samples collected at one time for bacterial analysis would provide an incomplete picture and potentially complicate analysis and results (Neher, 2001). The extraordinarily time-consuming nature, expert knowledge requirement, and complexity of such a comprehensive soil analysis precludes any practical application. The result is a need for bioindicator organisms, which, when measured, could provide information about the state of the entire soil food web. Such an organism should be common in soils to ensure its usefulness in multiple environments (Neher, 2001). It should occupy key niches within the soil food web and have different life

history strategies. These characteristics would allow the organism to provide information about the complexity and maturity of the soil food web. Such an organism should also be sensitive to changes in the soil environment, to reflect how these changes affect the soil food web. Lastly, it should be well-correlated with ecosystem services so as to provide an indication of the effects of management on soil functioning (Doran and Zeiss, 2000).

Nematodes meet the above requirements for useful bioindicator organisms. They are ubiquitous, occupy at least five trophic levels, from bacterivore to predator, and have life history strategies varying from opportunist to k-strategist (Bongers, 1999; Neher, 2001). Some taxa have resistant stages, such as cryptobiosis, allowing them to survive unfavorable conditions; others react quickly to changes in the environment (Bongers, 1999; Neher, 2001). Because of this differential response to soil conditions, the presence and absence of a variety of nematode taxa can indicate the state of disturbance in a soil system (Neher, 2001). Their generation times range from days to years, making them more temporally stable than bacteria and less likely to reflect transient changes (Neher, 2001).

Perhaps most importantly for agricultural systems, nematodes are well-correlated with ecosystem services, particularly nitrogen (N) cycling. In conventional farming systems, nematode activity is responsible for approximately 8% of N mineralization. In integrated systems, the number rises to 19% (Beare, 1997). Nitrogen mineralization occurs when nematodes prey on microbes and excrete ammonium, whereas N immobilization occurs when N is accumulated into nematode biomass (Ferris et al., 1998; Ingham et al., 1985). Immobilized N is then regulated by the feeding activities of predatory nematodes (Neher, 2001). The result of these cycles is N that becomes plant-available; systems which

contain nematode grazers have been shown to produce greater plant biomass than systems with less complex food webs (Ingham et al., 1985; Neher, 2001).

Unfortunately, simple measures of nematode abundance, proportions, or ratios of trophic groups are insensitive to qualitative differences between taxa. These measurements have not stood up to rigorous analysis when attempting to differentiate ecological condition at the regional scale (Neher, 2001). Likewise, simple diversity indices provide little to no information about ecosystem function (Ferris, 2010b). In response, more complex indices have been established for the analysis of nematode community structure, such as the Maturity Index, Enrichment Index, or Channel Index (Bongers, 1990; Ferris et al., 2001; Ferris, 2010b). These indices consider life history strategies, response to disturbance, and metabolic processing of C, as well as trophic levels and abundance. The utilization of these well-established indices can provide valuable information about the state of the soil food web and ecosystem functioning as well as diagnose changes in response to soil management (Bongers, 1999; Ferris et al., 2001; Neher, 2001; Vonk et al., 2013).

The impacts of the soil food web on soil ecosystem functioning and overall soil health is increasingly being recognized- not only by the scientific community, but also by agricultural producers, such as viticulturists and vintners. Many producers are adopting "sustainable" practices; such practices often include the declared goal of protecting soil health. By 2018, California had 142,065 acres of vineyards certified sustainable by the California Sustainable Winegrowing Alliance (CSWA). This accounts for 73% of the total cases of wine produced in the state ("California Sustainable Winegrowing Alliance | Certified Participants"). CSWA certified vineyards account for about 22% of statewide wine acreage, and an additional 10% of acreage are certified by other sustainability

programs, such as Sustainability in Practice (SIP) (Wine Institue, 2018). Sustainable certification in California vineyards generally requires the utilization of practices intended to protect soil, and dictates methods of fertilization, weed management, and cover crop use. Management practices encouraged by both the CWSA and SIP certification programs to benefit soil health include the use of equipment which lessens compaction, regular soil tests, organic matter addition, alternative tillage, and cover crops to reduce soil erosion and increase soil organic matter (CSWA, 2012; SIP Certified, 2018). SIP, in particular, requires integrated management of weeds, including monthly monitoring and herbicide rotation. Spot spraying and tillage swath widths are assessed, and guidelines recommend that fertilization be timed to maximize uptake (Sustainability in Practice (SIP) Certified, 2018).

These practices are known to generally have beneficial effects in soil physical and chemical properties by enhancing soil structure and improving soil organic matter, but the impacts on soil organisms and the soil food web is less clear (Magdoff, 2001; Forge et al., 2005; Birkhofer et al., 2008; Coll et al., 2011; Ito et al., 2015; Salomé et al., 2016).

Studies assessing the effects of agricultural management strategies on soil food webs using nematode indices have been attempted, but many of these studies produced varied results or were not correlated with either crop health or soil nutrient status (Coll et al., 2011; Ito et al., 2015; Salomé et al., 2016). Studies have also tended to look at results of a group of management practices implemented together, rather than a single practice in isolation. The results of such studies have been complicated by confounding factors, such as cropping density, pest pressure, climate, or soil type (Forge et al., 2005; Birkhofer et al., 2008, Tesic et al., 2007). Additionally, many studies that have contributed to knowledge about soil food webs were conducted in annual cropping systems, such as potatoes, rice, or

tomatoes (Ferris et al., 1996; Ito et al., 2015; Kimpinski et al., 2003). This highlights the need for field studies which control for complicating variables, and specifically address relevant practices for the wine industry in California.

In terms of weed management strategies, herbicide application (also referred to as chemical weeding) is a common practice in California, even though it is directly associated with soil and water pollution (Tesic et al., 2007). Tillage has often been used as an alternative to chemical weeding, especially by growers with sustainability in mind (Leap, 2017). However, tillage has been speculated to be the single most damaging practice for soil organisms in organic agriculture (Coll et al., 2012). Tillage has been shown to disturb organisms at higher trophic levels, encourage opportunistic taxa, lower soil carbon levels, and lessen fungal-mediated decomposition (Ferris, 2010; Ito et al., 2015; Salomé et al., 2016). The effects of herbicides on the soil food web have been shown to be smaller, possibly in part because, depending on their solubility and sorption characteristics, surface-applied chemicals may not come into contact with soil-dwelling organisms. Soils can recover after herbicide application, and herbicide-induced changes to the foodweb do not always affect soil function, or affect it in a negative way (Griffiths et al., 2008; Salminen et al., 1997). Despite evidence for these broad patterns of foodweb response to management strategies, these effects are type-specific for both herbicides and tillage. Different herbicide or machinery types have different effects on the soil foodweb (Ito et al., 2015; Salminen et al., 1997). Due to these differences, it is important for practices which are particular to California vineyards (i.e. specific herbicides and tillage types) to be studied.

In terms of fertilizer management, nutrient inputs are necessary for maintaining yields, but their use requires careful analysis as they can also be a source of environmental

contamination (Magdoff, 2001; Sims et al., 1999). The effects of fertilizers on below-ground organisms, and specifically nematodes, vary depending on the fertilizer type, amount, and the nematode taxa in question. Some organic amendments can have nematicidal effects (Forge et al., 2005) and reduce herbivorous nematodes, others have been shown to increase numbers of microbivorous, predatory and free-living nematodes after application (Birkhofer et al., 2008; Coll et al., 2011; Kimpinski et al., 2003; Neher, 1999). Inorganic fertilizers have been shown in some studies to reduce herbivorous and bacterivorous nematodes compared to organic amendments (Forge et al., 2005; Neher, 1999). Presumably, there are multiple mechanisms that control nematode populations, and it may not be possible to make broad generalizations on the effects of fertilizers on soil ecology. Rather, the effects of specific types of fertilizer must be studied in the cropping system to which they will be applied for meaningful conclusions to be made. The chemical composition of the fertilizer, in terms of variation of labile carbon fractions and C:N ratio, can change how it affects the food web. Inputs with low C:N ratios favor the growth of bacteria, which consume it; inputs with higher C:N ratios favor fungi. The response of either group of organisms is then reflected by increases in the abundance of their respective predators, including nematodes (Margenot and Hodson, 2016).

Finally, cover crops are generally used for the express purpose of environmental benefits, such as adding organic matter to the soil (Ito et al., 2015), but their use is contentious, especially in arid regions, as they may negatively affect crop yield and quality. Water competition is of particular concern in warm regions with low rainfall (Tesic et al., 2007), conditions that are common throughout much of California. For this reason, the choice of which cover crop to utilize should be carefully evaluated, as plant species which

require less water could have less detrimental effects on the cash crop. However, cover crops provide a continuous input of carbon to the soil food web, and the presence of a cover crop may have strong effects on soil functioning across all soil types (Salomé et al., 2016). Higher levels of soil carbon are correlated with greater nematode abundance and diversity (Ito et al., 2015; Salomé et al., 2016; Zhang et al., 2017). Because a robust community of microbial grazers, such as bacterivorous nematodes, is generally beneficial for the crop due to increased nutrient mineralization, and because grapes in particular are intentionally water stressed during certain periods of the growing season, and irrigated in the remainder of the season in California, it remains to be seen how cover crop types will affect crop and soil health in California vineyards (Zhang et al., 2017).

The main objective of this study was to determine the effects of current vineyard soil management strategies on soil food web structure and function, by using nematodes as bioindicators. The effects of (i) fertilizer management strategies (organic and inorganic), (ii) weed management (herbicide and tillage), and (iii) cover crops (high or low water requirements) on nematode community structure, soil nutrient content, crop health and yield were evaluated through a field trial in a Pinot Noir commercial vineyard in San Luis Obispo, California.

We hypothesized that, being a relatively disturbed soil ecosystem, the soil food web would also show relatively high levels of disturbance independently of the soil management strategy, with values near 2 on a scale of 1-5 for maturity and stability indicators. In addition, we hypothesized that fertilizer application would have a significant effect on the nematode food web, affecting the abundance and feeding preferences of the

nematode community, by changing soil physicochemical properties such as pH, C and N availability, and altering the composition of the rest of the soil community.

Tillage, compared to herbicide, is expected to reduce indicators of stability and alter the primary decomposition channel by changing soil carbon pools and disturbing the soil environment. Tillage is also expected to increase enrichment indices due to changes in nutrient availability and resulting changes in organisms in lower trophic levels.

Cover crop treatments are expected to lower stability indicators and decrease the Channel index compared to resident vegetation by increasing nutrient resources for opportunistic species, including bacteria. This is expected to be highest under the high-water use cover crop, which is dominated by legumes and should consequently support the greatest microbial biomass (Viketoft et al., 2005).

2. LITERATURE REVIEW

The mismanagement of soil is an ancient problem, dating back to the advent of agriculture and a shift away from hunter-gatherer societies. Even Plato noted the effects of soil erosion when he said, "The rich, soft soil has all run away, leaving the land nothing but skin and bone," (Montgomery, 2007). Soil degradation can result from the use of heavy agricultural machinery, fertilizer use and subsequent salt build up, overexploitation of resources through intensive cropping, or by stripping the land of plant cover and leaving soil prone to erosion by wind or water (Diacono and Montemurro, 2010; Kibblewhite et al., 2008; Oldeman, 1991). Despite the fact that soil degradation is an ancient problem, soils continued to be mismanaged and degraded well into the 20th century, and the Green Revolution has produced a state of continuous degradation (Singh, 2000). Since the 1940s, one third of all present cropland has been lost (Cameron et al., 2015). These soils have been abandoned after they became so badly degraded or eroded that they could no longer support crops (Montgomery, 2007). However, in the past few decades, mainstream agriculture has begun to shift away from typical management strategies which degrade soil. The concept of soil health has emerged and been refined as a worthy goal for growers to work towards, with the purpose of achieving agricultural sustainability (Doran and Zeiss, 2000).

Soil health refers to the ability of a soil to function as an intact ecosystem which supports plant productivity, animal health, and environmental quality (Doran and Zeiss, 2000; Kibblewhite et al., 2008). A crucial part of this concept is that soils are not sterile; they are living systems which require a suite of soil organisms in an interconnected food web to support its function and maintain productivity. Soil organisms are responsible for four functions which are termed ecosystem services: carbon transformations, nutrient

cycling, soil structure, and pest and disease regulation (Kibblewhite et al., 2008; Ferris, 2010a). The basal resource for the soil food web is generally complex carbohydrates produced by autotrophic fixation via photosynthesis which are rapidly transferred to soil organisms (Bardgett and van der Putten, 2014; Ferris, 2010a). These molecules are broken down by soil organisms via plant-, bacterial-, or fungal-feeding, followed by successive levels of parasitism and predation, thereby providing carbon, nitrogen, and energy to the food web. The energy bound within the molecules is released and the carbon and nitrogen can be immobilized in the tissues of the organisms, excreted, or respired (Ferris, 2010a).

As carbon, nitrogen, and energy cycle through the food web, the structure, dynamics, and activities of the web are affected (Ferris, 2010a). Pulses of resources trigger short-term increases in organism activity and N cycling, thereby increasing plant nutrient uptake and growth. For example, a fertilization or irrigation event is followed by pulses of microbial activity and subsequent increases in nitrogen mineralization and CO_2 release (Bardgett and van der Putten, 2014). Herbivory can also provide a resource pulse by stimulating root exudation. If the functional diversity of soil organisms is lost from the system, these functions (nutrient cycling and greenhouse gas release), as well as others, can be impacted (Ferris et al., 2001; Bardgett and van der Putten, 2014). Intensive land use, as occurs with agriculture, can alter the structure of the soil food web and consequently its function by changing the soil physical environment and inputs of C and N. It can shift decomposition pathways from fungal-dominated to microbial-dominated, for example, and slow nutrient and carbon cycling (Bardgett and van der Putten, 2014). Loss of functional diversity consistently slows carbon and nitrogen cycling and increases greenhouse gas emissions and nitrogen runoff (Bardgett and van der Putten, 2014). These changes in the

soil community and soil function can also affect crop fitness, reducing the capacity to compete, reproduce, and defend (Bardgett and van der Putten, 2014).

Anthropogenic pressures threaten the structure of soil communities, and knowledge of how soil microorganisms adapt to change is crucial for understanding how disturbances in the soil environment will affect agricultural sustainability (Bardgett and van der Putten, 2014). The capacity of the soil to function in agricultural systems, as well as the direction of change over time, indicates the sustainability of field management practices (Doran and Zeiss, 2000). Research is needed to identify the effects of soil management on soil organisms, and therefore soil function and agricultural sustainability.

The analysis of management effects on the soil food web can be accomplished by using bioindicator organisms. Nematodes, ubiquitous microscopic (generally 150µ – 10mm) roundworms, are particularly well-suited for this purpose. Nematodes live in a variety of environments, including soils, freshwater, and marine water (Ravichandra, 2008). Terrestrial nematodes occupy at least five trophic groups: bacterivores, fungivores, herbivores, predators, and omnivores (Neher, 2001). Nematode taxa can have varying life-history strategies within and between the trophic groups. Some nematodes, opportunists, have very short life cycles, respond very quickly to nutrient availability, and produce large numbers of progeny. Other nematodes have the opposite life history strategy, with long life cycles, low numbers of progeny, and a negative response to environmental perturbation. Still other taxa fall somewhere in between these two extremes (Neher, 2001). Nematodes are sensitive to management strategies, and consequently the structure of the nematode community will change in response to changes in field management (Ferris et al., 1996; Neher and Campbell, 1994; Neher, 1999; Vonk et al., 2013)

Nematode taxa prevalence and life history strategy can be used to calculate the status of a soil system, e.g. whether it is matured, disturbed, or enriched with nutrients, using established indices (Bongers, 1999; Ferris et al., 2001). These indices can also provide information about other organisms in the food web and the functioning of the soil, for example whether a fungal or bacterial channel of decomposition is dominating (Bongers, 1990, 1999; Bongers and Ferris, 1999a; Ferris et al., 2001; Ferris and Matute, 2003). High numbers of nematodes which respond quickly to food-rich conditions (enrichment opportunists) indicate high microbial activity. Higher values of opportunist fungivores, in proportion to bacterivores, indicates more fungal than bacterial decomposition, compared to sites with lower values (Ferris and Matute, 2003).

2.1 Nematode Indices

Nematode indices rely on the classification of nematodes along a "colonizer-persister" (cp) scale from 1 - 5, which loosely corresponds to the concept of r and k strategists in ecological succession. Taxa with a low cp value have a high colonization ability and are tolerant of disturbance. They are seen early in succession, have short life cycles, high fecundity and high metabolic activity. Cp-1 nematodes are enrichment opportunists which colonize food-rich conditions and their dominance in a community indicates enrichment. This class includes the bacterivorous family Rhabditidae (Figure 1).

Figure 1. A Rhabditidae nematode (left), cp class 1. A nematode in the family Aporcelaimidae (right), omnivores of cp class 5.

Cp-2 nematodes are general opportunists, and the dominance of this class (over both cp-1 and cp-3 to cp-5) indicate stress. Cephalobidae, bacterial feeders, is a family in this class (Ferris et al., 2001). Individuals of a higher cp value (cp-5) have longer life cycles and lower fecundity, are typically more sensitive to disturbance, and are less likely to be bacteria feeders. (Bongers, 1990; Bongers and Ferris, 1999b; Ferris et al., 2001). This class includes the family Aporcelaimidae, an omnivorous class that includes species that prey on worms (Godfrey, 1951).

There are 6 commonly used indices using the cp scale to evaluate nematode community structure: (i) maturity index, (ii) the plant parasitic index, (iii) the structure index, (iv) the channel index, (v) the enrichment index, and (vi) the basal index.

2.1.1 The Maturity Index (MI)

The MI is the weighted mean of the individual cp values. It is calculated as:

$$MI = \sum_{i=1}^{n} v_i f_i \qquad \text{Equation 1}$$

where v_i is the c-p value of taxon *i* and f_i is the frequency of that taxon in the sample (Bongers, 1990).

The MI is used to measure the disturbance or stability of a system (excluding herbivores) on a scale of 1 -5 and is considered one of the key indices for soil health (Bongers, 1999). Higher values indicate less disturbance. Pristine, undisturbed environments tend to have values around 4. Agricultural systems, which are subject to disturbance and nutrient-enriched, tend to have values less than 2 (Bongers and Ferris, 1999b). The MI value in agricultural systems drops following the incorporation of organic amendments, as this stimulates microbial activity and consequently opportunistic nematodes in class cp-1. As this flush of activity levels off, cp-2 nematodes begin to dominate the community structure, followed by a gradual increase in the MI as persisters increase in the system (Bongers and Ferris, 1999b).

2.1.2 The Plant Parasitic Index (PPI)

The PPI is calculated in the same way as the MI, but using only measures of herbivores:

$$PPI = \sum_{i=1}^{n} \hat{v}_i \hat{f}_i \qquad \text{Equation 2}$$

Where $\hat{v}_i$ is the c-p value of taxon *i* and $\hat{f}_i$ is the frequency of that taxon in the sample (Bongers, 1990).

Herbivores are omitted from the MI calculation, as their presence and abundance are generally dictated more by the host plant than the soil environment, and persister species can be found even under stress conditions. Consequently, the PPI, on a scale of 2 – 5, is indicative more of crop health than of the soil environment. Higher numbers indicate increased primary production, particularly from root growth, and may indicate crop vigor (Bongers, 1990; Ferris et al., 2001).

2.1.3 The Enrichment Index (EI)

The EI depicts whether the food web is enriched with nutrients or the availability of resources on a 0 – 100 scale. It is based on "expected responsiveness of opportunistic" guilds to food resource enrichment and indicates the amount and activity of primary detrital consumers (Ferris et al., 2001). It is calculated using the enrichment, *e,* and basal, *b,* components of the food web, and calculated as follows:

$$b = \sum_{b=1}^{n} k_i n_i \qquad \text{Equation 3}$$

$$e = \sum_{e=1}^{n} \hat{k}_i \hat{n}_i \qquad \text{Equation 4}$$

$$EI = 100\left(\frac{e}{e+b}\right) \qquad \text{Equation 5}$$

where k_i and $\hat{k}_i$ represent the weightings assigned to guilds that indicate basal and enrichment characteristics of the food web, respectively; n_i and $\hat{n}_i$ are the abundance of nematodes within those guilds. Weightings are assigned based on population increase rate in response to enrichment (Ferris et al., 2001).

Systems with regular inputs, such as conventional or organic agroecosystems, tend to have high EI values (Ferris et al., 2001). Higher EI values can indicate enhanced N

mineralization due to nematode grazing on microbial biomass, and are correlated with higher yields (Ferris et al., 1998, 2001). Values greater than 50 indicate a food web that has responded to a N-enriched environment (Margenot and Hodson, 2016).

