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Conservation agriculture improves the balance between beneficial free-living and plant-parasitic nematodes for low-input rainfed rice crop

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ABSTRACT

Conservation agriculture systems leaning on living mulch show particular promise thanks to their benefits on soil biological activity, but weed pressure in these cropping systems strongly depends on the amount of mulch. To assess the ability of these cropping systems to sustain soil health considering pest regulation, we investigated the combined influence of tillage and crop management (conventional, CONV and no-tillage with living mulch, NTLM) and weeding regimes (weekly hand-weeding and none) on soil free-living and plant-parasitic nematodes. To do so, we leant on a split-plot field experiment in Madagascar highlands 7 years after crop establishment. Overall, the abundance of soil free-living nematodes was 3.9 times higher in NTLM than CONV, primarily due to a preferential increase in fungal-feeders (+585 %) and in omnivores and predators (+633 %). Conversely, plant-parasitic nematodes had the same abundance in both systems, but not the same taxonomic composition, with a dominance of endoparasitic taxa in CONV, and of ectoparasitic taxa in NTLM. Weeding management affected only populations in NTLM, leading to increased abundance of fungal-feeders (+191 %) and lower abundance of semi-endoparasites (−89 %) in the unweeded systems, which were associated with changes in plant community diversity. In this context, conservation agriculture and no-weeding proved beneficial for promoting free-living nematode communities but also to decrease the overall plant parasitic pressure through plant diversification. As no weeding may nonetheless affect crop yield, a trade-off has therefore to be found to promote soil ecosystem services while maintaining crop production.

1. Introduction

Ecological intensification is a recognized strategy for maintaining the sustainability and resilience of agroecosystems, especially in smallholders' farms in developing countries with limited access to synthetic inputs (*e.g.* Tittonell, 2014). Agricultural practices that favor biodiversity, especially in soils, promote various agroecosystems services such as soil carbon storage, nutrient cycling or pest regulation (Bender et al., 2016). Nematodes are an interesting animal group due to their ubiquity (van den Hoogen et al., 2019) and their wide functional diversity within the soil food web (Yeates et al., 1993), linking them to numerous ecosystem services (*e.g.* biogeochemical cycling and pest regulation). Thus, using soil nematode indicators is highly useful to assess cropping systems impacts on soil health, contributing to sustainable food production (Du Preez et al., 2022; Trap and Blanchart, 2023).

In Madagascar highlands, rainfed rice cropping on acidic and nutrient-depleted Ferralsols face important limitations for plant nutrition and pest regulation, which are worsened by the restricted access in synthetic inputs (Raminoarison et al., 2020; Rodenburg et al., 2020; Ripoche et al., 2021). A cropping system based on no tillage and living mulch (NTLM) of *Stylosantes guianensis* cover crop was tested in this area and has proven effective in limiting weed pressure, while increasing crop yields (Dusserre et al., 2020; Rafenomanjato et al., 2023). The combination in this innovative cropping system of no soil disturbance

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and a permanent cover with a high quality leguminous green manure would maximize ecological services and could represent an achievement of conservation agriculture principles (He et al., 2023). However, although tillage reduction and vegetal diversity has the potential to enhance free-living nematode populations, it may also favor plant-parasitic nematodes (Henneron et al., 2015; Puissant et al., 2021), posing a potential threat to long-term crop sustainability. Whether the development of plant-parasitic nematodes could be mitigated under different weeding regimes in this specific context is unknown. To address this uncertainty, we assessed both soil free-living and plant-parasitic nematodes in a field split-plot experiment comparing no-tillage with living mulch (NTLM) and conventional (CONV) cropping systems combined with different weeding regimes 7 years after crop establishment. We assumed that the abundance of both free-living nematodes and plant parasitic nematodes would be promoted in the NTLM systems, yet that these increases would be mitigated by regular hand-weeding.

