



Effects of agricultural systems on ant diversity (Hymenoptera: Formicidae) in Central Morocco

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Key words. Ants, agricultural ecosystems, organic farming, traditional agriculture, conventional farming, bioindicators

Abstract. Ants are essential components of ecosystems, playing critical roles in nutrient cycling, pest control, and soil health. Agricultural practices significantly influence ant biodiversity, yet studies on this subject remain scarce in Morocco. This study examines the impact of three agricultural systems on ant diversity in Central Morocco: conventional (monoculture with intensive pesticide use), organic (no synthetic inputs and crop diversification), and traditional (low-input polyculture based on local practices), focusing on El Jadida and El Oualidia provinces. Using pitfall traps, a total of 1823 ants belonging to 4 subfamilies, 14 genera, and 21 species were sampled across the three systems. Organic agriculture exhibited the highest species richness (17 species; relative abundances dominated by *Tetramorium caldarium* and *Paratrechina longicornis*), and the highest Shannon diversity index, followed by traditional agriculture (11 species) and conventional agriculture (8 species). PERMANOVA and IndVal analyses revealed significant differences in species composition, with organic and traditional systems fostering distinct communities compared to conventional agriculture. Linear Discriminant Analysis highlighted clear separations among systems, reflecting the effects of habitat heterogeneity and management practices. The study underscores the ecological importance of organic and traditional practices in supporting ant biodiversity and calls for sustainable agricultural management to limit the negative impacts of biodiversity loss and homogenisation caused by conventional farming.

INTRODUCTION

Ants play a crucial role in ecosystems as pollinators, decomposers, and predators (Parr et al., 2016). They also improve soil structure, promote nutrient cycling, and help control pests (Agosti et al., 2000). Various agricultural practices, including monocultures, traditional agriculture, and organic farming, can influence ant diversity in different ways (Bos et al., 2007). However, agricultural intensification, characterised by crop monocultures, extensive soil disruption, and pesticide use, is associated with landscape simplification and biodiversity loss (Matson et al., 1997; Tilman et al., 2001). This phenomenon ultimately reduces the provisioning of essential ecosystem services, affecting agricultural sustainability (Tscharntke et al., 2005; Bianchi et al., 2006; Duru et al., 2017). The decline in biodiversity can be attributed to the homogenisation of habitats and the narrowing of available food resources, subsequently facilitating the prevalence of only a select few species with heightened adaptability or resistance (Baudron, 2011). On the other hand, more diversified agricultural systems,

such as traditional agriculture and organic farming, tend to promote higher ant diversity and evenness (Perfecto et al., 2014; Hevia et al., 2018). However, the effects on biodiversity also depend on crop type and habitat complexity, as some conventional agroforestry systems with high structural complexity can support greater arthropod diversity than organic monocultures with lower aboveground biomass (Tscharntke et al., 2011; Hevia et al., 2018).

Agriculture in Morocco is distributed across five major agroecosystems: mountains, favourable plains and hills, semi-arid and arid plains and plateaus, extensive irrigation areas, and pre-Saharan and Saharan regions, which together cover approximately 8.8 million hectares, or about 18% of the country's total area (Harbouze et al., 2019; Houssni et al., 2022). About 1.4 million hectares (15% of the total area) can be irrigated, while the remainder consists of rain-fed land, also referred to as “bour land” – a Moroccan term describing non-irrigated agricultural land that relies solely on rainfall. In this study, we classify agricultural systems into three main categories: traditional or subsistence agri-

culture, organic agriculture, and conventional agriculture. This classification considers the environmental impact and sustainability of the farming practices used. Additionally, it is important to note that the differences between these systems can vary significantly depending on the types of crops being cultivated.

Traditional agrosystems in Morocco predominantly consist of small family farms located in mountainous regions. These farms engage in subsistence agriculture and livestock farming, utilizing traditional techniques and extensive breeding, primarily of sheep and goats. They cultivate diverse crops, operate on small land holdings, and use local varieties with low yields (Ater & Hmimsa, 2008). Organic farming is a mode of agricultural production that excludes the use of synthetic substances such as chemical pesticides, synthetic fertilisers, genetically modified organisms (GMOs), and synthetic veterinary drugs (Gomiero et al., 2011). This production system was introduced in Morocco around 1990 and has since gained traction, particularly under the framework of the Green Morocco Plan (Sedraoui et al., 2011; El Bilali et al., 2021). It aims to promote environmentally friendly practices and sustainable agriculture. The expansion of organic farming in Morocco is part of a national strategy to enhance the value of agricultural products, especially those that are local and certified organic (Harbouze et al., 2019).