2.1.4 The Structure Index (SI)

The SI is calculated similarly to the enrichment index. However, the indicator guilds are those indicating structure rather than enrichment (such as higher cp classes, e.g. 3-5, as well as omnivores and carnivores) and weightings are assigned based on the indication of food web complexity provided by the guilds present. Weightings indicate the relative importance of that indicator. For example, cp-2 taxa are found in all food webs, but taxa of cp-5 are usually only found in undisturbed environments (Ferris et al., 2001). The structure index is calculated using the formula:

$$SI = 100\left(\frac{s}{s+b}\right) \qquad \text{Equation 6}$$

where:

$$s = \sum_{s=1}^{n} \bar{k}_i \bar{n}_i \qquad \text{Equation 7}$$

where k_b and k_s represent the weightings assigned to guilds that indicate basal and structure characteristics of the food web, respectively; n_b and n_e are the abundance of nematodes within those guilds, and b is calculated using Equation 3 (Ferris et al., 2001).

The SI is also a 0 – 100 scale and it depicts the length of the micro-food web. High SI values can be found in natural grasslands or forests, and indicate greater food web linkages, diversity, stability, and structure. This indicates the possibility of increased regulatory functions, such as buffering of opportunistic guilds and herbivore regulation (Ferris et al., 2001).

The structure and enrichment indices can be plotted together for a visual assessment of where a soil community lies along the continuum of structure and enrichment (Figure 2).

Soil communities are most structured if their values fall in the right side of the square, most enriched in the top of the square, and vice versa. The quadrants can be used to interpret other factors about the soil community, like whether it is likely to be conducive or suppressive of disease, or has a high, moderate, or low C:N ratio.

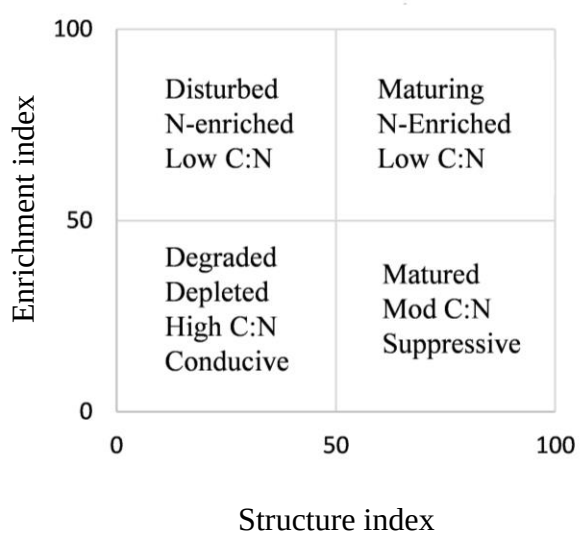

Figure 2. Soil food web analysis according to nematode structure and enrichment indices.

2.1.5 The Channel Index (CI)

The CI improves upon simple fungal- to bacterial-feeding nematode ratios by integrating nematode traits such as generation time, survival capabilities and response to C and N ratios in soil amendments. It uses the abundance of nematodes in the Ba_1 and Fu_2 guilds. Ba_1 nematodes are enrichment opportunists and indicate bacterial response to low C:N ratio inputs and eutrophic conditions. Fu_2 nematodes are fungal feeders with relatively short generation times, are tolerant of extreme conditions, and can succeed in both basal or stable environments. The Fu_2 guild contains the 3 most commonly found fungivorous

nematodes. The percentage of these nematodes (Ba_1 and Fu_2) are weighted by their relative fecundity and life course characterizes to indicate whether the fungal or bacterial channel of decomposition is dominating. Higher values indicate more fungal decomposition is occurring; lower values indicate more bacterial decomposition. The CI is on a 1 – 100 scale and is calculated as:

$$CI = 100 \times \frac{0.8Fu_2}{3.2Ba_1 + 0.8Fu_2} \quad \text{Equation 8}$$

(Ferris et al., 2001). The channel index is correlated with low soil pH, indicating that at low pH fungal decomposition dominates (Ferris et al., 2001). Higher CI has been experimentally demonstrated following incorporation of high C:N amendments compared to low C:N amendments (Ferris and Matute, 2003).

2.1.6 The Basal Index (BI)

The BI is calculated as:

$$BI = 100 \times \frac{b}{e+s+b} \quad \text{Equation 9}$$

where *e*, *s*, and *b* represent the weighted abundance of nematodes in the enrichment, structure, and basal food web components (Ferris et al., 2001). For example, bacterial- and fungal-feeding nematodes with a cp-2 value are weighted with 0.8 (Berkelmans et al., 2003). The basal index indicates the prevalence of opportunistic taxa which are tolerant of disturbance. Higher values indicate more nematodes in this class (Sánchez-Moreno et al., 2006).

2.1.7 Additional Indices

Some additional indices are in use, expanded from the above six. The ΣMI merges free-living and plant parasitic nematodes. The MI2-5 is the Maturity Index with cp-1 taxa excluded (Neher, 2001). This measurement is more indicative of heavy metal contamination, as cp-2 nematodes are more resistant to heavy metal pollution than class cp-1 (Sieriebriennikov et al., 2014).

2.2 Sustainable Soil Management Practices in the Wine Industry

Nematode analysis has become increasingly useful as the sustainability of agricultural industries has become suspect. Agricultural practices have caused the loss of natural ecosystems, added significant pollutants to the environment, and degraded soil and water quality (Tilman et al., 2002). In the wine industry, sustainability is also threatened by climate change (Mozell and Thach, 2014), as growers are faced with multi-faceted changes in the environment, such as increased temperature, reduced precipitation, increased evaporation, and increased atmospheric CO_2 levels, all of which are hypothesized to have negative impacts on wine production. Drought and accelerated salinization (driven by increased evaporation, reduced precipitation, and declining water availability) are considered the biggest threats in arid regions such as California (Keller, 2010). In the face of these challenges, growers are turning to practices that reduce environmental impacts and including appropriate soil management as a key component of maintaining sustainability (Keller, 2010). Vineyards have been shown to sequester significantly more carbon than other systems, even other perennial systems, and consequently have higher potential at mitigating climate change (Suddick et al., 2013).

Fertilization, weed management, and cover crops all have the potential to further exacerbate environmental issues or unfavorably affect the crop. Despite this, or in some cases, because of this, recommended sustainable practices include nutrient analysis to inform fertilizer application, organic amendments (including manure), limiting fertilizer volatilization by disking in (or other methods), reduced tillage, avoiding herbicides with high leaching potential, reducing passes made for weed control, maintaining a narrow berm, spot spraying instead of treating the entire berm, and the use of cover crops (Aguirre et al., 2012). While some of these practices have been well studied in other agricultural systems, there is not comprehensive research on the effects of the practices on the whole soil ecosystem for Mediterranean vineyards. Although other management practices are also employed that may be of environmental significance (such as insecticide or fungicide use), they are beyond the scope of this review.

Organic amendments are suggested to preserve organic matter. Less soil tillage is promoted to preserve structure and thus organic matter, and spot sprays and narrow berms are suggested to minimize herbicide use (Aguirre et al., 2012). Cover crops or resident vegetation are suggested to cool the canopy microclimate (Keller, 2010), minimize soil erosion, and maximize water and nutrient storage (Mozell and Thach, 2014). However, cover crops can compete with the cash crop for water and nutrients, and may require additional fertilization to prevent competition (Keller, 2010; Tesic et al., 2007). The use of cover crops, fertilization, and soil tillage on the complete soil ecological system in Californian vineyards is largely unknown. Defining which of these practices are the most beneficial to crop yields and soil ecology in vineyards could result in major environmental

benefits, as vineyards occupy a large geographic area and are a major part of the economic sector, both in California and globally.

2.3 Fertilizer Management Strategies and their Effects on Soil Food Webs and Crop Yields

In this review, two broad categories of fertilizers are examined. The first is inorganic, i.e. fertilizers from a non-plant or non-animal source, also called synthetic. Inorganic nitrogen fertilizers are manufactured from atmospheric N_2 (Mikkelsen, 2012). Potassium and phosphorus inorganic fertilizers are usually mined, which makes them non-renewable (Crop Life Staff, 2017). Agricultural systems which use mostly inorganic fertilizers are termed conventional. The second category of fertilizer is organic, i.e. fertilizers which are obtained originally from a plant or animal source; this category includes manure or compost. Many conventional growers, in acknowledgement of the benefits of organic fertilizers, have begun to also incorporate organic fertilizers into their systems. However, because organic fertilizers are applied in conjunction with inorganic fertilizers, the system is still termed conventional.

The addition of plant nutrients through fertilization has significant short- and long-term effects on soil organisms (Diacono and Montemurro, 2010; Lazcano et al., 2013; Gueisseler and Scow, 2014). Additions of readily available source of nutrients may favor early successional microbial species with high turnover rates. Increases in these prey species following fertilization may also result in an increase in predators (Birkhofer et al., 2008), therefore increasing the abundance of bacterivorous nematodes. However, fertilizer addition also constitutes a disturbance to the soil environment, causing those nematode taxa sensitive to disturbance, such as omnivores and predators, to decline, regardless of

fertilizer type, when compared to systems which receive no fertilization (Forge et al., 2005).

The addition of inorganic or organic fertilizers can affect soil organisms differentially. The addition of organic fertilizers in particular has been shown to benefit bacteria and results in higher microbial biomass compared to soils treated with inorganic fertilizers (Birkhofer et al., 2008). Conventional systems, that receive only inorganic fertilizers, have shown low amounts of omnivores as compared to soils that receive organic fertilizers (Birkhofer et al., 2008). These reductions in omnivores and predators can be reflected by reduced values in the structure index (SI) and maturity index (MI) (Neher, 1999; Li et al., 2010).

Conventional agricultural systems, that receive solely inorganic fertilizers, typically support low densities of fungal biomass, but some research has reported significantly more abundant fungivores in conventional systems compared to organic (Birkhofer et al., 2008; Li et al., 2010). Relative increases in fungivores following inorganic fertilizer application, compared to organic fertilizer, is reflected by increases in the channel index (CI). This suggests that fungivores may be feeding on alternate sources (such as root hairs), that the fungi are of particularly high quality, or it could be the indirect result of fertilizer-induced changes in soil pH (Birkhofer et al., 2008; Li et al., 2010). However, increases in soil carbon over long-term application of organic fertilizers could be beneficial for mycorrhizal fungi (Birkhofer et al., 2008).

Herbivores have not shown a consistent response to fertilization, and much of the evidence is contradictory (Birkhofer et al., 2008; Coll et al., 2011, 2012; Forge et al., 2005; Neher, 1999; Salomé et al., 2016). Research suggests that the herbivore response is case

specific and varies with the crop type, soil type, root response to fertilization, and type and quantity of amendment. For example, poultry manure has been correlated with reduced herbivores, and dairy manure has been correlated with increased herbivores. There also appears to be differences in the types of herbivores affected. Manure fertilizers have resulted in increased numbers of *Pratylenchus* (Forge et al., 2005) (Figure 3) but not *Helicotylenchus* (Birkhofer et al., 2008; Forge et al., 2005). Organic systems commonly have higher levels of herbivores than conventional, and these increases have been theorized to be the result of more feeding sites provided by an increased root system (Birkhofer et al., 2008). It does not appear to be due to different N concentrations, as differences in nematodes were seen in plots fertilized with organic and mineral fertilizer which received the same amount of N (Forge et al., 2005).

Herbivore community structure is reflected by the plant parasitic index (PPI). Higher PPI values, indicating greater primary production, have been recorded in organic plots compared to conventional (Neher, 1999).

Yield and crop quality may be the most crucial factors in a grower's choice of fertilizer type. Although neither organic nor mineral fertilizers consistently produce higher yields than the other, the type of organic amendment added may have a significant effect on the yield (Figure 4) (Birkhofer et al., 2008; Döring et al., 2015; Forge et al., 2005). Berry quality does not appear to be affected by fertilizer type (Döring et al., 2015). The results of several studies are obscured by complications which make direct comparisons more difficult, such as low stand densities, different inputs of nutrients with different fertilizer types, or higher pest or disease pressure under one fertilizer type (Figure 5) (Birkhofer et al., 2008; Forge et al., 2005; Tesic et al., 2007).

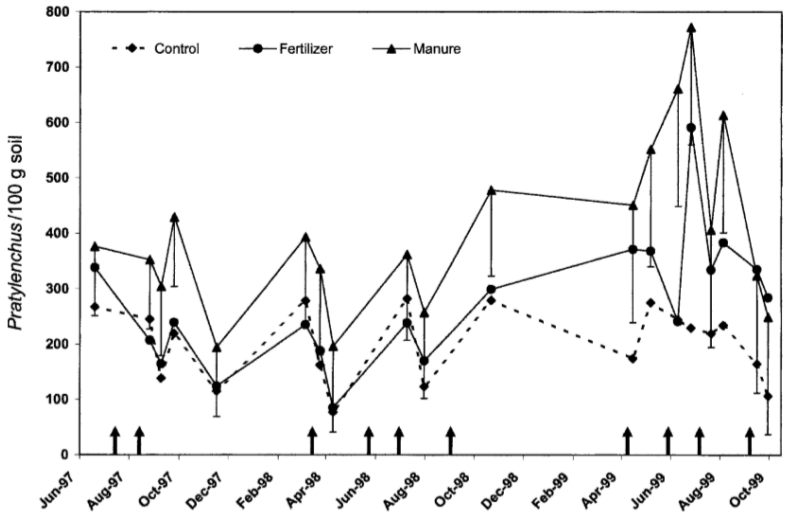

Figure 3. Change in *Pratylenchus penetrans* population over time, in plots treated with inorganic fertilizer (circle) or manure (triangle), or no fertilizer (diamond). Excerpted from Forge et al. 2005.

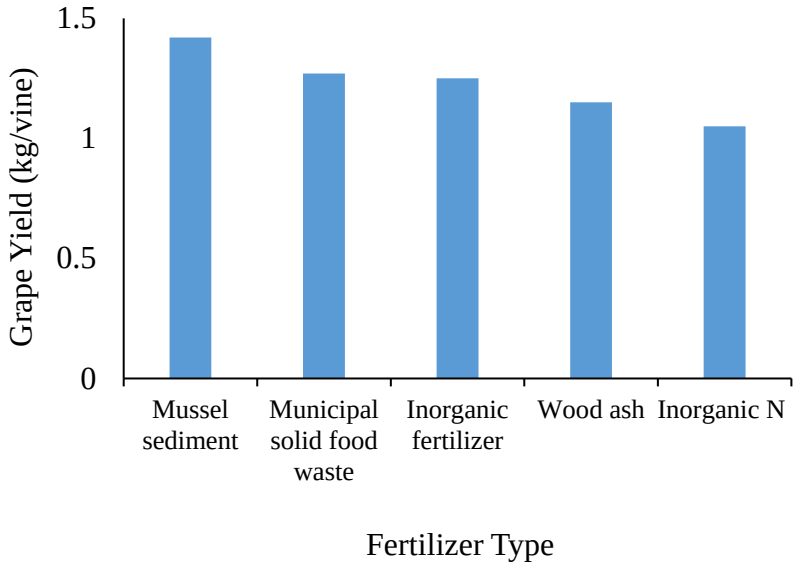

Figure 4. Grape yield in kg/vine for plots receiving inorganic fertilizer without N, full inorganic fertilizer, or organic fertilizer from different sources, from a study in Nova Scotia, Canada (adapted from Messiga et al., 2016).

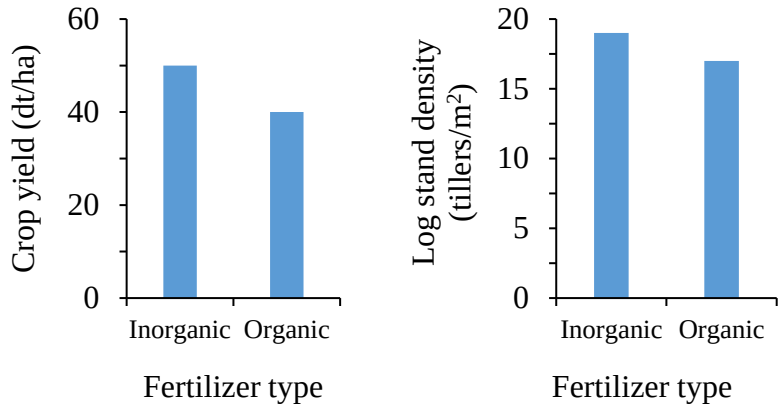

Figure 5. Wheat yield and stand density for the same plots receiving mineral or organic fertilizer (modified from Forge et al., 2005)

2.4 Weed Management Strategies and their Effects on Soil Chemical Properties, Nematode Food Webs and Crop Yields

Weed management is most commonly accomplished by one of two methods: herbicide application or tillage. Herbicides can be applied as a pre-emergent, in which case they are sprayed on bare ground before weeds appear, or as a post-emergent, in which case they are sprayed on young, growing weeds. Tillage, likewise, can occur before or after weeds appear. However, tillage before weeds appear is generally to prepare soils for new plantings. Once crops are established, soils are tilled after weeds appear to remove them. In vineyards, soil can be tilled under the vine, in the tractor row, or both. There are many different types of equipment that can be used for tillage, such as a moldboard plow, which turns over topsoil and brings subsoil to the top, a chisel plow, which rips and agitates soil but does not invert it, or deep ripping, which break up very deep layers of soil to combat compaction.

Tillage effects on soil and the soil food web vary over time, with the type of equipment used, and with soil type (Freckman and Ettema, 1993; Ito et al., 2015; Zhang et

al., 2017). Chiseling instead of moldboard plowing, for example, may decrease the loss of SOC after tillage (Ito et al., 2015). However, over the long-term, tillage has been shown to decrease soil organic matter (SOM). The accompanying increase in SOM decomposition also decreases soil organic carbon (SOC) (Ito et al., 2015). This potentially increases soil bulk density and could be detrimental to soil structure. It is also correlated with decreased nematode abundance and decreases in the fungal-dominated channel of decomposition, compared to the bacterial-mediated channel (Ito et al., 2015).

Tillage is also detrimental for organisms of higher trophic levels (i.e. predators and omnivores), which are generally more sensitive to disturbance, such as that which occurs with tillage (Ferris, 2010b; Ito et al., 2015). Additionally, tillage may release nutrients in the short-term by releasing soil organic matter from aggregates and incorporating surface residue, which encourages opportunistic taxa (Salomé et al., 2016).

When using nematode ecological indicators to analyze the effects of tillage on the soil food web, Ito et al. (2015) found that overall, tillage tended to lower indicators of environmental stability (Figure 6), and bacterivore, predator, and herbivore abundance. However, rotary cultivation appeared to be less detrimental to fungivores and facultative root feeders than moldboard plowing; moldboard plowing resulted in the lowest abundance at most times (Figure 7) (Ito et al., 2015). They also found that tillage increased the enrichment index, which represents the abundance and activity of primary detrital consumers. These results are in line with the short-term response of the food web seen above.

Herbicides are also associated with changes in the soil food web, but it is possible that such effects are small compared to those caused by other agricultural management

practices, and that soils may recover over time (Griffiths et al., 2008). Surface-applied herbicides may be less likely to affect soil organisms due to the location of application (Salminen et al., 1997). Overall, soils treated with herbicides tend to be dominated more by bacteria than fungi (Salomé et al., 2016). Additionally, although herbicides can affect ecosystem processes, the results are not always negative. Increased nitrogen mineralization has been shown to occur in soils treated with herbicide (Salminen et al., 1997). Some changes in the soil food web may not affect its functionality (Griffiths et al., 2008). For example, decreased respiration in soils treated with herbicide compared to other weed management or to controls was not correlated with any changes in plant growth (Griffiths et al., 2008). Effects of herbicide are also type-specific. Some herbicides are directly toxic to soil fauna, others can alter fauna behavior, potentially altering predation through changes in hunting behavior (Salminen et al., 1997).

Herbicide use, in comparison to mowing, has been shown to decrease nematode abundance, especially fungivores, although this can vary with soil type (Salomé et al., 2016). Fungi abundance has also been shown to decrease with herbicide use (Wilkinson and Lucas, 1969), so the decline of fungivores follows logically. However, herbicides appear to be less detrimental to nematode ecological indicators than tillage (Figure 8) (Salomé et al., 2016).