2. Material and methods

The study was conducted at the experimental site described in Rafenomanjato et al. (2023), set up in 2015 in Mid-West Madagascar (19°33'26"S, 46°24'55"E, elevation of 930 m a.s.e), with the soil characterized Oxisol (USDA classification), with an annual rainfall of 1330 mm and an average temperature of 24 °C (Rodenburg et al., 2020). Briefly, a split-plot design replicated in six blocks was set up from 2015 to 2018 to compare different soil and fertilization managements for a rice/maize biannual rotation. In this trial, we sampled soil in the 0–10 cm layer in March 2018 at rice flowering stage in four blocks, fertilized with 10 t Dry Matter (DM) ha^{-1} of organic manure, under two tillage managements (conventional-tilled CONV and non-tilled with *S. guianensis* living mulch NTLM) combined with two weeding regimes (weekly hand-weeding and no weeding), resulting in four treatments. Nematodes were extracted using the Oostenbrink direct cottonwood filter method (Townshend, 1963) from 100 g of fresh soil samples. The nematodes were then counted with a stereomicroscope and approximately 200 individuals per sample were randomly selected and studied under a compound microscope to identify their taxonomic identity at the genus or family level. Taxa were assigned to trophic groups as described by Yeates et al. (1993). All statistical analyses were performed using R software R-4.3.1 (R Core Team, 2023) with *agricolae* (de Mendiburu, 2023), *car* (Fox and Weisberg, 2019) and *stats* (R Core Team, 2023) packages. Differences between treatments were tested by one-way ANOVAs, followed by *post hoc* Tukey HSD tests to compare data from all treatments. When conditions of normality were not met, Kruskal-Wallis tests were used instead of ANOVAs.

3. Results and discussion

In line with our expectations, the total abundance of free-living nematodes increased significantly in the NTLM cropping systems (+295 %, Fig. 1a). We attribute these changes to two main mechanisms: (i) the enrichment in soil carbon (Balesdent et al., 2000; Autret et al., 2016) and hence soil microbial biomass (Helgason et al., 2009; Sun et al., 2023) in the superficial soil layer with the presence of a permanent plant cover and no tillage, and (ii) the reduction of soil physical disturbance thanks to the presence of a mulch and no tillage, which favors soil biota in the soil layer (Roger-Estrade et al., 2010; Betancur-Corredor et al., 2022; Coulibaly et al., 2022).

We assumed that the first mechanism played an important part on the soil carrying capacity toward the soil nematode communities. Indeed, a recent study conducted in a similar Ferrallitic soil from Madagascar showed that free-living nematodes are firstly limited by carbon, highlighting the importance of regular organic matter restitution on this community (Trap et al., 2024). Also, NTLM systems in Madagascar are known to increase soil C content and microbial biomass