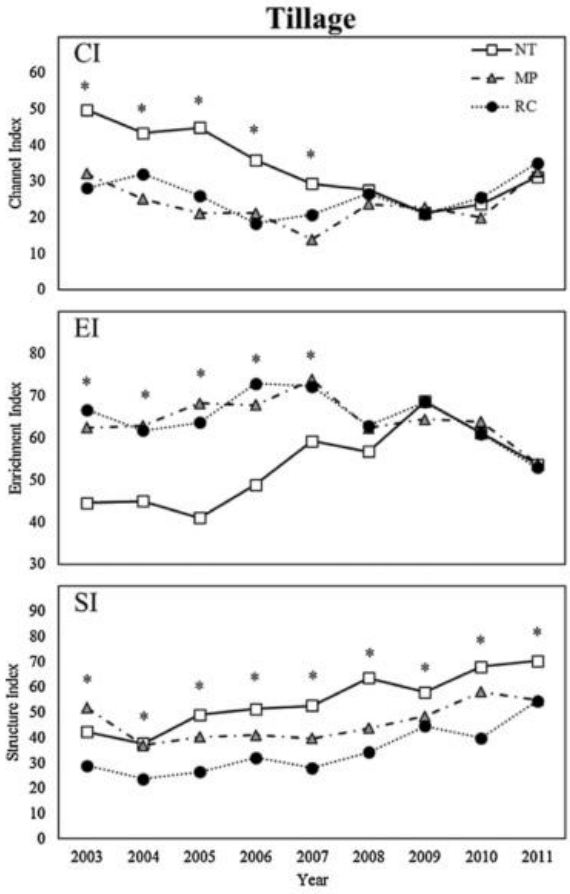

Figure 6. Channel Index (CI), Enrichment Index (EI) and Structure Index (SI) over time in agricultural plots under different tillage regimes: no-till (NT), moldboard plowed (MP), or plowed with a rotary cultivator (RC) in Ibaraki, Japan (adapted from Ito et al., 2015).

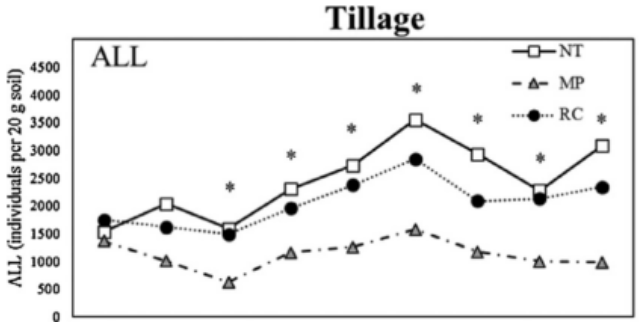

Figure 7. Number of individual nematodes per 20 g of soil in a long-term experiment in Ibaraki, Japan. NT= no till, MP= moldboard plow, and RC= rotary cultivator (adapted form Ito et al., 2015)

Yield and berry physiology do not appear to be affected by the choice of herbicide or cultivation for weed control as shown in previous studies (Pool et al., 1990; Smith et al., 2008). However, weed control only under the vine, rather than both under the vine and in the tractor row, can negatively affect crop yield (Tesic et al., 2007).

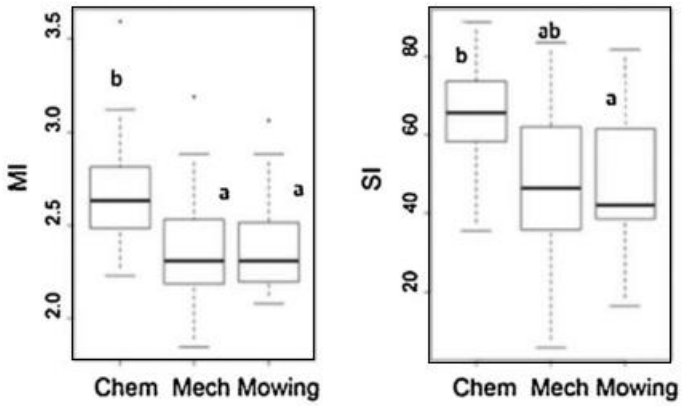

Figure 8. Effects of weed management strategies on maturity index (MI) and structure index (SI) in Southern France vineyards. Different letters indicate significant differences ($p<0.05$). The three treatments were herbicide (Chem), Mechanical weeding (Mech) and Mowing (Mowing) (adapted from Salomé et al., 2016).

2.5 Cover Crops Effects on Food Webs and Crop Yields

The supply of energy for soil microbial communities comes from root exudates, which stimulate a bottom-up adjustment to the food web. It follows that cover crops lead to an increase in microbial activity and microbial biomass carbon (MBC) (Nakamoto et al., 2012; Salomé et al., 2016). Permanent cover crops also increase the soil organic matter to microbial biomass C ratio, compared to fallow plots, which indicates resource availability to microorganisms (Salomé et al., 2016), and fungal biomass (Ito et al., 2015), potentially increasing microbivore nematodes, and indeed, nematodes are responsive to changes in

plant cover. Nematode densities increase somewhat as cover crops are maintained over time, as shown by a recent study by Ito et al. (2015). This study found that opportunistic bacterivores, facultative root feeders, and fungivores all increased under cover crops compared to fallow plots (i.e. native weeds) (Figure 9). The increase in opportunistic bacterivores may be responsible for an interesting decrease in nematode indicators of ecological stability under temporary cover crops, compared to a bare soil, observed by Salomé et al. (2016) (Table 1). The exudates of fast-growing cover crops may favor taxa with a low cp value, thereby lowering stability indices. However, Salomé et al. (2016) also observed that cover crops increased the numbers of predators in most years compared to fallow plots, and predators tend to have higher cp values (Ferris et al., 2001).

The increase in opportunistic bacteria under cover crops, and consequently bacterivorous nematodes, would also explain the observation in the study by Ito et al. (2015) that cover cropped plots had a lower channel index compared to fallow, indicating the decomposition pathway in these plots is dominated more by bacteria than fungi. The channel index also differed by cover crop type. Cover crops with a higher C:N tend to promote more fungi and fungal decomposition, and in turn more fungivores (Ito et al.,2015) (Figure 9). However, effects of cover crops on ecological indices seems to vary greatly depending on the year samples were taken.

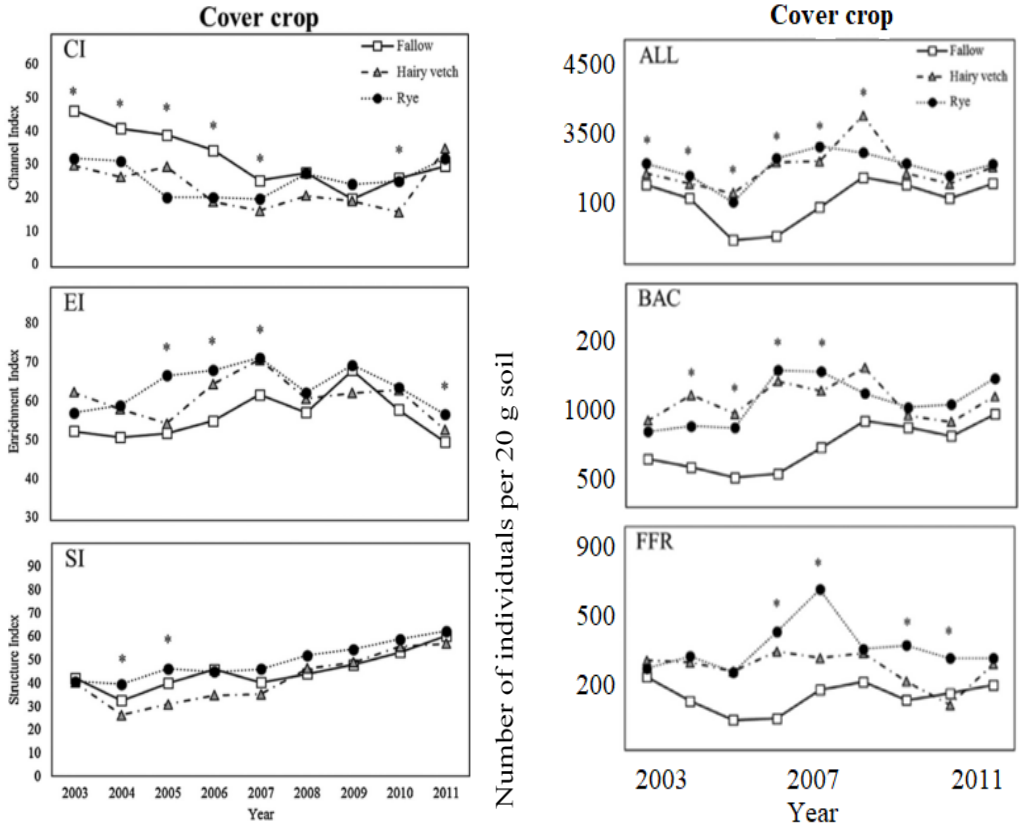

Figure 2. Results from an long-term experiment in Ibaraki, Japan looking at nematode response to cover crops. The square represents fallow plots, the triangle, hair vetch, and the circle is rye. BAC is bacterial feeders, FFR is facultative fungal feeders and ALL is all trophic levels (adapted from Ito et al., 2015). Number of individual nematodes per 20 g of soil over time (right) and Channel Index (CI), Enrichment Index (EI) and Structure Index (SI) over time (left) (adapted from Ito et al., 2015).

Table 1. Values for maturity index (MI) and structure index (SI) for a cover crop experiment in Southern France. Letters a and b within a column indicate significant differences between the three durations of plant cover.

Treatment	**MI**		**SI**	
No plant cover	2.7	b	72.3	b
Temporary plant cover	2.2	a	46.7	a
Permanent plant cover	2.3	ab	60.3	ab

Cover crops may delay important grapevine physiological stages, reduce vigor, and negatively affect canopy structure, although this may be dependent on climate and soil type. Vines may suffer from reduced water and nutrient uptake, especially phosphate and boron (McGourty et al., 2008; Smith et al., 2008). Over time, the use of cover crops may also reduce yield (Tesic et al., 2007). Because vineyards are often drip irrigated, roots distribution tends to be concentrated under the drip line, and therefore may not benefit from any beneficial effects of cover crops on soils in the tractor rows between vines (Smith et al., 2008). However, the negative effects of cover crops on grapevine canopies may end up having a favorable effect on berry and wine quality, as reduced energy invested in vegetative tissues may result in increased energy invested in the berry. It may also reduce titratable acidity and increase soluble sugars, phenols, and anthocyanins, ultimately producing a higher quality wine (Xi et al., 2011).

The choice of which cover crop to plant is also an important consideration. Some crops are suggested to maintain grapevine vigor, others to decrease or increase vigor. Grasses, for example, may decrease vigor, whereas legumes with a small percentage of grasses are suggested to increase it. Vetches are suggested to maintain vigor (Aguirre et al., 2012).

2.2 Conclusion

Soil organisms are directly responsible for soil processes, such as nutrient cycling, and therefore are valuable indicators of soil health that could be used to evaluate the sustainability of agricultural production. Nematodes can be used as bioindicators to evaluate the state of the soil community.

Although much research has been done on the effects of fertilization strategies, weed management, and cover crops on soil nematodes and nematode food webs, there are currently no thorough assessments of the effects of these practices on the whole soil ecosystem in Mediterranean vineyard systems. Furthermore, many of the studies suffer from conflicting results, confounding factors, such as crop density or pest pressure, or data that was not correlated with crop yield. Research is needed to fill these knowledge gaps, especially for vineyards in California, where there is the potential for large environmental and economic impacts.

3. MATERIALS AND METHODS

3.1 Site Description

This study was carried out in a commercial Pinot Noir vineyard owned by Paragon Vineyard Company, Inc in San Luis Obispo, California (Figure 10). Mean annual precipitation in this area is 38 – 63.5 cm; mean air temperature is 15°C (Soil Survey Staff, 2017). The soil is classified as Los Osos-Diablo complex, with 9-15% slopes. These soils are typically well-drained with clay texture overlaying weathered bedrock at 99 cm. They are non-saline to very slightly saline and non-calcareous. The parent material is residuum weathered from mudstone, sandstone, and/or shale (Soil Survey Staff, 2017).

Figure 3. Approximate site location in San Luis Obispo County, CA.

3.2 Experimental Design

Three main soil management practices currently in use by the wine industry in California, (*i*) cover crops, (*ii*) fertilizer usage, and (*iii*) weed management, were evaluated in this study in three adjacent trials within a 3.5 acre vineyard section (Figure 11).

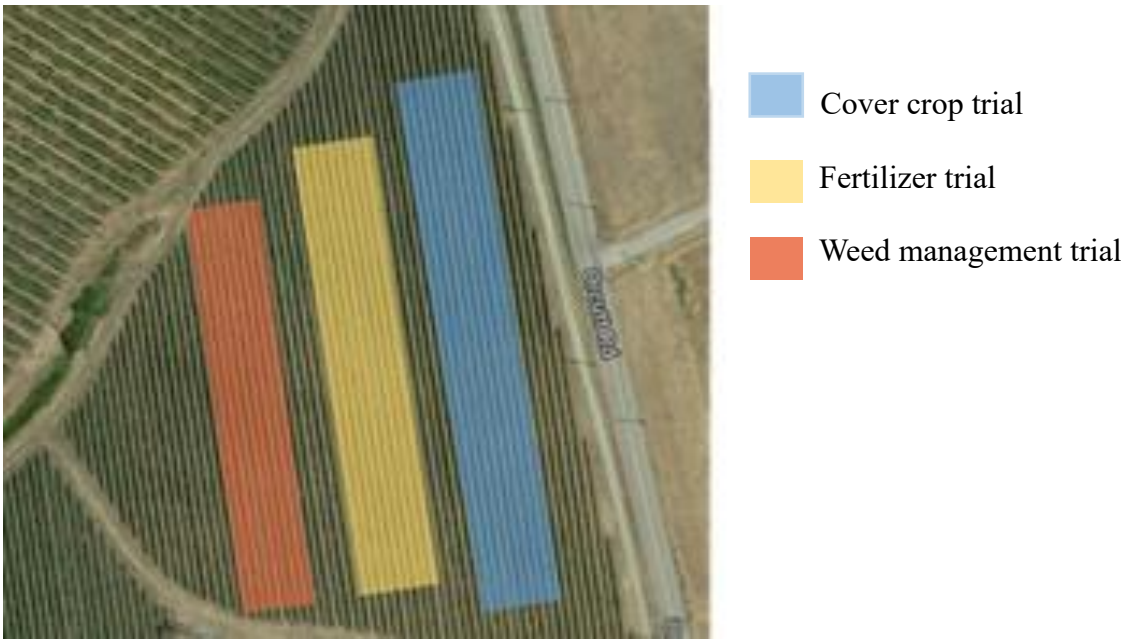

Figure 11. Experiment set up showing all three trials: cover cropping, fertilizer, and weed management.Within the cover cropping trial, three treatments were compared: high or low water-use cover crops, or no cover crop (i.e. resident vegetation).

The fertilizer trial compared organic to inorganic fertilization treatments, and the weed management trial compared herbicide application and tillage for weed control. A total of 8 soil management treatments were implemented, with 6 replicates per treatment. Treatments were applied in spring 2016 to plots that were 4 rows wide, with a length evenly divided amongst the length of the row. Of the 6 replicates (plots) per treatment, 2 plots were randomly assigned within each of the same 4 rows for a randomized complete block design within each of the three trials. All trials received the same foliar-applied fungicides

and insecticides (Appendix A) and were subject to other standard industry practices for commercial production.

3.3 Fertilizer Trial

Three fertilization treatments were compared in this trial, inorganic fertilization, organic fertilization, or no fertilizer application (control). Replicate layout is shown in Figure 12.

Inorganic	None	None	Organic	Inorganic	Organic
Inorganic	Organic	None	None	Inorganic	Organic
None	Organic	Inorganic	Organic	None	Inorganic

Figure 12. Layout of fertilizer treatment replicates for the fertilizer trial in a Pinot Noir vineyard in California.

The inorganic fertilization plots received 400 lb/acre of a 15-15-15 fertilizer derived from Monoammonium Phosphate, Urea, Ammonium Sulfate and Muriate of Potash (Agropell, JR Simplot, Boise, ID, USA). Fertilizer was side-dressed along the vine row on June 17, 2017, before veraison samples were taken. The total nutrients applied were 60.4, 60.41 and 60.32 lbs/acre of N, P, and K respectively. Of this, 60, 60 and 60 lbs of N, P, and K per acre were applied to the soil; the rest were applied as a foliar treatment.

Organic plots received 1000 lb/ac of an organic fertilizer derived from dehydrated poultry manure, feather meal, rock phosphate and potassium sulfate (Organic Farms 4-4-2P, Organic Farms Fertilizers, Livingston, CA, USA). The organic fertilizer was side-dressed along the vine row on June 17, 2017, before veraison. Total nutrient inputs were 40, 40, and 20.09 lbs/acre of N, P, and K respectively. Of this, soil-applied fertilizer was

40, 40, 20 lbs/acre of N, P, and K, respectively; the remainder was applied as a foliar treatment.

Both the inorganic and organic plots received foliar fertilizers consisting of 2 applications in the spring of a 2-2-0 + 2% Micros custom blend from Valley Farm Supply (Santa Maria, CA, USA) at 1 gal/ac, and 3 foliar applications of Organic Triggrr (0-0-1; derived from kelp and plant extracts, includes 0.45% Humic Acid derived from Kelp) (Westbridge Agricultural Products, Vista, CA, USA) at 8 oz/ac. Three foliar applications of Acadian 0.1-0-5.0 were applied in the summer (Acadian Seaplants Ltd., Nova Scotia, Canada) at 1 qt/acre.

The no fertilizer control received no foliar or soil applied fertilizer.

3.4 Weed Management Trial

Two treatments were compared in this trial: the use of herbicide and the use of tillage. Replicate layout is shown in Figure 13.

Herbicide	Tillage	Tillage	Herbicide
Herbicide	Herbicide	Tillage	Herbicide
Herbicide	Tillage	Tillage	Herbicide

Figure 13. Replicate layout for herbicide trial treatments.

The herbicide treatment received one application of Rely 280 Herbicide in the spring on May 6, 2017 (Bayer CropScience, Leverkusen, Germany) at 3.5 pts/acre (active ingredient: glufonsinate-ammonium) in a 81 cm wide band underneath the vine with PHT Crop Oil Concentrate CA (JR Simplot, Boise, ID, USA; petroleum oil based). Glufosinate

is a broad-spectrum contact herbicide, first derived from cultures of soil bacteria *Streptomyces viridochromogenesa*. This herbicide works by inhibiting the enzyme glutamine synthetase (BASF, 2018). The tilled plots were tilled under the vine once per month from April to July, with a radius cultivator (Clemens Vineyard Equipment, Inc., Woodland, CA, USA).

3.5 Cover Crop trial

Three treatments were compared in this trial, a high-water use cover crop mixture, a low-water use cover crop mixture, compared to non-seeded plots (control). Replicate layout is shown in Figure 14.

High	Low	Low	None	High	None
None	None	High	Low	High	Low
Low	High	None	Low	None	High

Figure 14. Replicate layout of cover crop treatments in a Pinot Noir vineyard in California. "High" is a high-water use cover crop, "Low" is a low-water use cover crop, and "None" is the control, which was not seeded.

The high-water use cover crop mix was Oso Plowdown Plus (Helena Chemical, Collierville, TN, USA), a 60% legume, 20% grass mix. This mixture contains 30% maple pea (*Pisum sativum* L.), 10% daikon radish (*Raphanus sativus* var. *niger),* 10% mustard (*Brassica juncea*), 30% bell beans (*Vicia faba),* and 20% barley (*Hordeum vulgare*). It was seeded at 100 lbs/acre in a 6’ wide band. The total calculated seed required was 45 lbs; the actual seed used was 50lbs.

The low-water use mix was Double Hitter Plus (Helena Chemical), a mixture that is approximately 70% grasses and 25% legumes. It contains 30% meadow brome (*Bromus erectus)*, 40% creping red fescue (*Festuca ruba)*, 10% rose clover (*Trifolium hirtum*) and 15% crimson clover (*Trifolium incarnatum*). It was seeded at 35 lbs/acre in a 6' wide band. The total calculated required amount of seed was 16 lbs. However, the actual total amount of seed used was 25 lbs.

The no cover control was not seeded, and contained resident native and non-native vegetation, largely *Trifolium dichotomum, Lolium multiflorum,* and *Oxalis californica*. Some species present could have been remnants or volunteers from a previous year's seeded cover crop.

Figure 4. Low water use cover crop (left) and no cover crop (right). The apparent pattern present in the control plots could be volunteers from previous years' seeded cover crops.

Figure 5. High water use cover crop (left) and low water use cover crop (right).

3.6 Soil Sampling

Soil samples (20 cm depth) were collected during the 2017 season at bloom (May 11, 2017), veraison (July 25, 2017) and harvest (September 13, 2017) for the cover crop trial, and at veraison and harvest for the fertilizer and weed management trial. Using a shovel, three samples were collected per plot under the vine, and three were collected from the tractor row. At each plot, the three samples for each location (vine and tractor row) were separately homogenized for a composite sample. Samples were stored in plastic bags and immediately transported to the lab where they were stored at 4º C.

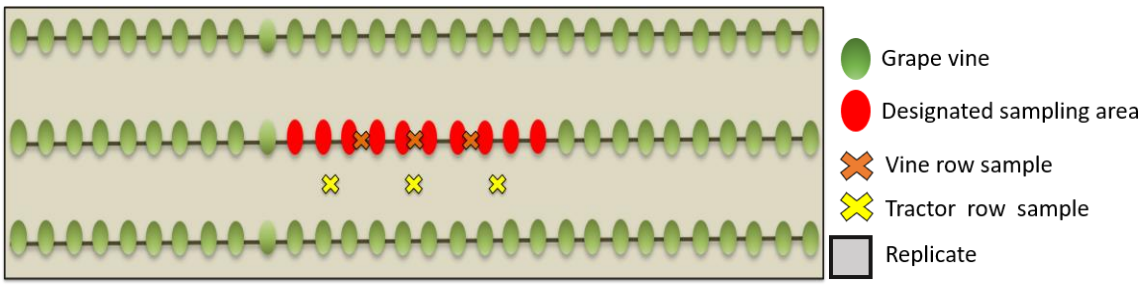

Figure 17. Soil sampling set up for each plot. The orange samples were homogenized for one replicate, and the yellow samples were homogenized for one replicate, resulting in two samples total per replicate (one from the vine row and one from the tractor row).

3.6.1 Analysis of Soil Chemical Parameters

3.6.1.1 Soil pH and Electrical Conductivity

To measure pH and electrical conductivity (EC), 20 grams of field moist soil was combined in a 1:1 ratio with deionized (DI) water then left to settle for one hour. The pH was measured by immersing a pH electrode (Accumet Combination Glass Electrode, Fisher Scientific, Waltham, MA) into the solution until the suspension covered the bottom of the electrode. When the pH meter was stable on the 100ths place for 10 seconds, the pH value was recorded. EC was measured with a Field Scout EC meter (Spectrum Technologies, Inc., Aurora, IL, USA*)* on the same suspension that was used for pH. The tip of the meter was inserted below the surface of the suspension and used to gently stir until the soil was completely suspended. EC was recorded to the nearest 0.1 dS m^{-1} after the readings stabilized.

3.1.6.2 Nitrate Nitrogen (NO_3^--N)

Nitrate was extracted from soils using an aluminum sulfate solution and quantified using an Accumet nitrate ion specific electrode (Fisher Scientific, Waltham, MA, USA). Briefly, 10 grams of air-dried, ground and sieved soil were extracted with 25 ml of

aluminum sulfate extracting solution by shaking on a reciprocating mechanical shaker for 10 minutes. The mixture was then filtered through a P4 paper filter (Fisher Scientific, Hampton, NH, USA) and the concentration recorded in mV by inserting the nitrate electrode in the resulting clear extract. A calibration curve using known standards was created for converting mV readings into concentration. Total NO_3^--N mg kg^{-1} was calculated as

$$(NO_3\ in\ filtrate - method\ blank) * 2.5. \quad \text{Equation 10}$$

where NO_3^- is in mg L^{-1}.

3.1.6.3 Total Soil Carbon and Nitrogen

Total Carbon and Nitrogen were measured in air-dried, ground and sieved (2mm) soil samples by combustion on a Vario Max CNS analyzer (Elementar, Langenselbold, Hesse, Germany*).*

3.1.6.4 Permanganate Oxidizable Carbon (POXC)

Permanganate oxidizable carbon or POXC, was measured as a proxy of active soil carbon (Culman et al., 2012). Briefly, 2 grams of air-dried soil were combined with 18 ml of DI water and 2 ml of 0.2M $KMnO_4$. Each sample was shaken to ensure soil dispersion within the solution and then placed on a mechanical shaker at 240 oscillations per minute for 2 minutes. Samples were then allowed to settle for 10 minutes and subsequently 0.5 ml of the supernatant was transferred to 49.5 ml of DI water. Absorbance of the final solution was analyzed on a spectrophotometer (Milton Roy, Houston, TX) at 550 nm. Total POXC in the soil samples was calculated as:

Equation 11

$$POXC = [0.02\ mol\ L^{-1} - (a + b\ \times Abs)] * \left(9000\ \frac{mg\ C}{mol}\right) * (\frac{0.02\ L\ solution}{wt})$$

where a = intercept of the standard curve, b = slope of the standard curve, Abs= absorbance reading, and wt= weight of air-dried sample in kg. POXC is in ($mg\ kg^{-1}$).

3.1.6.5 Water-Soluble Organic Carbon (WSOC) and Nitrogen (WSN)

Total dissolved organic carbon and total soluble nitrogen were measured on a TOC-V CPH/CPN Total Organic Analyzer (Shimadzu, Kyoto, Kyoto Prefecture, Japan). Fifty ml of DI water was added to 5 grams of field moist soil, placed on a reciprocating shaker for 30 mins, then centrifuged at 3500 rpm for 30 minutes. The supernatant was filtered through a 0.25 µm syringe filter (Environmental Express, Charleston, SC, USA) and acidified to pH 2 with concentrated H_2SO_4 before being run through the analyzer. The analyzer produced final concentrations as mg/L.

3.1.6.7 Quality Control

Replicates and duplicates were performed for 10% of samples for each of the chemical analyses. Acceptable values for relative difference at the method level were ≤ 20%. Acceptable values for relative difference at the instrument level were ≤ 10%. If results exceeded acceptable values the analysis was performed again.

3.6.2 Nematode Analysis

3.6.2.1 Nematode Extraction

Nematodes were extracted from 200 cc of field moist soil following the sucrose centrifugation procedure modified from Byrd et al., 1966. DI water was added to soil for a total volume of 400 ml and mixed, then allowed to sit for 30 minutes. An additional 300 ml of DI water was added, and the soil was transferred back and forth between 1 L cups 10 times. The water was poured through a No. 40 sieve (420 µm) and retained, leaving soil at

the bottom of the 1 L cup. This process was repeated 2 more times. The retained water was brought up to a total volume of 3.5 L, stirred, and allowed to settle for 1 minute. It was then poured over a No. 400 (37 µm) sieve. Material maintained on the sieve was washed into a falcon tube, vortexed, and centrifuged at 1700 for 5 minutes. After 15 minutes, the supernatant was siphoned off and discarded. The soil was then brought to 35 ml with a sucrose solution and shaken until all the sediment was in solution, vortexed, and centrifuged. The centrifuge was brought up to 1000 rpms and then slowed to a stop. The suspension was sieved through a No. 500 sieve (25 µm) and rinsed thoroughly with DI water to remove any remaining sucrose. Material maintained on the sieve was collected using 50 ml of DI water for nematode identification. After settling for at least 30 minutes, all but 10 ml was siphoned and discarded.

3.6.2.2 Nematode Quantification and Identification

Total nematodes in 1 ml were counted using a dissecting scope then multiplied by the total extraction volume to get total nematodes in the soil sample. Identification was done under a light microscope to family by morphology (Goodey, 1951; Bongers, 1988). Different nematode families have distinct features that allow for visual differentiation; the stylet, tail, esophagus region, and head in particular vary greatly between some taxa. Stylets may be present or absent, strong or delicate, long or short, and with or without basal bulbs. For example, Xiphinema, known colloquially as dagger nematode, is an obligate migratory ectoparasite which has an extraordinarily long, strong stylet for puncturing plant roots (Ravichandra, 2008). Helicotylenchus, or spiral nematode, is another plant parasite with a strong stylet, but is clearly different from Xiphinema based on its head and lip shape (among other characteristics) (Figure 18). Nematode tails can be bulbous, flat, conical,

asymmetrical, filiform, and so on. (Figure 19). The esophageal region is composed of several parts (Figure 20), which can vary in size, shape, and distinctness Figure 21).

Nematode community structure was analyzed using NINJA (Nematode INdicator Joint Analysis) (Sieriebriennikov et al., 2014), which automatically calculates Equations 1-9 for the following indices: Maturity, ΣMaturity, Maturity 2-5, Plant Parasitic, Structure, Channel, Enrichment, and Basal. It also calculates trophic groups, metabolic rates, and total biomass.

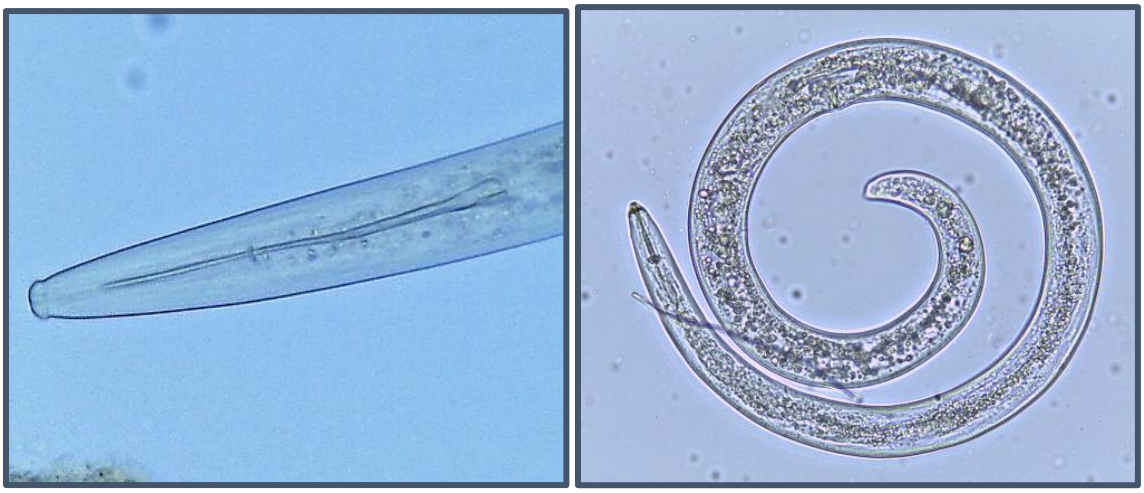

Figure 18. A Xiphinema nematode (left), colloquially called a dagger nematode, showing a key identifying characteristic: the long, strong stylet with a knobbed base. A Helicotylenchus nematode (right), colloquially called a spiral nematode, showing the characteristic spiral shape, strong stylet with knobbed base, and distinct lip region.

Figure 19. Examples of varying nematode tail shapes: bulbous (left) and tapered (right).

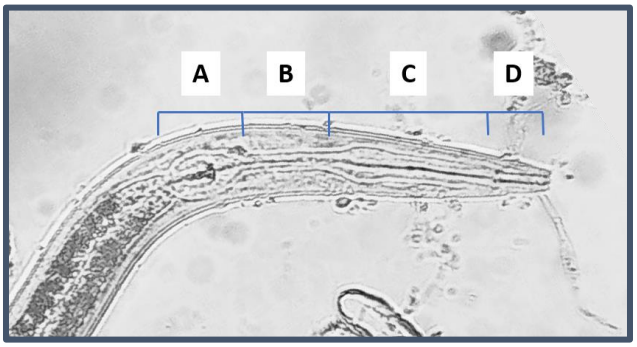

Figure 20. Parts of a nematode esophagus: postcorpus with posterior bulb (A), isthmus (B) and corpus (C). (D) is the head.

Figure 21. Varying esophageal structure and separation between esophagus and intestinal region: overlapping with a distinct elongated lobe (left), non-overlapping (middle), and indistinct overlapping regions (right) with rectangular median bulb present (arrow).

3.1.8 Crop Yield and Quality

Harvested fruit was analyzed for brix, pH, titratable acidity, and individual berry weight according to standard laboratory practices. Total weight in tons of each trial was also recorded.

3.7 Statistical Analysis

All three trials were analyzed separately in JMP Pro 13 (SAS, Cary, NC). Statistical significance was determined using a standard least squares restricted maximum likelihood method (REML). Post-hoc Tukey's HSD or Student's tests were then run on significant differences. Correlations were run using multivariate Spearman's ρ.

For the fertilization trial, significance of family abundance was calculated as:

Equation 12

$$y = sample\ location + sample\ date + treatment + date * treatment + location * treatment + row + replicate + \varepsilon$$

where row was a random variable, replicate was a random variable nested within row, and ε was model error. The significance of nematode ecological indices for the fertilizer and weed management trials were also calculated using Equation 8.

Significance of family abundance for the weed management trial was calculated as:

Equation 13

$$y = sample\ location + sample\ date + treatment + replicate + row + \varepsilon$$

where row was a random variable and replicate was a random variable nested within row, and ε was model error.

Cover crop models were slightly different, as samples were only taken in the tractor row, so location was eliminated from the model. Significance of family abundance and nematode ecological indices was calculated as:

Equation 14

$$y = sample\ date + treatment + date * treatment + replicate + row + \varepsilon$$

where row was a random variable and replicate was a random variable nested within row, and ε was model error.

4. RESULTS AND DISCUSSION

4.1 Fertilization Experiment

4.1.1 Effects of Fertilization Strategies on Soil Nematode Community Structure

Twenty nematode families were identified from soil samples across all plots and treatments in the fertilizer trial. Of these, 7 families were bacterivores, 4 were fungivores, 2 were omnivores, 7 were plant parasites, and 1 was a predator (Table 2).

Table 2. Number of nematode families identified in each cp class from soils in a California vineyard. One family is listed twice, due to the presence of two subfamilies of different cp classes.

CP class	Number of families	CP class	Number of families
Ba-1	2	Pp-2	2
Ba-2	3	Pp-3	4
Ba-3	1	Pp-5	1
Ba-4	1	Om-4	1
Fu-2	3	Om-5	1
Fu-3	1	Pr-3	1

Ba: bacterivore
Fu: fungivore
Pp: plant parasite
Om: omnivore
Pr: predator.

Aphelenchoididae (fungivore) was the most abundant family overall, followed by Cephalobidae and then Rhabditidae (bacterivores) (Table 3). Only location or sample date had a significant effect ($p \leq 0.05$) on average nematode abundance for any family when all locations were considered in the standard least squares model (Table 4).

Table 3. Average (n=6) and absolute abundance of nematode families per 200 cm^3 soil collected in a California vineyard at two times: veraison and harvest, under three fertilization strategies (inorganic, organic and no fertilizer).

		Veraison						Harvest						
		Tractor row			Vine row			Tractor row			Vine row			
Family	**Trophic group-cp**	None	Organic	Inorganic	None	Organic	Inorganic	None	Organic	Inorganic	None	Organic	Inorganic	**Total Abundance**
Rhabditidae	Ba-1	179.9	38.5	109.3	10.2	121.8	0.0	433.1	275.1	298.8	3.4	30.8	67.6	9411.3
Cephalobidae	Ba-2	485.5	301.5	358.9	181.4	164.6	105.1	563.9	479.8	773.1	113.9	125.1	121.5	22646.0
Plectidae	Ba-2	17.1	0.0	7.8	3.3	0.0	0.0	0.0	32.5	15.0	9.8	20.9	33.1	837.4
Monhysteridae	Ba-3	11.5	11.1	15.9	8.2	36.5	25.5	36.1	14.0	18.6	19.4	14.3	14.6	1354.0
Alaimidae	Ba-4	18.7	45.6	12.2	3.3	3.6	0.0	3.0	35.0	77.7	0.0	0.0	0.0	1195.1
Aphelenchoididae	Fu-2	719.8	1246.5	539.1	163.5	210.4	46.6	950.6	961.2	665.9	143.8	435.0	301.7	38305.4
Neotylenchidae	Fu-2	6.9	0.0	0.0	26.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	198.9
Diphtherophoridae	Fu-3	0.0	0.0	0.0	3.3	0.0	11.2	0.0	0.0	0.0	23.2	16.9	0.9	332.9
Tylenchidae	Pp-2	239.1	232.9	494.2	82.9	68.1	66.3	523.8	284.5	647.5	39.3	290.6	544.7	9165.0
Tylenchulidae	Pp-2	0.0	8.0	5.4	305.0	247.0	534.1	0.0	0.0	16.0	260.8	66.3	84.8	21083.5
Belonolaimidae	Pp-3	74.9	41.1	10.6	14.9	5.8	0.0	43.7	51.7	55.3	97	0.0	14.3	1932.5
Heteroderidae	Pp-3	0.0	11.1	0.0	0.0	0.0	40.3	0.0	16.5	7.1	0.0	0.0	0.0	449.8
Hopolaimidae	Pp-3	2.2	0.0	0.0	85.5	19.8	0.0	0.0	0.0	0.0	331.7	49.3	158.4	3881.4
Pratylenchidae	Pp-3	97.0	269.2	47.5	14.6	0.0	28.87	189.6	138.1	163.6	3.2	0.0	6.8	5750.2
Longidoridae	Pp-5	0.0	0.0	0.0	27.2	31.9	37.1	14.1	0.0	0.0	88.7	77.6	48.1	1947.4
Qudsianematidae	Om-4	0.0	0.0	0.0	2.3	2.2	0.0	5.0	52.5	8.8	0.0	2.4	0.9	444.2
Aporcelaimidae	Om-5	11.5	0.0	0.0	0.0	0.0	0.0	8.0	34.1	41.2	10.2	9.0	5.8	719.0
Tripylidae	Pr-3	25.6	92.9	15.7	0.0	0.0	0.0	14.1	63.0	29.7	13.0	0.0	6.8	1564.1

Ba: bacterivore
Fu: fungivore
Om: omnivore
Pp: plant parasite
Pr: predator.

Table 4. Model significance ($p \leq 0.05$) for abundance of nematode families in a California vineyard under three fertilization treatments (organic, inorganic, or none), sampled at two times (veraison or harvest), from two locations, either the tractor or vine row.

Family	Treatment	Location	Time	Treatment*Location	Treatment*date
Rhabditidae		*			
Cephalobidae		*			
Plectidae					
Monhysteridae					
Alaimidae		*			
Aphelenchoididae		*			
Neotylenchidae					
Diphtherophoridae		*			
Tylenchidae					
Tylenchulidae		*			
Belonolaimidae		*			
Heteroderidae					
Hopolaimidae		*			
Pratylenchidae		*			
Longidoridae		*			
Qudsianematidae			*		
Aporcelaimidae			*		
Tripylidae		*			

Nematode ecological indices were generally in line with expected values for disturbed agricultural soils (Table 4), averaging 2.0, 2.1, and 2.2 for MI, MI 2-5, and SMI respectively. They showed, on average, low structure (mean SI=16.46) and intermediate enrichment (mean EI=50.1).

Table 4. Nematode index means (n=6) for soil samples collected in a California vineyard under different fertilization treatments (either organic, inorganic, or no fertilizer) at two times, veraison or harvest, from either the vine or tractor row.

	Veraison						Harvest					
	Tractor			Vine			Tractor			Vine		
Index	**None**	**Organic**	**Inorganic**	**None**	**Organic**	**Inorganic**	**None**	**Organic**	**Inorganic**	**None**	**Organic**	**Inorganic**
Maturity	1.94	2.06	1.99	1.98	1.94	2.12	1.77	2.03	2.02	2.19	2.02	1.98
Maturity 2-5	2.07	2.08	2.04	2.04	2.08	2.12	2.04	2.19	2.17	2.26	2.09	2.10
Σ Maturity	2.01	2.19	2.06	2.33	2.10	2.28	1.86	2.09	2.09	2.80	2.31	2.43
Plant parasitic	2.47	2.57	2.32	2.83	2.73	2.32	2.32	2.42	2.36	3.08	2.99	2.70
Channel	56.80	89.54	83.46	77.08	64.51	100.0	36.51	52.38	56.85	78.12	77.05	68.63
Basal	41.78	49.40	56.13	56.15	45.38	52.38	32.96	36.12	39.53	39.17	44.60	40.82
Enrichment	55.03	46.07	41.58	40.92	50.32	36.61	65.79	57.04	53.15	49.25	51.60	56.31
Structure	12.82	13.80	7.89	7.20	12.25	20.49	7.28	29.05	24.25	33.50	14.32	15.99

Most ecological indices were significantly affected by time, location, or both (Table 5). Significant effects of the fertilization treatments were observed for some indices, depending on the location considered. Maturity (MI) and Sigma Maturity (ΣMI) indices were significant for the treatment by location interaction. The MI was highest under the vine when no fertilizer was applied, and lowest in the tractor row under the no fertilizer treatment ($p < 0.03$; $F = 4.2$) (Figure 22). The ΣMI was highest in the vine row under no fertilizer, and lowest in the tractor row under the same treatment ($p = 0.04$; $F = 3.7$) (Figure 23). The ΣMI, Plant Parasitic Index (PPI), and Channel Index (CI) were all significantly different by location ($F = 15.1, 7.1, 5.9$, respectively) and had higher average values in the vine row as compared to the tractor row (Figure 24). The MI 2-5, CI, Basal (BI), and Enrichment Indices (EI) were significantly different by date (Figure 25). MI2-5 and EI were higher at harvest than veraison. The CI and BI were lower at harvest than at veraison.