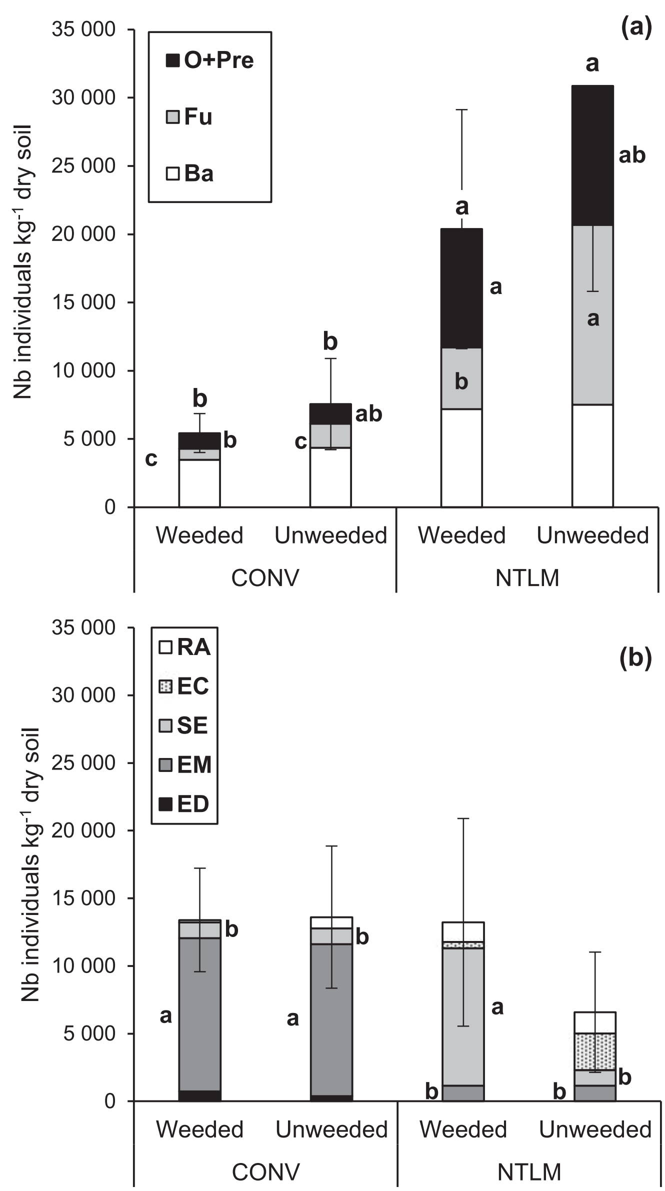

Fig. 1. Soil nematode free-living (a) and plant-parasitic (b) abundances. Values are means ($n = 3$). Significant differences were tested with one-way ANOVAs between treatments, followed by a Tukey post-hoc HSD test; different letters indicate significant differences among treatments ($p \leq 0.05$). CONV: conventional system; NTLM: No-tilled system with living mulch; Ba: bacterial-feeders; Fu: fungal-feeders; O + Pre: omnivores and predators; RA: Root-associated nematodes; EC: ectoparasites; SE: semi-endoparasites; EM: *endo*-migratory; ED: endo-sedentary.

in the superficial soil layer (Rabary et al., 2008; Zemek et al., 2018; Dusserre et al., 2020). These increases, along with presence of permanent plant cover, likely benefited to both fungal-feeders (+585 %) and their predators (+633 %), but not to bacterial-feeders (ANOVA, $p >$ 0.05, Fig. 1) (Henneron et al., 2015; Puissant et al., 2021). In addition to carbon, the NTLM system can provide other elements that limit the growth of nematodes, in particular nitrogen (Trap et al., 2024). Indeed, *S. guianensis* is a legume that fixes large quantities of N (70 to >200 kg ha^{-1} $year^{-1}$) (Zemek et al., 2018). The absence of physical disturbance may also have favored the promotion of free-living nematodes in NTLM systems (Treonis et al., 2010; Ito et al., 2015; Sun et al., 2023). In particular, fungal communities are highly sensitive to the mechanical breaking of their hyphae during soil tillage (Roger-Estrade et al., 2010; Ryan and Graham, 2018), likely resulting in negative bottom-up impacts on fungal-feeders, but also through indirect effects on mycorrhizal fungi and their effects on soil-plant interactions (Kabir, 2005). This assumption is reinforced by the additional negative impact of weeding on the abundance of fungal-feeders in the no-till systems (−66 %, Fig. 1), which also exert a physical disturbance during the operation, although of a lesser strength than tillage. On the contrary, the increase of omnivores and predators in NTLM may be due to the rise in the abundance of their preys, a bottom-up effect, as suggested by the positive correlation of this group with both microbial-feeders and free-living nematodes (Fig. 2a, b), but also to their high sensitivity to physical disturbance. Omnivores and predators may be more sensitive to tillage than microbial-feeders (Puissant et al., 2021; Betancur-Corredor et al., 2022), due to their bigger size among nematode taxa (Kladivko, 2001; Postma-Blaauw et al., 2010). Considering the role of predation played by these large nematodes on species that are parasitic on plants, it is likely that the suppressive capacity of the soils under NTLM will increase in the long term (Sánchez-Moreno and Ferris, 2007; Steel and Ferris, 2016).