Table 5. Model significance for nematode indices in a Californian vineyard at harvest and veraison at two locations, under the vine or in the tractor row. * or ** indicates $p < 0.05$ or $p < 0.001$ respectively. Empty cells were not significant.

	Treatment	**Location**	**Date**	**Treatment*Location**
Maturity				*
Maturity 2-5			*	
Σ Maturity		**		*
Plant Parasitic		*		
Channel		*	*	
Basal			**	
Enrichment			*	
Structure				

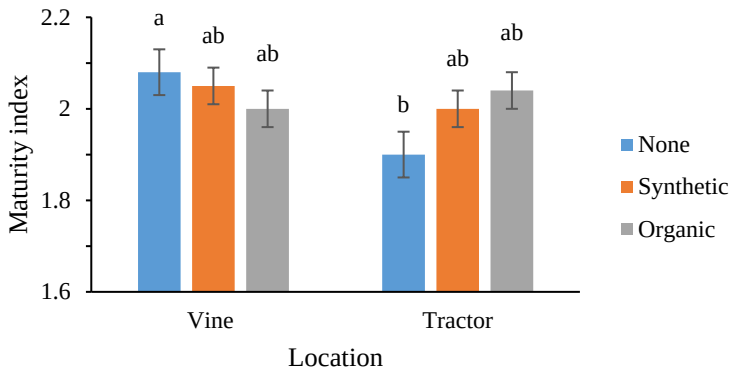

Figure 22. Maturity index (LS Mean ± standard error) for soil samples collected from a California vineyard under three fertilizer treatments (none, inorganic, or organic), under the vine or in the tractor row. Columns with different letters indicate significant differences according to Tukey's HSD (α = 0.05)

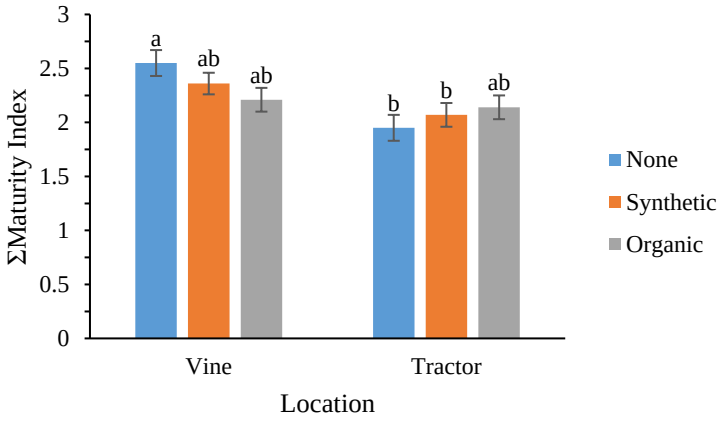

Figure 23. Sigma maturity index (LS Mean ± standard error) for soil samples collected from a California vineyard under three fertilizer treatments (none, inorganic, or organic), from under the vine or in the tractor row. Bars with different letters indicate significant differences according to Tukey's HSD (α = 0.05).

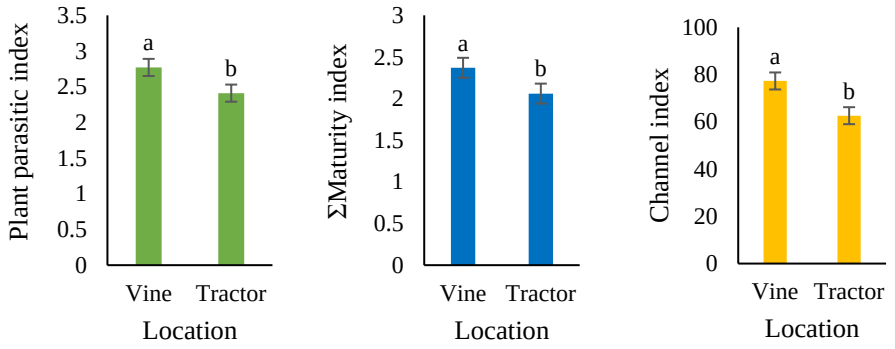

Figure 24. Nematode ecological index (LS Means ± standard error, n=35) for soil samples from a California vineyard, from either the vine row or the tractor row. Different letters above bars indicate Student's t test significant differences (α=0.05).

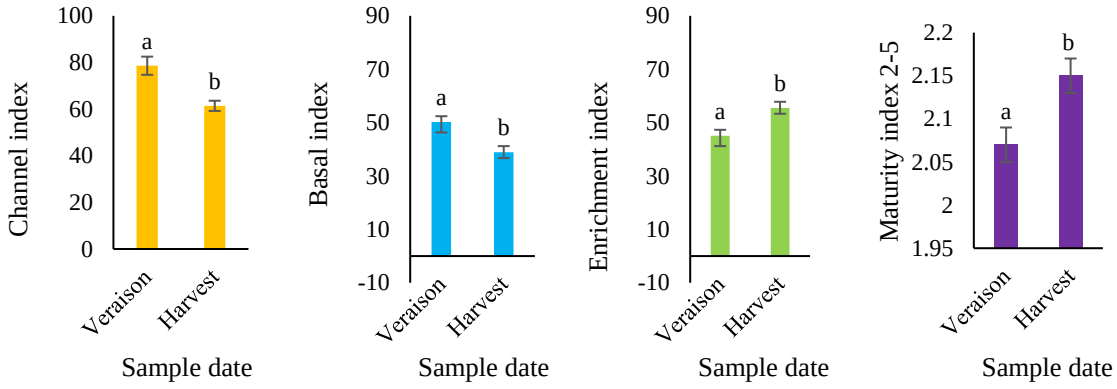

Figure 25. Channel index (CI), Basal index (BI), Enrichment index (EI), and Maturity index 2-5 (MI 2-5) LS Mean for soil samples from a California vineyard collected at two times, veraison or harvest. Error bars indicate standard error. Bars with different letters indicate significant differences according to Tukey's HSD (α=0.05)

Food web analysis using enrichment and structure indices showed that at veraison, all samples clustered near the low-structure, intermediate enrichment quadrants, regardless of the treatment or location, indicating a disturbed soil food web (Figure 26). At harvest, samples tended towards higher enrichment values than at veraison.

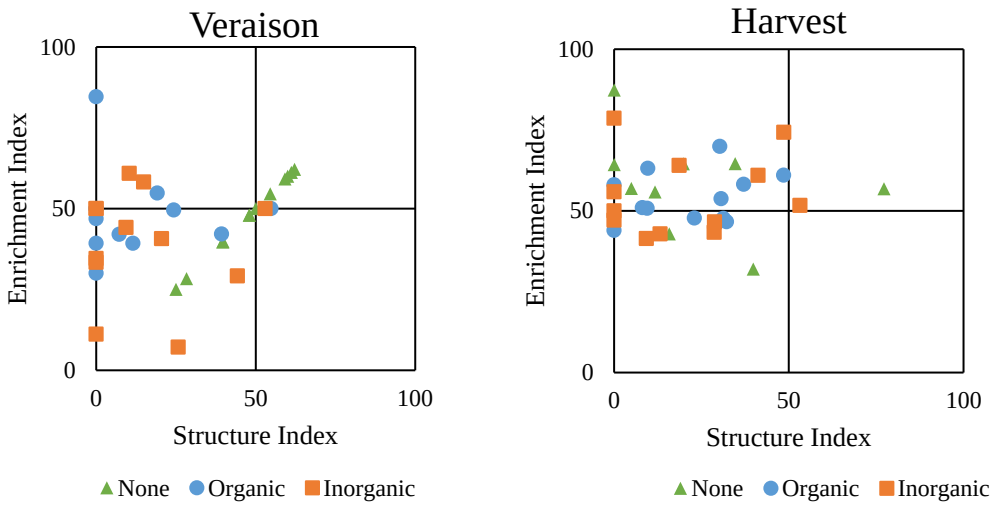

Figure 26. Enrichment and structure indices for nematode communities in soils from a California vineyard under 3 different fertilizer treatments (none, organic, or inorganic) collected either at veraison or at harvest.

4.1.2 Effects of Fertilization Strategies on Soil Chemical Parameters

Average values for soil chemical parameters measured in this study are given in Table 6. Overall the fertilization treatments did not significantly affect any of the measured soil chemical parameters regardless of the sampling date or location (Table 7). However, sampling date and location seemed to have a significant effect on most of the soil chemical parameters analyzed (Table 7).

Table 6. Average (n=6) measurements ± SE for soil samples collected from a California vineyard under 3 different fertilization strategies. Samples were collected twice: once at veraison and once at harvest, either under the vine or in the tractor row. WSC is water-soluble carbon and WSN is water-soluble nitrogen.

	Veraison						Harvest					
	Tractor			Vine			Tractor			Vine		
	Organic	**Inorganic**	**None**	**Organic**	**Inorganic**	**None**	**Organic**	**Inorganic**	**None**	**Organic**	**Inorganic**	**None**
pH	6.26 ±0.4	6.39 ±0.3	6.35 ±0.1	7.8 ±0.1	7.71 ±0.1	7.71 ±0.2	6.82 ±0.15	6.72 ±0.13	6.86 ±0.16	7.9 ±0.27	8.17 ±0.08	8.09 ±0.1
EC (dS/m)	2.37 ±0.4	2.22 ±0.4	2.20 ±0.5	1.98 ±0.2	2.06 ±0.2	1.97 ±0.2	2.28 ±0.43	2.10 ±0.22	2.03 ±0.29	2.50 ±0.23	2.02 ±0.41	2.26 ±0.25
NO_3^- (mg/kg)	24.9 ±12.2	31.7 ±14.6	39.6 ±15.1	15.8 ±3.0	2.2 ±0.8	8.3 ±2.8	46.8 ±4.1	53.2 ±7.6	48.4 ±10.7	9.8 ±2.8	7.6 ±3.4	7.2 ±1.6
POXC (mg/kg)	473.9 ±78.0	464.3 ±47.3	484.3 ±72.7	443.5 ±69.3	396.4 ±65.2	439.7 ±48.1	554.4 ±92.17	511.6 ±51.52	573.1 ±151.0	621.3 ±88.56	644.1 ±106.4	643.9 ±89.54
C (%)	1.32 ±0.1	1.50 ±0.2	1.47 ±0.18	1.28 ±0.2	1.31 ±0.2	1.29 ±0.06	1.37 ±0.09	1.32 ±0.15	1.29 ±0.12	1.43 ±0.22	1.46 ±0.26	1.46 ±0.13
N (%)	0.14 ±0.0	0.14 ±0.0	0.12 ±0.02	0.11 ±0.0	0.11 ±0.0	0.11 ±0.01	0.11 ±0.01	0.11 ±0.02	0.10 ±0.01	0.12 ±0.03	0.12 ±0.03	0.11 ±0.02
WSC (g/kg)	218.9 ±21.3	196.6 ±6.0	272.4 ±25.3	170.6 ±6.8	202.3 ±16	197.5 ±10.5	166.2 ±6.8	205 ±8.4	174.8 ±13.7	172 ±23.8	190.3 ±18.3	188.9 ±28.5
WSN (g/kg)	123.8 ±25.9	133 ±30	157.4 ±27.2	77.5 ±4.8	93.6 ±10.6	95.6 ±5.9	81.9 ±4.4	110.3 ±9.4	89.5 ±10.9	71.2 ±16.7	81.4 ±12.6	79.8 ±17.8

Table 7. Model significance ($p < 0.05$) indicated with an asterisk for measured chemical parameters in plots under different fertilization treatments in a California vineyard. Empty cells were not significant.

	Treatment	Location	Date	Treatment*Location	Treatment*date
pH		*	*		
EC (ds/m)					
NO_3^- (mg/kg)		*			
POXC (mg/kg)			*		
Total C (%)					
Total N (%)					
Total WSC (g/kg)			*		
Total WSN (g/kg)		*	*		

Significant differences were observed for water soluble nitrogen (WSN), nitrate (NO_3^-) and pH, between the different locations within each plot. Nitrate and WSN were both lower in the vine row than in the tractor row (Nitrate: $F=52.6$, $p<0.0001$; WSN: $F=11.08$, $p=0.0025$). However, pH was higher in the vine row than in the tractor row ($F=731.5$; $p<0.0001$) (Figure 27). Permanganate oxidizable carbon (POXC) was lower at veraison than at harvest (sampling date: $F=45.8$, $p<0.0001$), but water-soluble organic carbon (WSOC) and WSN were higher (WSC $F=45.8$, $p<0.001$; WSN $F=8.9$, $p=0.0053$) (Figure 27). No significant differences were observed for other variables.

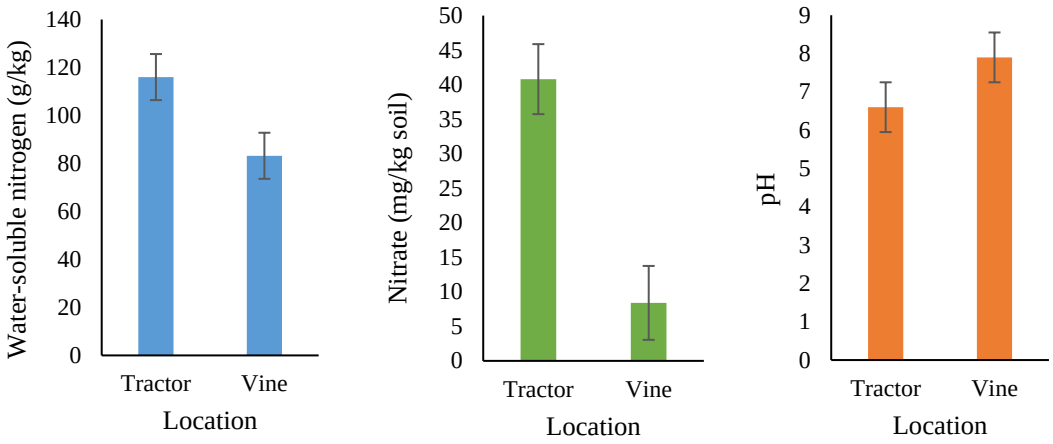

Figure 27. Chemical parameters (LS mean ± standard error, n=36) for soil samples collected from a California vineyard in either the tractor row or under the vine.

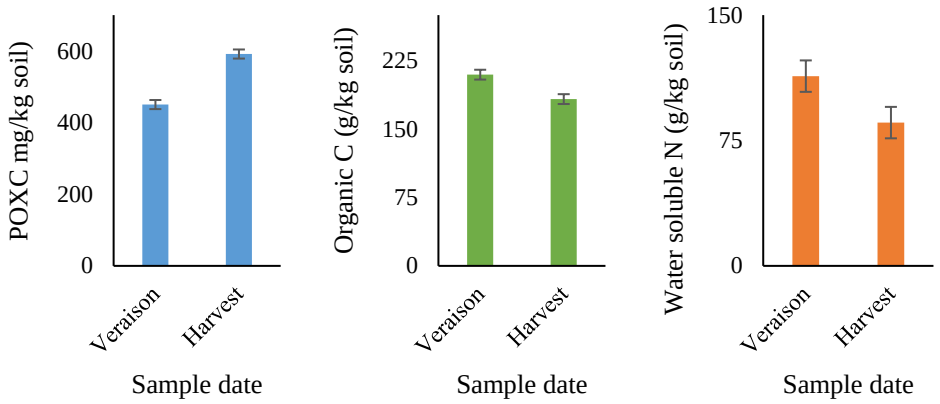

Figure 28. Chemical parameters (LS Mean ± standard error, n=36) for soil samples from a California vineyard, collected at two times, either at veraison or harvest.

Some chemical parameters were significantly correlated with nematode ecological indices (Table 8). The ΣMI and Plant parasitic (PPI) indices were positively correlated with soil pH. Maturity (MI) and channel (CI) indices were positively correlated with EC.

The ΣMI, CI, and Basal (BI) indices were all negatively correlated with NO_3-. The CI and BI were negatively correlated with POXC, and the EI was positively correlated.

4.1.3 Effects of Fertilization Strategies on Berry Quality and Yield

The fertilization treatment applied had no effect on the quality of the berries based on brix, pH, TA, or berry weight (n=3). There were significant differences in total yield (n=3). Plots with no fertilizer produced a significantly higher tonnage than organic fertilizer. Inorganic fertilizer was intermediate (Table 9).

Table 8. Correlations between soil chemical parameters and nematode ecological indices, indicated by Spearman's ρ values, for soil samples collected from a California vineyard.

Index	pH	EC (ds/m)	WSN (g/kg)	Total N (%)	NO_3- (mg/kg)	WSC (g/kg)	Total C (%)	POXC (mg/kg)
Maturity	0.075	0.240 *	-0.044	0.123	-0.076	-0.181	-0.012	-0.023
Σ Maturity	0.394 **	0.177	-0.029	0.044	-0.283 *	-0.154	-0.063	0.037
Maturity 2-5	0.016	0.062	-0.015	0.007	0.212	-0.158	0.068	0.220
Plant parasitic	0.291 *	0.113	0.039	0.088	-0.062	-0.014	0.072	0.069
Channel	0.068	0.238 *	0.005	0.221	-0.390 **	-0.053	-0.025	-0.237 *
Basal	-0.002	0.09	-0.034	0.202	-0.283 **	-0.014	-0.088	-0.367 **
Enrichment	-0.032	-0.139	0.026	-0.211	0.235	0.085	0.092	0.342 **
Structure	0.039	0.057	-0.030	0.008	0.188	-0.164	0.071	0.219

*Significant at the 0.05 level
**Significant at the 0.005 level

Table 9. LS Means (n=3) ±SE. Significance ($p<0.05$) indicated by *. Different letters within a row indicate significant differences according to Tukey's HSD.

	F	p value	None	Organic	Inorganic
Brix	0.2	0.9	25.9 ± 0.25	25.9 ± 0.25	26.1 ± 0.25
pH	1.1	0.4	3.4 ± 0.03	2.5 ± 0.03	3.5 ± 0.03
TA (g/l)	0.1	0.9	5.4 ± 0.15	5.3 ± 0.15	5.4 ± 0.15
Berry weight (g/berry)	1.0	0.4	1.0 ± 0.03	0.9 ± 0.03	1.0 ± 0.03
Yield (tons/rep)	5.3	0.05	0.15 ± 0.01 a	0.13 ± 0.01 b	0.14 ± 0.01 ab

4.1.4 Fertilizer Discussion

The structure of the soil food web in soil samples collected in the fertilizer trial reflected a moderate level of disturbance as compared to other agricultural systems (Bongers and Ferris, 1999b). Both fertilization treatments (inorganic and organic) were expected to increase measurements of disturbance, through the increase in soil nutrient contents and food web analysis using enrichment and structure indices showed that samples clustered near the low-structure, intermediate enrichment quadrants, regardless of the treatment or location, indicating a disturbed soil food web responding to nutrient inputs. However, no clear effect of the fertilization treatments on nematode abundance and food web structure were observed in this study.

No differences in the plant parasitic index were seen based on treatment. This is in agreement with Coll et al., 2011, Salomé et al., 2016, and Ferris et al., 1996, who saw similar results. This is likely because plant parasites are more dependent on the status of the host plant than on the surrounding environment, and persister species can be found even under stressed conditions (Bongers, 1990). The lack of significant differences in this index under different treatments may also be due to the perennial nature of the crop; parasitic species could already have been established before the experiment establishment and remained relatively unchanged throughout the treatment. This also could indicate little change in the crop's root system in response to fertilization.

Partial effects of the fertilization treatments depending on the location were observed for the MI and ΣMI, which were highest under the vine when no fertilizer was applied, and lowest in the tractor row under the same treatment. All other treatment/location combinations were intermediate between these lowest and highest values. This could be

indicating that the fertilizer treatment is acting as a disturbance to the soil food web, as expected, but that it is tempered somewhat by a more stable environment underneath a perennial crop (the vine). The strongest differences observed were between the tractor row and the vine row in the 'no fertilizer' treatment; this is probably a result of the different soil management applied at the two locations over the long term. The lack of clear effects of the fertilization treatments on the nematode abundance and food web structure could be attributed to the fact that the treatment time may have been too short to see differences. Similarly, a previous study by Salomé et al. (2016) found that differences in the Maturity or Structure index between conventionally and organically managed vineyards were weak and dependent on site specific and soil-dependent properties.

Nematode abundance and food web structure within the fertilizer trial changed with time. At harvest, samples tended towards higher enrichment index (EI) values than at veraison, potentially indicating greater N content and labile C sources (Sánchez-Moreno et al., 2008; Zhang et al., 2017). In fact, a significant correlation was observed between EI and the soil active carbon, measured as POXC. Opportunistic taxa, such as bacteria, utilize labile carbon as a food source. As these taxa multiply, so do their predators, thereby raising the enrichment index (Ferris and Matute, 2003; Margenot and Hodson, 2016). Margenot and Hodson (2014) also observed a correlation between POXC and the bacterial channel of decomposition. Nitrogen, as NO_3-, was not significantly correlated with the EI, but it was significantly negatively correlated with the ΣMI, CI, and BI. Each index decreased with increasing NO_3-; these changes could be attributed to changes in the biology of SOM decomposition and extracellular enzymes produced by soil organisms (Sinsabaugh et al., 2005; Grandy and Neff, 2008). For example, N addition has been shown to increase the

decomposition of labile carbon and inhibit the expression of enzymes required to breakdown lignin (Sinsabaugh et al., 2005). Both of these factors could contribute to a decrease in the maturity of the soil food web and the fungal channel of decomposition, reflected by decreases in the ΣMI and CI.

The Channel index (CI) and pH were not significantly correlated, but both were significantly different by location, and the CI was highest where pH was highest. Moderately higher CI values were seen under the vine (where pH was the highest) than in the tractor row, indicating that more fungal decomposition is occurring under the vine than in the tractor row. Channel index is not a quantitative measurement, so it cannot be used to objectively determine how fungal decomposition is occurring; it can only be used to compare the measured plots and locations (Ferris et al., 2001).

Opposite to previous studies (Malusà et al., 2004), the fertilizer treatment had a significant short term impact on vine yield. Yield under organic fertilizer was significantly lower than the control (no fertilizer), but yields between the inorganic and organic treatments were indistinguishable. This is difficult to interpret because there were no significant differences in soil chemical parameters between treatments. However, considering that the control plots received no soil-applied fertilizers for two growing seasons (the year before this study, and the year of this study) with no decrease in yield during the second year warrants further study. Other studies which have observed significant decreases in yield of organically fertilized vineyards attributed the differences primarily soil water-holding capacity, erosion, and potassium deficiencies, which were not measured in this study (Pool and Robinson, 1995). In spite of these differences in yield,

the treatments did not affect berry quality or chemistry significantly, in accordance with Döring et. al. (2015).

Results from this trial were likely obscured by several factors. The difference between the tractor row and the vine were very distinct but unrelated to the treatment and may have masked the variability explained by treatment. Additionally, strong effects of sampling date indicate that there are seasonality effects which are not related to management. Although nematodes are more temporally stable than some other soil microorganisms (Neher, 2001), further studies of soil food webs should include the effects of seasonality. Organic carbon, for example, has been shown to be highest in the summer when root exudates and microbial metabolites increase (Marschner and Kalbitz, 2003) Changes in chemical parameters due to different locations and time may drive stronger changes in nematode populations than short-term applications of fertilizers.

4.2 Weed Management Trial

4.2.1 Effects of Weed Management Strategies on Soil Nematode Community Structure

Seventeen families were identified from soil samples across all plots and treatments in the weed management trial. Of these, 6 were bacterivores, 2 were fungivores, 6 were plant parasites, 2 were omnivores, and 2 were predators (Table 10).

Aphelenchoididae (fungivore) was the most abundant family overall, followed by Rhabditidae and then Cephalobidae (bacterivores). The average number of individual nematodes, by location and treatment, are shown in Table 11.

Table 10. Number of nematode families identified in each cp class from soils in a California vineyard. One family is represented twice due to the presence of two subfamilies in different cp classes.

CP class	Number of families	CP class	Number of families
Ba-1	2	Pp-3	5
Ba-2	3	Om-4	1
Ba-4	1	Om-5	1
Fu-2	2	Pr-3	1
Pp-2	1	Pr-4	1

Ba: bacterivore
Fu: fungivore
Pp: plant parasite
Om: omnivore
Pr: predator

Nematode ecological indices were generally in line with expected values for disturbed agricultural soils (Table 13), averaging 1.98, 2.09, and 2.15 for the Maturity index (MI), MI2-5, and ΣMI, respectively (n = 48). They showed, on average, very low structure (mean structure index = 12.51, n = 48) and intermediate enrichment (mean enrichment index = 50.58, n = 48).

Significant effects of weed management treatment were observed only for the plant parasite index treatment*time and treatment*location interactions. Most ecological indices were significantly affected by location (Table 14). The tractor row samples had a significantly lower mean Maturity Index (MI), ΣMI, Plant Parasitic Index (PI), Channel Index, and Basal Index, and a higher mean Enrichment Index than the vine row samples (Figure 29).

Table 11. Average (n=6) and absolute abundance of nematode families collected in 200cm^3 of soil collected from a California vineyard either in the vine row or the tractor row, at two different times (veraison or harvest), in plots which were either treated with an herbicide or tilled for weed control. Trophic-cp indicates the trophic group and the colonizer-persister class.

		Veraison				Harvest				
		Tractor		Vine		Tractor		Vine		Total
Family	Trophic-cp	Herbicide	Tilled	Herbicide	Tilled	Herbicide	Tilled	Herbicide	Tilled	Abundance
Rhabditidae	Ba-1	364.5	216.0	29.1	43.3	348.9	302.1	0.0	6.4	7861.8
Cephalobidae	Ba-2	353.6	126.6	77.6	198.9	554.0	546.4	67.9	98.1	12139.6
Plectidae	Ba-2	0.0	0.0	0.0	0.0	7.9	0.0	11.6	21.8	248.5
Monhysteridae	Ba-3	26.7	1.8	0.0	0.0	21.5	12.7	40.8	2.9	638.1
Alaimidae	Ba-4	0.0	0.0	0.0	0.0	7.9	24.1	0.0	2.9	209.3
Aphelenchoididae	Fu-2	955.6	647.1	129.7	210.6	1643.9	1186.6	69.9	102.5	29675.1
Tylenchidae	Pp-2	333.6	398.0	48.5	5.9	629.7	292.2	31.6	101.8	11046.5
Tylenchulidae	Pp-2	23.8	92.3	42.0	58.0	0.0	2.4	174.2	61.1	2723.0
Belonolaimidae	Pp-3	31.4	0.0	0.0	145.0	0.0	23.5	3.5	2.9	1237.4
Heteroderidae	Pp-3	0.0	17.3	13.8	0.0	8.3	0.0	0.0	2.9	254.1
Hopolaimidae	Pp-3	0.0	0.0	0.0	0.0	0.0	0.0	17.9	425.3	2659.4
Pratylenchidae	Pp-3	67.7	42.8	0.0	58.0	57.4	50.6	0.0	43.1	1917.0
Tripylidae	Pr-3	0.0	0.0	0.0	0.0	4.0	21.6	0.0	0.0	153.4
Longidoridae	Pp-5	0.0	0.0	0.0	47.7	6.6	0.0	47.5	31.7	800.6
Qudsianematidae	Om-4	0.0	9.2	0.0	0.0	6.8	0.0	14.4	0.0	182.3
Aporcelaimidae	Om-5	19.7	5.6	4.4	5.9	34.6	3.6	4.5	0.0	469.9
Mononchidae	Pr-4	0.00	0.00	0.00	0.00	0.00	0.0	4.49	0.00	26.9

Ba: bacterivore
Fu: fungivore
Pp: plant parasite
Om: omnivore
Pr: predator

Table 12. Model significance ($p \leq 0.05$) for abundance of nematode families from soil samples collected in a California vineyard on two dates (at veraison or harvest) and from two locations (under the vine or in the tractor row). Empty cells were not significant.

Family	Treatment	Location	Date
Rhabditidae		*	
Cephalobidae		*	
Plectidae			
Monhysteridae			
Alaimidae		*	*
Aphelenchoididae		*	
Tylenchidae		*	
Tylenchulidae			
Belonolaimidae			
Heteroderidae			
Hopolaimidae			
Pratylenchidae			
Tripylidae			
Longidoridae		*	
Qudsianematidae			
Aporcelaimidae			
Mononchidae			

Table 13. Average nematode index values for soils in a California vineyard under two different weed management strategies (herbicide or tillage), in two locations (vine row or tractor row), measured either at Veraison or at Harvest.

	Veraison				Harvest			
	-- Tractor row --		-- Vine Row --		-- Tractor row --		-- Vine row --	
	Herbicide	Tilled	Herbicide	Tilled	Herbicide	Tilled	Herbicide	Tilled
Maturity	1.9	1.9	1.9	2.0	1.9	1.9	2.3	2.0
Maturity 2-5	2.1	2.0	2.0	2.1	2.1	2.1	2.3	2.0
Σ Maturity	2.0	1.9	2.0	2.4	2.0	2.0	2.5	2.5
Plant Parasitic	2.5	2.3	2.1	4.2	2.3	2.3	3.1	2.8
Channel	50.6	56.6	71.7	71.0	52.9	52.4	100.0	93.3
Basal	37.4	38.4	47.4	57.3	36.9	39.4	44.7	58.7
Enrichment	60.7	61.0	50.9	39.6	60.2	58.4	35.4	38.5
Structure	12.8	5.7	6.0	8.2	17.1	10.7	33.9	5.6

Table 14. Model significance for nematode indices from a California Pinot Noir vineyard under two weed management strategies, herbicide or tillage, depending on sampling date or sample location (under the vine or from the tractor row). Empty cells were not significant.

	Nematode index model significance				
	Treatment	**Date**	**Location**	**Treatment * Date**	**Treatment * Location**
Maturity			*		
Maturity 2-5					
Σ Maturity			*		
Plant Parasitic			*	*	*
Channel			*		
Basal			*		
Enrichment			*		
Structure					

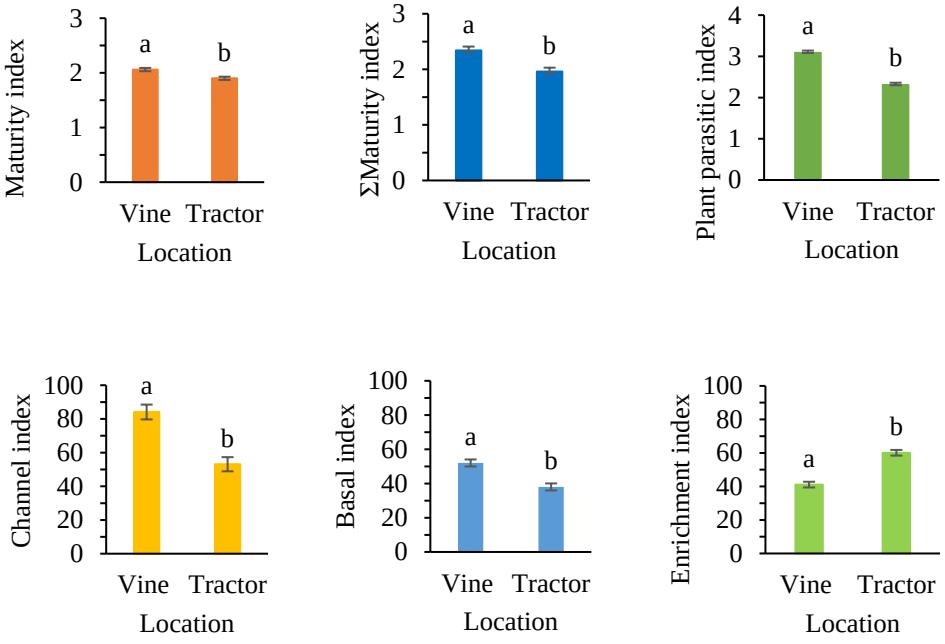

Figure 29. Nematode ecological index LS means (n=24) for soil samples collected from a California vineyard in two locations: under the vine or in the tractor row. Different letters indicate significant differences according to a Student's t test (α=0.05)

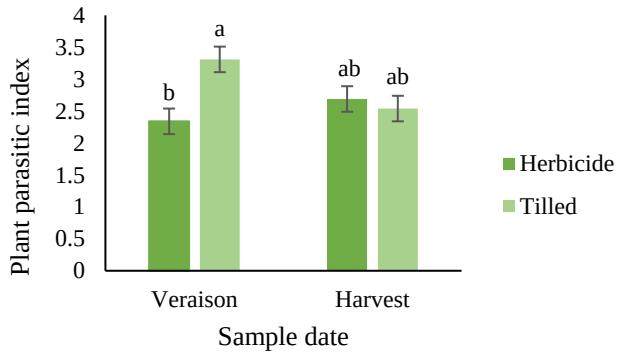

Figure 30. Plant parasitic index (LS mean ± standard error, n=12) for soils collected from a California vineyard under tillage or herbicide weed management treatments, collected at veraison and at harvest. Different letters indicate significant differences according to Tukey's HSD test (α=0.05).

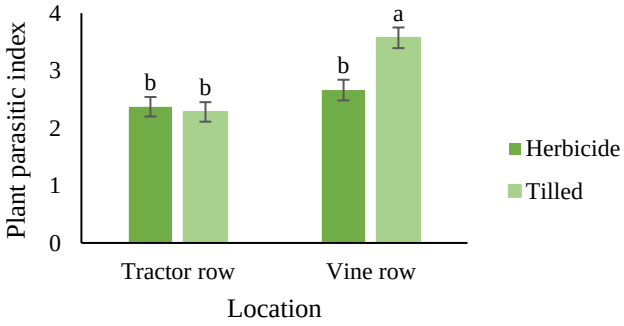

Figure 31. Plant parasitic index (LS mean ± standard error, n=12) for soils collected from a California vineyard under tillage or herbicide weed management treatments, collected either from the tractor row or under the vine. Different letters indicate significant differences according to Tukey's HSD test (α=0.05).

Food web analysis using enrichment and structure indices showed that samples tended to all have low structure indices regardless of location, although it was more pronounces in the vine row (Figure 32). However, there were differences in enrichment

values between the tractor and the vine row, with higher enrichment values in the tractor row regardless of treatment. Samples for the tractor row clustered in the disturbed but N-enriched quadrant; samples for the vine row were more diffuse, but generally clustered in the N-depleted quadrants.

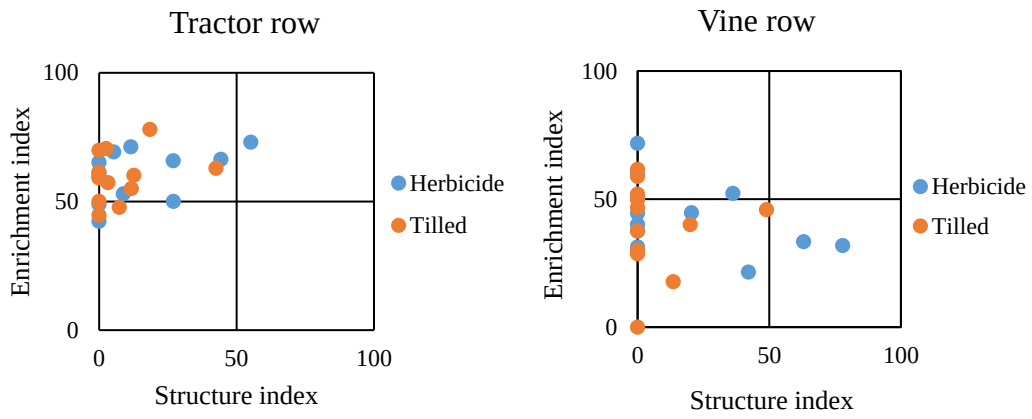

Figure 32. Enrichment and structure indices for nematode communities in soils from a California vineyard under tillage or herbicide treatments for weed control, collected either in the tractor row or beneath the vine, at veraison and harvest.

4.2.2 Effects of Weed Management Strategies on Observed Chemical Parameters

Average values for soil chemical parameters measured in this study are given in Table 15. Overall, the weed management treatment significantly affected total C%, and the treatment*location and treatment*sampling date interactions were also significant for some parameters (Table 16). Location and sample date were significant for most parameters.

Table 15. Average (n=6) measurements ±SE for soil samples collected from a California vineyard under 2 weed management strategies. Samples were collected twice: once at veraison and once at harvest, either under the vine or in the tractor row.

	---------- Veraison ----------				---------- Harvest ----------			
	------ Tractor row ------		-------- Vine row --------		------ Tractor row------		-------- Vine row --------	
	Tilled	**Herbicide**	**Tilled**	**Herbicide**	**Tilled**	**Herbicide**	**Tilled**	**Herbicide**
pH	6.4 ±0.1	6.4 ±0.2	7.7 ±0.0	7.9 ±0.1	6.9 ±0.1	6.7 ±0.0	8.0 ±0.2	8.3 ±0.0
EC (dS/m)	2.0 ±0.1	2.1 ±0.1	1.5 ±0.0	1.7 ±0.1	2.2 ±0.1	2.2 ±0.1	2.3 ±0.2	2.3 ±0.1
NO_3- (mg/kg)	8.0 ±1.1	10.1 ±2.7	7.0 ±1.2	5.0 ±1.2	40.1 ±7.9	59.9 ±7.7	9.7 ±0.9	7.8 ±1.7
POXC (mg/kg)	480.9 ±19.3	521.2 ±19.6	502.1 ±24.6	464.6 ±21.3	638.2 ±25.6	623.8 ±12.3	618.7 ±17.5	556.1 ±18.0
C (%)	1.3 ±0.0	1.4 ±0.1	1.3 ±0.0	1.2 ±0.0	1.6 ±0.1	1.5 ±0.1	1.5 ±0.0	1.3 ±0.1
N (%)	0.1 ±0.0	0.1 ±0.0	0.1 ±0.0	0.1 ±0.0	0.1 ±0.0	0.1 ±0.0	0.1 ±0.0	0.1 ±0.0
WSC (g/kg)	238.1 ±26.5	181.2 ±15.3	118.8 ±3.7	108.3 ±3.0	197.1 ±6.5	183.8 ±3.0	162.4 ±4.3	170.4 ±6.8
WSN (g/kg)	99.5 ±10.2	95.2 ±8.0	53.9 ±4.7	54.3 ±4.2	67.1 ±3.0	66.7 ±15.1	48.8 ±12.6	43.9 ±6.5

Table 16. Model significance ($p \leq 0.05$) indicated with an asterisk for measured chemical parameters in plots under different weed management treatments (herbicide or tillage) in a California vineyard. Empty cells were not significant.

	Treatment	**Location**	**Date**	**Treatment*Location**	**Treatment*date**
pH		*	*		
EC (ds/m)			*		
NO_3^- (mg/kg)			*		
POXC (mg/kg)			*		
C (%)	*	*	*		*
N (%)		*			
WSC (g/kg)		*			
WSN (g/kg)		*	*		

Average total carbon % was slightly, but significantly, higher in tilled plots than in plots which were sprayed with herbicide (1.4 and 1.3, respectively; n =23) (Figure 33). Measurements were generally higher in the tractor row than in the vine row, except for pH, which was higher in the vine row (Figure 33). In general, values were higher at harvest

than at veraison, except for water-soluble nitrogen, which was higher at veraison (Figure 34).

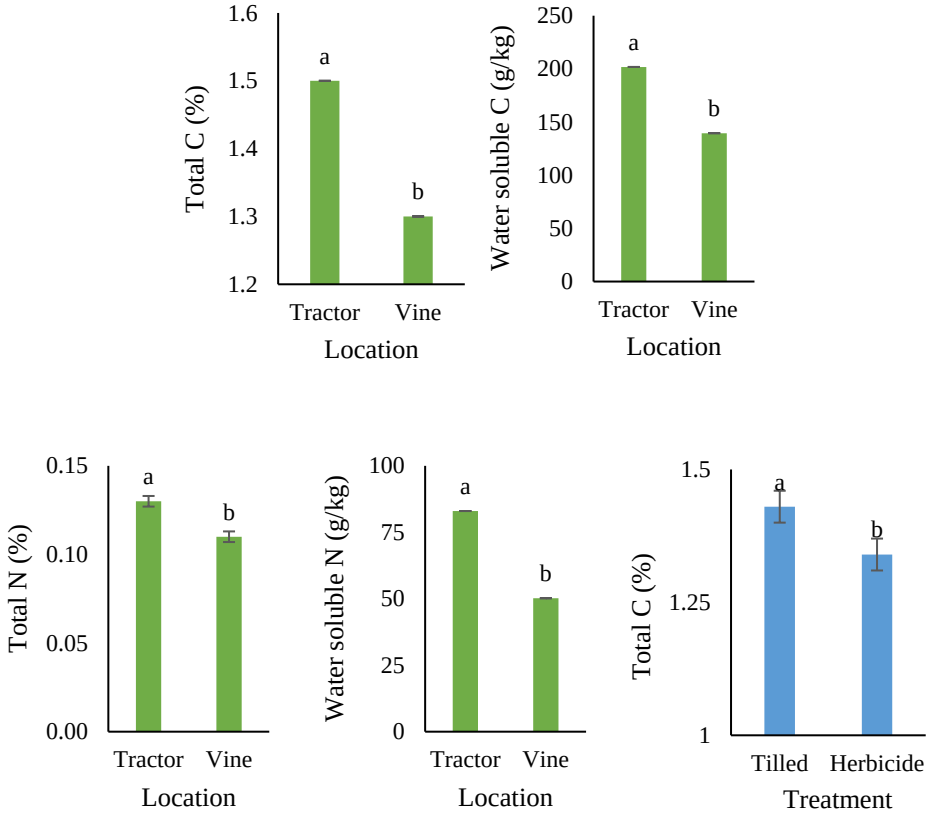

Figure 33. Chemical parameters (LS mean ± standard error, n=23) for soil samples collected in a California vineyard under tillage or weed management treatments for weed control; or from two locations, under the vine or in the tractor row. Bars with different letters are significantly different according to Tukey's HSD ($p<0.05$).