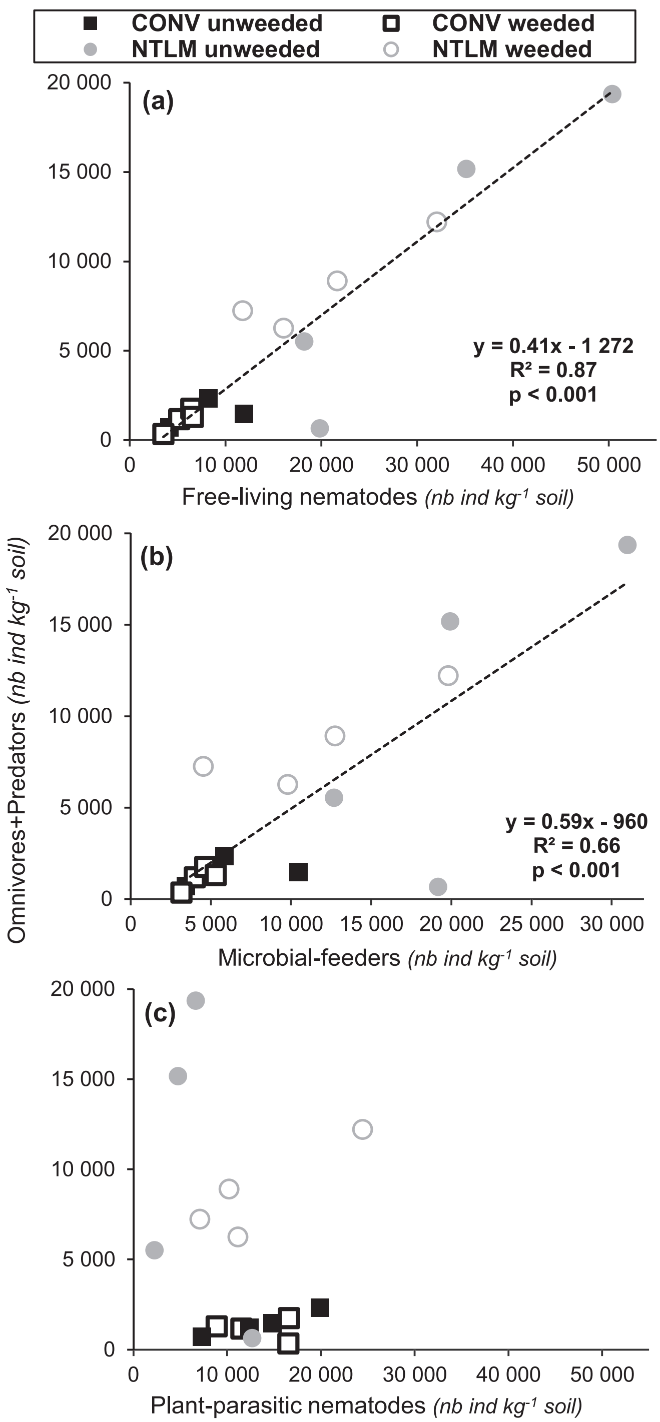

Fig. 2. Correlations between nematode omnivores and predators' abundance with the abundance of (a) free-living nematodes, (b) nematode microbial-feeders, and (c) plant-parasitic nematodes.

However, the abundance of plant-parasitic nematodes did not differ between the CONV and the NTLM systems (Fig. 1). While tillage management does not have clear trends on plant-parasitic nematodes (Sun et al., 2023), we expected that the presence of the permanent plant cover in NTLM will favor their development (Puissant et al., 2021). As discussed above, practices promoting omnivores and predators may in turn regulate the abundance of plant-parasitic nematodes (Tabarant et al., 2011), yet the absence of correlations between these two groups (Fig. 2c) suggests otherwise in the case of our study at this sampling date. NTLM plant community composition may have played an important role into the regulation of plant-parasitic nematodes; for instance, a previous trial evidenced lower plant-parasitic nematodes abundance when rainfed rice was diversified with plant mixtures including legume species (Ripoche et al., 2021). In line with this assumption, plant-parasitic communities presented contrasted composition between the CONV systems (weeded and unweeded), dominated by *endo*-migratory nematodes (83 ± 7 % of the plant-parasites), the weeded NTLM system, dominated by semi-endoparasitic nematodes (75 ± 5 % of the plant-parasites), and the unweeded NTLM system, presenting an equal proportion of the four groups of parasites studied (RA, EC, SE and EM, Supplementary Fig. S1). These differences could be linked to their contrasted weed community's composition, as Rafenomanjato et al. (2023) evidenced a shift between weeds dominated by grass species in CONV toward a dominance of broad-leaved species in NTLM systems. On a lesser note, tillage absence may also have favored the semi-endo, ectoparasitic and root-associated nematodes in the NTLM systems because of their higher sensitivity to physical disturbance due to their different life strategies, as a longer time of their life cycle occurs outside of plant roots.

We conclude that NTLM under this specific context can effectively enhance soil fertility without increasing plant-parasitic pressure, both important aspects to consider for cropping systems sustainability. While increased biological fertility thanks to permanent soil cover and organic mulch is expected from conservation agriculture systems, parasitic pressure is often more uncertain, and in our case appears to depend more on the nature of the living cover used than the absence of tillage or weeding management. These findings strongly encourage to focus more on the impacts of plant communities' composition – and agroecosystem diversification – on nematode plant parasitic pressures, which are less studied than free-living nematodes in this area due to strong soil fertility deficiency.

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CRediT authorship contribution statement

Marie Sauvadet: Writing – review & editing, Writing – original draft, Visualization, Validation, Formal analysis. **Patrice Autfray:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Antsa Rafenomanjato:** Writing – review & editing, Methodology, Investigation. **Aude Ripoche:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Jean Trap:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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