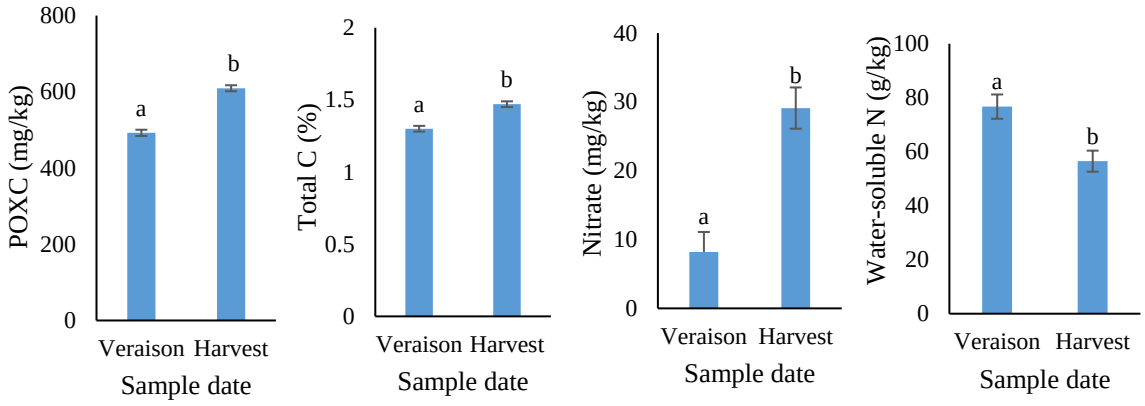

Figure 34. Chemical parameters (LS mean ± standard error) in soil samples taken from a California vineyard at veraison or harvest. Different letters above a column indicate significant differences according to Tukey's HSD ($p<0.05$).

Soil pH was positively correlated with Maturity (MI), ΣMI, and Basal indices, and negatively correlated with the enrichment index (EI). Water-soluble nitrogen (WSN) was negatively correlated with MI, ΣMI, and CI, and positively correlated with the EI. Total N (%) was negatively correlated with the MI, MI 2-5, and SI. Water-soluble carbon was negatively correlated with BI and positively correlated with EI.

4.2.3 Effects of Weed Management Strategies on Berry Quality and Yield

There was no significant difference between herbicide and tillage for brix, pH, TA, berry weight, or total yield (Table 18).

Table 17. Correlations between soil chemical parameters and nematode ecological indices, indicated by Spearman's ρ values, for soil samples collected from a California vineyard.

Index	pH	EC	WSN (g/kg)	Total N (%)	NO_3- (mg/kg)	WSC (mg/kg)	Total C (%)	POXC (mg/kg)
Maturity	0.491**	0.1311	-0.394*	-0.307*	-0.066	-0.214	-0.187	-0.005
Maturity 2-5	-0.026	0.19	-0.017	-0.306*	0.209	0.118	0.065	0.225
Σ Maturity	0.521**	0.029	-0.396*	-0.133	-0.152	-0.249	-0.172	-0.106
Plant parasitic	0.195	-0.074	-0.193	0.135	-0.211	-0.057	-0.086	-0.164
Channel	0.572**	0.23	-0.368*	-0.067	-0.093	-0.297	-0.103	-0.053
Basal	0.394**	-0.001	-0.228	0.083	-0.138	-0.295*	-0.043	0.026
Enrichment	-0.638**	-0.078	0.462**	0.136	0.208	0.401*	0.101	0.016
Structure	-0.025	0.193	-0.021	-0.301*	0.211	0.121	0.069	0.223

*Significant at the 0.05 level
**Significant at the 0.005 level

Table 18. Berry chemistry and total yield (LS Means ± standard error, n=3) for fruit harvested from a California vineyard under tillage or herbicide treatments for weed management.

	F	p value	Tilled	Herbicide
Brix	0.6	0.5	21.9 ±0.2	22.2 ±0.2
pH	0.004	1.0	3.4 ±0.04	3.4 ±0.04
TA (g/l)	0.1	0.7	6.5 ±0.1	6.4 ±0.1
Berry weight (g/berry)	0.02	0.9	1.1 ±0.02	1.1 ±0.02
Yield (tons/rep)*	3.4	0.1	0.15 ±0.01	0.18 ±0.01

4.2.4 Weed Management Discussion

Food web structure in soil samples collected from the weed management trial reflected a similar level of disturbance compared to other agricultural systems (Bongers and Ferris, 1999b). Food web analysis using enrichment and structure indices showed that most sampled clustered near the low-structure quadrants and appeared N-depleted under the vine. The tillage treatment was expected to increase measures of disturbance due to the reduction in organisms at higher trophic levels, but for most nematode indices there was no clear effect of weed management treatment on nematode family abundance or food web structure. Zhang et al. (2012) saw similar results and hypothesized that disturbance-tolerant taxa could have been selected for over years of the same management (tillage). Because this was a short-term experiment, and tillage was generally practiced in this vineyard, a similar situation could have occurred in this trial.

The plant parasitic index (PPI) was the only ecological measurement that had a significant interaction effect between treatment and location or date. The PPI was lowest under the herbicide treatment at veraison, but treatments were indistinguishable by the end of the growing season. In soil under the vine, the PPI was also lowest under the herbicide treatment, compared to the tilled plots. This could indicate reduced crop vigor and decreased primary production, partially from root growth, where herbicide was applied. Because the herbicide plots only received one treatment of herbicide, but tilled plots were maintained with monthly treatments, it is possible that the reduction in PPI under the herbicide treatment is due in part to vine competition with new weeds. Tesic et al. (2007) observed reduced vine vigor when vines were in competition with floor cover. The PPI was not correlated with any soil chemical parameters; however, where PPI was lowest

(herbicide treatment, under the vine) total N (%) was also significantly lower and soil pH was significantly higher than other location and treatment combinations. Salome et al. (2016) found that lime application in some soils was a stronger driver of soil organisms than weeding strategy (whether by herbicide, tillage, or weeding), and pH was strongly correlated with several other nematode indices.

Although previous studies observed higher enrichment indices (EI) in tilled plots compared to no-till (Ito et al., 2015) there were no differences in EI between treatments in this study. Salomé et al. (2016) saw differences in EI between weeding treatments only in non-stony, calcareous soils. This soil was non-calcareous, and so our results are in agreement with Salomé et al. EI was positively correlated with water-soluble Nitrogen, as predicted by Sanchez-Moreno et al. (2008). N addition has been shown to increase the decomposition of labile carbon and inhibit the breakdown of lignin (Sinsabaugh et al., 2005). Both of these factors could contribute to a soil community which favors opportunistic taxa that feed on labile nutrient sources, thereby increasing the EI. This also could explain why water-soluble nitrogen was also correlated with reduced values for the Maturity and Σ Maturity indices.

Although total C (%) was not significantly different by treatment at veraison, by harvest it was highest under tillage than compared to herbicide, in contrast to findings by Ito et al. (2015) that soil C was reduced under tillage. However, Griffiths et al. (2008) saw effects of herbicide varied by soil type, so it is possible that, like with EI, soil effects are confounding treatment results. As was seen in both Pool et al. (1990) and Smith et al. (2008), herbicide or tillage had no effect on berry quality or yield.

The difference between the tractor row and the vine row were very distinct but unrelated to the treatment. Location was a significant factor for most nematode indices and most chemical parameters. It appears that any differences between the effects of herbicide and tillage on the soil food web is less pronounced than the difference between the vine row environment and the tractor row environment. This could be because the tractor row in this particular vineyard has been managed the same way for several years, resulting in accumulating effects of the disturbance.

4.3 Cover Crop Experiment

4.3.1 Effects of Cover Crop on Soil Community Composition

Overall, 19 families were identified from soil samples in all plots across all treatments. Of these, 6 were bacterivores, 3 were fungivores, 2 were omnivores, 7 were plant parasites and 1 was a predator (Table 19).

Table 19. Number of nematode families identifies in each colonizer-persister (cp) class from soils in a California vineyard. One family is represented twice due to the presence of two subfamilies with difference cp classes.

Cp class	No. of families	Cp class	No. of families
Ba-1	2	Om-4	1
Ba-2	2	Om-5	1
Ba-3	1	Pp-2	2
Ba-4	1	Pp-3	4
Fu-2	3	Pp-5	1
Fu-3	1	Pr-3	1

Ba: bacterivore
Fu: fungivore
Pp: plant parasite
Om: omnivore
Pr: predator

Aphelenchoididae (fungivore) was the most abundant family, followed by Cephalobidae (bacterivore), and then Tylenchidae (fungivore/herbivore). The abundance of 3 nematode families were significantly different ($p \leq 0.05$) by treatment using the standard least squares model: Monhysteridae (Ba-3), Tylenchidae (Pp-2 and Fu-2 subfamilies), and Qudsianematidae (Om-4) (Table 21). These families responded differently to the treatments (Figure 35). The abundance of some families was also significantly different by time (Table 21). The average number of individual nematodes by treatment and location are shown in (Table 20).

Nematode ecological indices were generally in line with expected values for disturbed agricultural soils (Table 22), averaging 1.93, 2.1, and 2.1 for the maturity, maturity 2-5, and Σ maturity indices, respectively (n = 53). They showed, on average, intermediate enrichment (mean enrichment index = 55.87; n = 53) and very low structure (mean structure index = 15.87; n = 53).

Treatment, sample date, or both, significantly affected about half of the indices ($p \leq 0.05$) (Table 23). Treatment was significant for the Maturity (MI, $F=10.8$, $p <0.001$), Channel (CI, $F=5.7$, $p\leq0.02$), Basal (BI, $F=4.3$, $p\leq0.04$), and Enrichment (EI, $F=5.8$, $p\leq0.02$) indices (Figure 36). For these indices, the low-water use plots drove the significance; the high-water use cover crop and the resident vegetation were not significantly different. All significantly different indices, except EI, were lower in the low water use plots than in the other treatments. EI was highest in the low-water use plots compared to the other treatments (Figure 36).

Table 20. Average (n=6) and absolute abundance of nematodes by family in 200 cm^3 of soil from a Pinot Noir vineyard in California, under three cover crop treatments: resident vegetation ("None"), low-water use seed mix ("Low"), or high-water use seed mix ("High").

	Trophic	-------- Bloom --------			-------- Veraison -------			--------- Harvest --------			Total
Family	**-cp**	**None**	**Low**	**High**	**None**	**Low**	**High**	**None**	**Low**	**High**	**abundance**
Panagrolaimidae	Ba-1	275.4	226.9	377.2	373.7	449.7	559.8	859.1	686.8	837.7	1,498.8
Rhabditidae	Ba-1	0	0	0	18.9	35.4	10.1	47.4	100.6	7.7	11,714.5
Cephalobidae	Ba-2	741.2	315.5	881.8	782.4	929.3	784.5	834.2	1061.1	616.5	27,650.9
Plectidae	Ba-2	48.3	0	2.1	0	17.1	29.8	7.3	14.5	11.7	447.2
Monhysteridae	Ba-3	0	0	0	0	8.6	0	0	0	0	1,985.0
Alaimidae	Ba-4	0	0	0	0	0	7.7	0	0	0	1,321.3
Aphelenchoididae	Fu-2	0	0	0	27.4	8.6	0	0	0	0	41,363.1
Neotylenchidae	Fu-2	0	36.2	0	0	0	0	0	0	0	215.8
Diphtherophoridae	Fu-3	0	0	0	27.4	0	11	0	9.8	26.3	51.5
Qudsianematidae	Om-4	0	11.7	0	0	0	7.7	14	8.4	0	156.9
Aporcelaimidae	Om-5	64.6	30.3	0	76.6	22.6	69.9	153.5	88.2	145.6	785.2
Tylenchidae	Pp-2	46.7	0	97	4.8	0	19.1	52	28.5	82.8	15,324.5
Tylenchulidae	Pp-2	316.2	386.3	286.6	107.2	193.1	178.7	129.9	306.4	112.3	239.3
Pratylenchidae	Pp-3	0	0	0	13.5	32.6	78.4	72.6	25.4	48.2	3,877.3
Belonolaimidae	Pp-3	253.7	64.8	228.9	352.7	171.7	280.4	553.3	393.4	266.1	2,382.3
Heteroderidae	Pp-3	25.3	18	6.9	11.7	21.7	41.3	113.9	114.5	46.7	180.9
Hopolaimidae	Pp-3	0	0	0	3.7	2.7	0	15.9	3.7	0	46.5
Longidoridae	Pp-5	0	0	0	0	0	0	12	3.7	0	94.5
Tripylidae	Pr-3	0	0	0	0	0	0	0	0	0	1,624.4

Ba: bacterivore
Fu: fungivore
Pp: plant parasite
Om: omnivore
Pr: predator

Table 21. Model significance ($p \leq 0.05$) indicated by * for abundance of nematode families in a California vineyard under three cover crop mix treatments (none, low-water use, or high-water use), sampled at three times (bloom, veraison, and harvest). Empty cells were not significant.

	Treatment	**Time**	**Treatment*date**
Panagrolaimidae			
Rhabditidae		*	
Cephalobidae		*	
Plectidae			
Monhysteridae	*		
Alaimidae			
Aphelenchoididae			
Neotylenchidae			
Diphtherophoridae			
Tylenchidae	*	*	
Tylenchulidae			
Belonolaimidae		*	
Heteroderidae			
Hopolaimidae			
Pratylenchidae		*	
Longidoridae			
Qudsianematidae	*		
Aporcelaimidae			
Tripylidae		*	

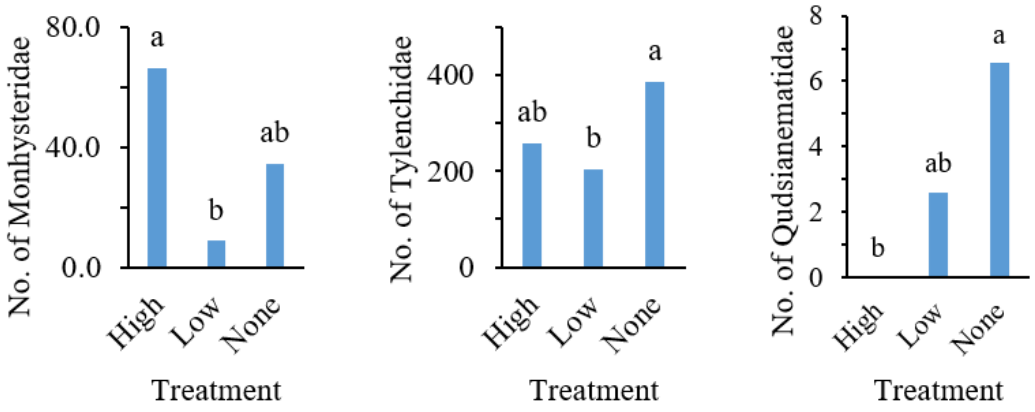

Figure 35. Number (LS Mean) of individuals collected per 200 cc^3 soil in a California vineyard under three cover crop mix treatments (high-water use, low-water use, or none).

Table 22. Nematode index means (n=6) for soil samples from a California vineyard under different cover crop treatments, resident vegetation (“None”), a low-water use seed mix (“Low”), or a high-water use seed mix (“High”), collected at 3 times, bloom, veraison or harvest.

	---------- Bloom ----------			---------- Veraison ----------			---------- Harvest ----------		
Index	**None**	**Low**	**High**	**None**	**Low**	**High**	**None**	**Low**	**High**
Maturity	1.9	1.6	1.9	2	1.9	2	2	2	2
Maturity 2-5	2.2	2	2.1	2.1	2.1	2.1	2.1	2.2	2.1
ΣMaturity	2	1.7	1.9	2	2	2	2.1	2.1	2.1
Plant Parasitic	2.3	2.6	2.1	2.3	2.4	2.3	2.5	2.5	2.4
Channel	47.8	17.4	47.2	65.6	45.4	54.9	61.7	51.4	67.9
Basal	34.4	23.3	37.5	46.2	36.4	42.1	45	40.8	51.7
Enrichment	64	76.7	59.8	50.6	60.3	52.9	48.5	52.3	41.4

Table 23. Model significance for nematode indices in a California vineyard under three different cover crop treatments (resident vegetation only, a low-water use seed mix, or a high-water use seed mix), sampled at three times: bloom, veraison, and harvest. Empty rows were not significant.

	Treatment	**Time**	**Treatment*time**
Maturity	*	*	*
Maturity 2-5			
Σ Maturity		*	
Plant Parasitic			
Channel	*	*	
Basal	*	*	
Enrichment	*	*	
Structure			

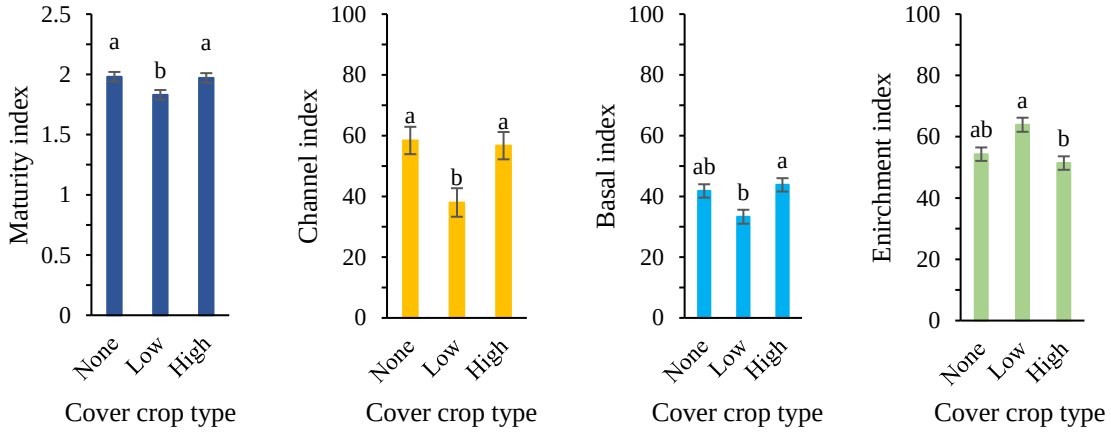

Figure 36. Nematode ecological indices (LS mean ± standard error) for soil samples from a California vineyard under three different cover crop treatments, resident vegetation ("None"), a low water use seed mix ("Low"), or a high water use seed mix ("High"). Columns not connected by the same letter are significantly different according to Tukey's HSD test.

Sample date was significant for MI ($F=10.8$, $p\leq0.0003$), ΣMI ($F=12.5$, $p\leq0.0001$), CI ($F=6.3$, $p\leq0.005$), BI ($F=8.6$, $p\leq0.001$), and EI ($F=17.02$, $p\leq0.0001$). Except for the EI, these indices increased from the beginning of the growing season to the middle (bloom to veraison), then held steady (Figure 37). The EI decreased from the beginning to the middle of the growing season, then held steady (Figure 37).

Food web analysis using enrichment and structure indices showed that the low cover plots tended to be the most enriched compared to the other treatments. High and no cover crop plots tended to fall somewhere between the enriched and depleted quadrants. Structure values for all treatments, however, fell into the disturbed or degraded quadrants. At bloom, plots had very low structure that increased later in the season, although

enrichment dropped. Regardless of season, plots fell into the disturbed or degraded quadrants (Figure 38).

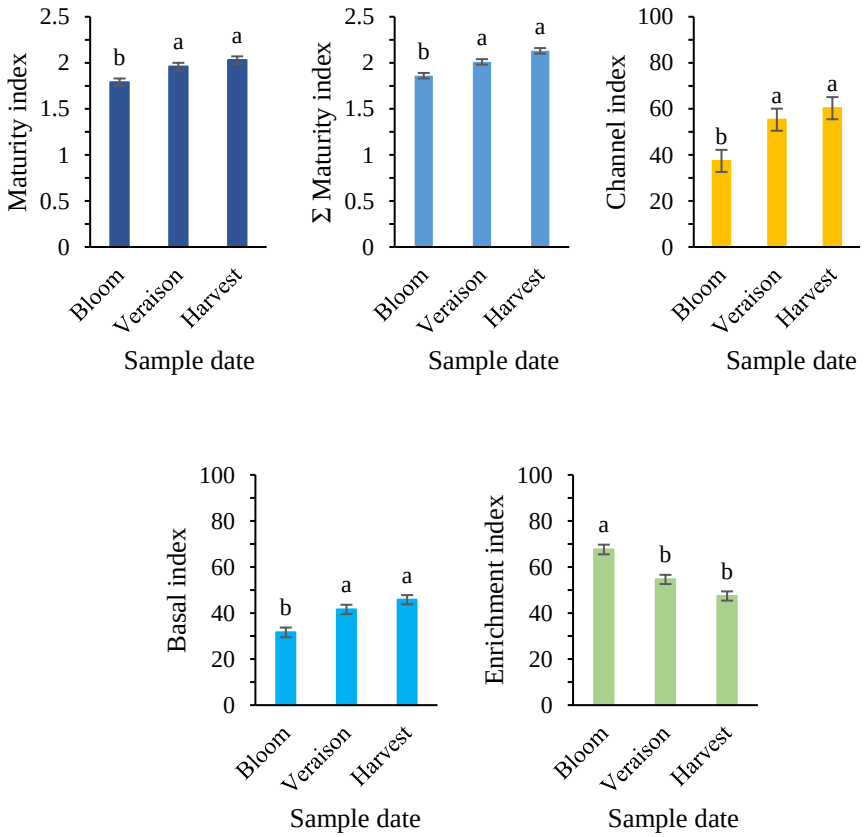

Figure 37. Nematode ecological indices (LS mean ± standard error) for soil samples from a California vineyard collected at three different times: bloom, veraison, or harvest. Columns not connected by the same letter are significantly different according to Tukey's HSD test.

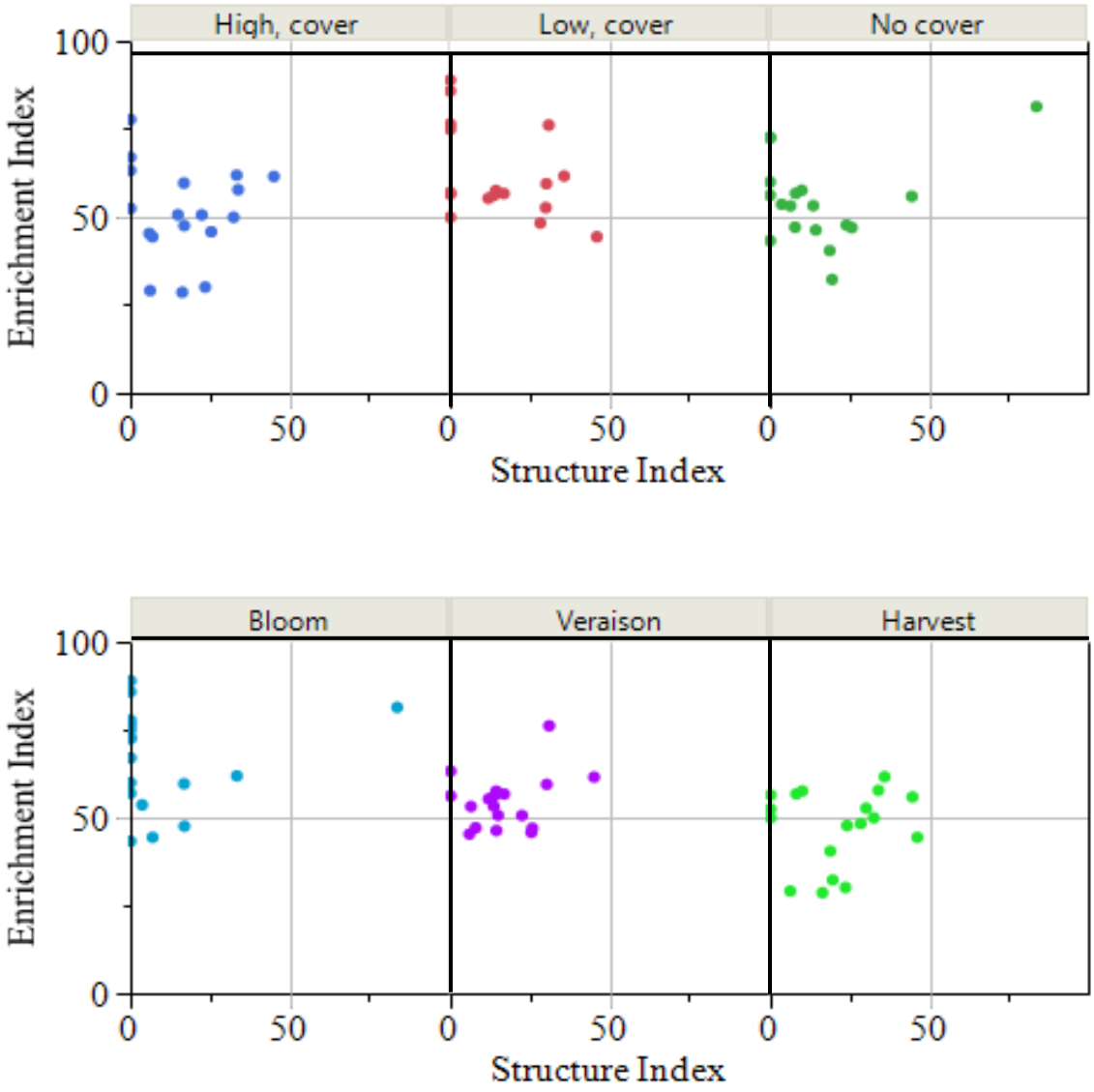

Figure 38. Enrichment and structure indices for nematode communities in soil samples from a California vineyard, with colors indicating either cover crop treatments- high water use mix (“High, cover”), low water use mix (“Low, cover”), or none (“No cover”) - or sample date (bloom, veraison, or harvest).

4.3.2 Effects of Cover Crop on Soil Chemistry

Average values for soil chemical parameters measured in this study are given in Table 24. Treatment significantly affected pH, water-soluble carbon (WSC) and water-soluble nitrogen (WSN) (Table 25). Date also significantly affected most parameters (Table 25).

The low-water use cover crop mix had significantly lower pH and higher WSC and WSN than either the high-water use cover crop or the resident vegetation (Figure 39). Sample date significantly affected several parameters, with values generally increasing as the growing season progressed (Figure 40).

Most nematode ecological indices were correlated with water-soluble carbon, pH and NO_3- (Table 26). Only 2 indices, the Maturity index 2-5 and the Structure index, were correlated with EC.

Table 24. Average (n=6) measurements ±SE for soil samples collected from a California vineyard under 3 different cover crop mixes, either high-water use species (High), low-water use species (Low), or resident vegetation only (None). Samples were collected 3 times: at bloom, veraison and harvest, from under the tractor row.

	---------- Bloom ----------			---------- Veraison ----------			---------- Harvest ----------		
	None	**Low**	**High**	**None**	**Low**	**High**	**None**	**Low**	**High**
pH	7.2 ±0.1	7.0 ±0.1	7.2 ±0.1	6.4 ±0.1	5.9 ±0.2	6.1 ±0.2	6.7 ±0.1	6.6 ±0.1	6.8 ±0.1
EC (dS/m)	1.4 ±0.1	1.5 ±0.0	1.5 ±0.1	2.4 ±0.2	2.4 ±0.2	2.1 ±0.2	1.9 ±0.1	1.9 ±0.1	1.8 ±0.1
NO3 (mg/kg)	20.7 ±7.2	12.4 ±4.0	18.7 ±15.8	63.2 ±20.9	45.5 ±22.2	33.0 ±19.4	67.1 ±14.0	72.7 ±15.1	52.9 ±18.7
POXC (mg/kg)	454.6 ±17.4	438.3 ±56.7	475.5 ±25.5	566.1 ±23.3	551.9 ±19.9	481.7 ±10.2	521.5 ±16.8	490.6 ±36.9	498.9 ±18.0
C (%)	1.40 ±0.0	1.30 ±0.1	1.35 ±0.1	1.43 ±0.1	1.38 ±0.1	1.27 ±0.1	1.48 ±0.0	1.41 ±0.0	1.39 ±0.1
N (%)	0.12 ±0.0	0.11 ±0.0	0.12 ±0.0	0.13 ±0.0	0.13 ±0.0	0.12 ±0.0	0.13 ±0.0	0.12 ±0.0	0.11 ±0.0
NPOC (g/kg)	114.1 ±9.7	138.0 ±14.2	141.4 ±13.7	180.2 ±6.0	203.6 ±18.9	160.5 ±7.3	244.4 ±8.1	287.4 ±2.3	241.6 ±8.2
(TN g/kg)	na	na	na	105.1 ±14.8	105.6 ±28.3	91.8 ±18.8	108.4 ±6.6	156.8 ±6.5	99.7 ±9.1

Table 25. Model significance ($p \leq 0.05$) indicated with an asterisk for measured chemical parameters in plots under different cover crop mixes in a California vineyard. Empty cells were not significant.

	Cover crop mix	Date	Cover crop mix*date
pH	*	*	
EC (ds/m)		*	
NO_3-ˡmg/kg)		*	
POXC (mg/kg)		*	
Total C (%)		*	
Total N (%)			
WSC (g/kg)	*	*	
WSN (g/kg)	*	*	

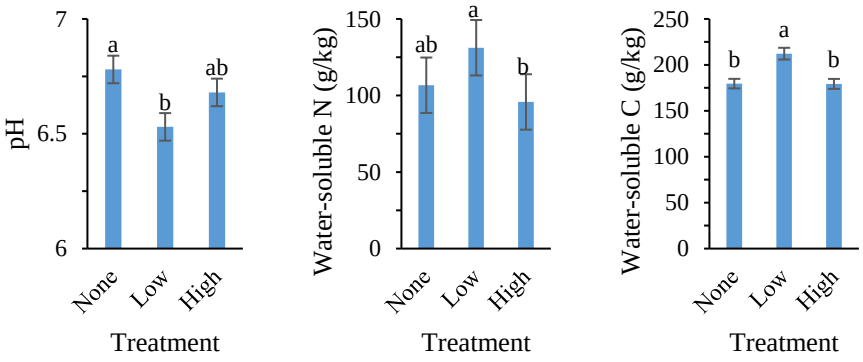

Figure 39. Chemical parameters (LS mean ± standard error, n=18) for soil samples collected in a California vineyard under different cover crop treatments: resident vegetation ("None"), low water use seed mix ("Low"), or high water use seed mix ("High").

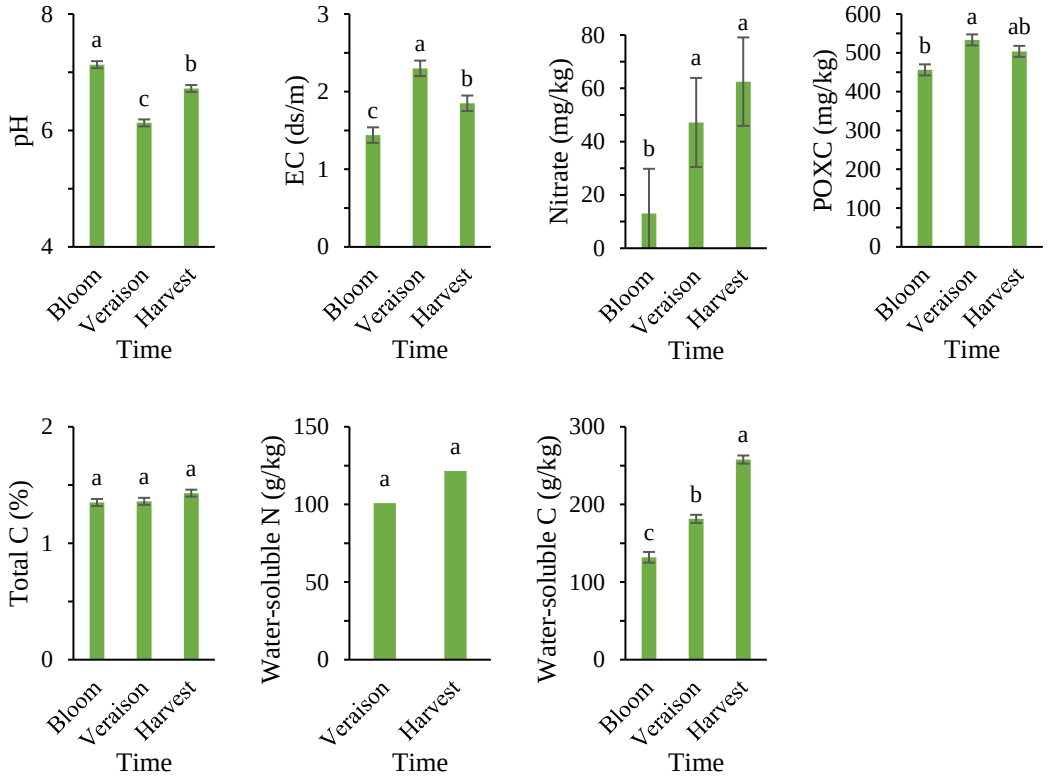

Figure 40. Chemical parameters (LS mean ± standard error, n=23) for soil samples collected in a California vineyard sampled over a growing season, at bloom, veraison, and harvest. Bloom samples were not available for water-soluble nitrogen.

4.3.3 Effects of Cover Crop on Berry Quality and Yield

Cover crop treatment did not have significant effect on brix, pH, TA, berry weight, or total yield (n=3) (Table 27).

Table 26. Correlations between soil chemical parameters and nematode ecological indices, indicated by Spearman's ρ values, for soil samples collected from a California vineyard.

Index	pH	EC (ds/m)	Total N (%)	WSN (g/kg)	NO_3- (mg/kg)	Total C (%)	WSC (g/kg)	POXC (g/kg)
Maturity	-0.301*	0.249	0.032	0.19	0.442*	-0.07	0.383*	0.077
Σ Maturity	-0.335*	0.243	0.079	0.289	0.483*	-0.052	0.476*	0.022
Maturity 2-5	-0.343*	0.404*	0.174	0.299	0.435*	0.026	0.408*	0.12
Plant parasitic	-0.207	0.078	-0.008	0.211	0.119	-0.165	0.175	-0.059
Channel	-0.236	0.196	-0.158	-0.052	0.244	0.008	0.318*	0.073
Basal	-0.224	0.051	-0.310	-0.310	0.149	-0.060	0.213	-0.009
Structure	-0.319*	0.391*	0.178	0.284	0.430*	0.031	0.395*	0.221
Enrichment	0.316*	-0.118	0.016	0.167	-0.299*	0.083	-0.343*	-0.188

*Significant at the 0.05 level

**Significant at the 0.005 level

Table 27. Berry chemistry and total yield (LS Means ± standard error, n=3) for fruit harvested from a California vineyard under different cover crop treatments: resident vegetation ("None"), low water use seed mix ("Low"), or high water use seed mix ("High").

	F	p value	None	Low	High
Brix	0.7	0.5	26.2 ±0.12	26.0 ±0.12	26.2 ±0.12
pH	0.06	0.9	3.6 ±0.06	3.5 ±0.06	3.5 ±0.06
TA (g/l)	0.2	0.8	5.6 ±0.16	5.7 ±0.16	5.8 ±0.16
Berry weight (g/berry)	0.2	0.8	0.9 ±0.02	0.9 ±0.02	0.9 ±0.02
Yield (tons/rep)	3.2	0.1	0.2 ±0.01	0.2 ±0.01	0.2 ±0.01

4.3.4 Cover Crop Discussion

Food web structure in soil samples collected from the cover crop trial reflected a similar level of disturbance compared to other agricultural systems (Bongers and Ferris, 1999b). Food web analysis using enrichment and structure indices showed that all plots fell into the disturbed or degraded quadrants, indicating a disturbed and immature soil food web. Both cover crop treatments (high and low water use mixes) were expected to lower stability indicators by supplying energy for soil microbial communities from root exudates (Ito et al., 2015; Salomé et al., 2016). Differences between the cover crop treatments were observed in this study, and the high-water use crop (dominated by legumes) showed greater ecological stability than the low water use crop (dominated by grasses). However, the high water use crop did not lower stability compared to the control (resident vegetation).

The Channel Index (CI) was lower in the low-water use (grass-dominated) treatment than in the high-water use (legume-dominated) or control plots. Based on the literature, it was expected that the cover crop treatment would result in a higher Channel index (CI) than the resident vegetation (Ito et al., 2015). Other studies, however, have shown that soil communities are shaped more by plant species than by plant functional group (Porazinska et al., 2003; Viketoft et al., 2005), so soil organisms could be responding to individual species within each treatment more so than the presence or absence of a planted cover crop. Because the effects of plant on the soil community are driven primarily by exudates into the soil environment, further research on the effects of cover crops could incorporate cover crop physiology for clearer results. Fast-growing cover crops, for example, may encourage opportunist taxa. The short-term nature of this project, combined with biennial ripping of the field, could also have complicated our results. Strong differences between cover crop

treatments in Zhang et al., 2017, for example, were analyzed after 16 years of a continuous management strategy.

Cover crop treatment neither decreased yield nor increased berry quality, as was observed by Tesic et al. (2007) and Xi et al. (2011), respectively. The types of negative effects of cover crop on a grapevine that could lead to increased berry quality could have been avoided by appropriate soil nutrient levels and regular irrigation (McGourty et al., 2008; Smith et al., 2008).

5. CONCLUSIONS

Overall, nematode ecological indices proved to be less useful for measuring subtle differences in soil management over the short-term than previously thought. They did not differentiate between herbicide and tillage, showed few differences between organic or inorganic fertilizer, and produced hard to interpret results for the cover crop trial. In general, the most pronounced differences were seen by location and date, rather than treatment.

Some management practices in the studied vineyard were unknown or hard to control for, for example, prior years' fertilization strategies, or if other activities were occurring that could have complicated results. While this makes interpreting data difficult, it also presents a true-to-life situation, which generally has more interdependent factors than a controlled research experiment. While it is possible that clearer results could be had under tighter control, the results of this experiment may be interpreted to mean that some changes to vineyard management have little effect on soil health in isolation and/or in the short-term. Much like the soil food web, an agroecosystem is an interdependent system made up of many working parts, and changes to one aspect of management may be buffered by other aspects of the system.

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APPENDIX

Table 28. Complete list of fungicides and herbicides applied to all trials in 2017.

Date Completed	Type of Application	Product	EPA/California Registration No.	Manufacturer	Rate/acre
3/6/2017	Foliar	Miller Spur Shield	EPA Exempt	Miller Chemical and Fertilizer, LLC	2 qt
		Topsin M WSB	73545-16-AA-70506	United Phosphrus Inc.	1 lb
4/4/2017	Foliar	JMS Stylet Oil	65564-1-AA	JMS Flower Farms, Inc.	2 qt
		Kocide 3000	352-662-ZA	E.I. DuPont de Nemours & Co Inc.	1 lb
4/25/2017	Foliar	Mettle 125ME	80289-8-AA	Isagro USA, Inc.	5 oz
		PHT Ad-Max 90	7001-50537-AA	J.R. Simplot Company	3 oz
5/5/2017	Foliar	Quintec	62719-375-AA	Dow AgroSciences	5 oz
		Microthiol Disperss	70506-187-AA	United Phosphrus Inc.	3 lb
		PHT Ad-Max 90	7001-50537-AA	J.R. Simplot Company	4.5 oz
5/18/2017	Foliar	Luna Experience	264-1091-AA	Bayer CropScience LP	8 oz
		Movento	264-1050-AA	Bayer CropScience LP	6 oz
		Microthiol Disperss	70506-187-AA	United Phosphrus Inc.	3 lb
		Vintre	72662-50004-AA	Oro Agri Inc.	1 qt
6/2/2017	Foliar	Vivando	7969-284-AA	Bayer CropScience LP	12 oz
		Microthiol Disperss	70506-187-AA	United Phosphrus Inc.	3 lb
		PHT Ad-Max 90	7001-50537-AA	J.R. Simplot Company	6 oz
6/16/2017	Foliar	Torino	8033-103-AA-10163	Gowan Company	3.4 oz
		Microthiol Disperss	70506-187-AA	United Phosphrus Inc.	3 lb
		Movento	264-1050-AA	Bayer CropScience LP	6 oz
		Vintre	72662-50004-AA	Oro Agri Inc.	1 qt
6/29/2017	Foliar	Quintec	62719-375-AA	Dow AgroSciences	5 oz
		Microthiol Disperss	70506-187-AA	United Phosphrus Inc.	3 lb
		Vintre	72662-50004-AA	Oro Agri Inc.	1 qt