Conventional agriculture is the most widely practiced agricultural system in Morocco and globally (Mrabet et al., 2012). This system typically involves the use of synthetic fertilisers, pesticides, and genetically modified organisms to maximise crop yields and efficiency (Prusak et al., 2014). In conventional agriculture, farmers apply various synthetic chemicals, including fertilisers, herbicides, and pesticides, to manage crop diseases and control insect pests, thus enhancing crop yields and ensuring production efficiency (Sumberg & Giller, 2022).

Numerous global studies indicate that agricultural intensification typically reduces ant diversity and alters community composition (Andersen, 2000; Bestelmeyer & Wiens, 2001; Gibb & Parr, 2010). In Morocco, agricultural landscapes include diverse agroecosystems, traditional farming methods, and distinct climatic conditions (Zina et al., 2022), which may influence these global patterns. This diversity makes Morocco a particularly relevant setting to investigate how different agricultural systems might affect ant diversity and community structure.

Agricultural practices significantly impact ant diversity and ecosystem health. Studies across continents have shown that intensive farming often reduces ant species richness and abundance by altering habitat structure and resource availability (Gibb & Parr, 2010). For example, in Costa Rica, ground-foraging ant diversity declined in coffee plantations with reduced vegetational complexity, although ant diversity on coffee bushes remained unchanged (Perfecto & Snelling, 1995). In Sudan, soybean monocultures reduced ant diversity and threatened rare species, while organic farms supported up to 61% of native ant species compared to just 17% in monocultures (Eisawi et al.,

2022). Similarly, in Indonesia, organic maize farms hosted greater ant diversity than conventional farms, with *Odon-toponera* sp. emerging as a bioindicator of agroecosystem health (Widhiono et al., 2017). In the Moroccan context, Houssni et al. (2022) found that conventional farming in the Middle Atlas significantly decreased ant diversity, likely due to habitat simplification and loss of vegetative cover. These findings collectively emphasise the global and regional need to adopt biodiversity-friendly practices in agrosystems to preserve ant communities and sustain ecosystem functioning.

The aim of this study is to assess the impact of different farming systems on ant diversity in Central Morocco, through a preliminary investigation conducted in the provinces of El Jadida and El Oualidia. Based on existing research showing that reduced synthetic chemical inputs and more complex habitat structure in low-input agroecosystems support greater ant diversity (Helms et al., 2021; De Souza-Campana et al., 2022; Estrada et al., 2023), we hypothesise that ant diversity will be higher in organic and traditional systems compared to conventional ones. This study was conducted in fields cultivating a variety of annual vegetable crops, including zucchini, tomato, and pepper, grown under the three farming systems: conventional, traditional, and organic. These diverse agroecosystems provide a valuable context to evaluate how different agricultural practices affect ant diversity in Central Morocco.

MATERIAL AND METHODS

Study sites

We conducted the research across five distinct locations within the El Jadida region (33°15'N, 8°30'W), each representing a different farming method (Fig. 1). Surveys were conducted in conventional, traditional, and organic fields cultivating mostly annual vegetable crops such as zucchini, tomato, and pepper. Each agricultural system included two replicated fields, where pitfall traps were installed and monitored between April and June 2022 for a duration of six weeks. The conventional system consisted of fields covering ca. 4 ha, primarily used for monoculture and irrigated through drip or gravity systems, with moderate to high pesticide input. The traditional system consisted of fields of ca. 3 ha, characterised by minimal to moderate pesticide use and diversified cropping practices. Finally, the organic system comprised ca. 15 ha, managed under polyculture with drip irrigation and no synthetic pesticide applications. These fields were primarily used for monoculture and irrigated using either drip irrigation, which is a system that delivers water directly to plant roots through tubes, or gravity irrigation, which relies on water flowing naturally from a higher source. Pesticides were applied with moderate to high intensity, meaning application occurred more than once per crop cycle, with high doses and a broader spectrum of active ingredients. The conventional system consisted of fields covering ca. 4 ha, primarily used for monoculture and irrigated through drip or gravity systems, with moderate to high pesticide input. The traditional system consisted of fields spanning 3.6 ha, also using drip or gravity irrigation, characterised by minimal to moderate pesticide use (one or two applications per crop cycle with relatively lower doses and a narrower range of products). Lastly, the organic farms covered 15.1 ha, exclusively irrigated via the drip technique, with no synthetic pesticides and practicing polyculture, cultivating multiple vegetable crops simultaneously to en-

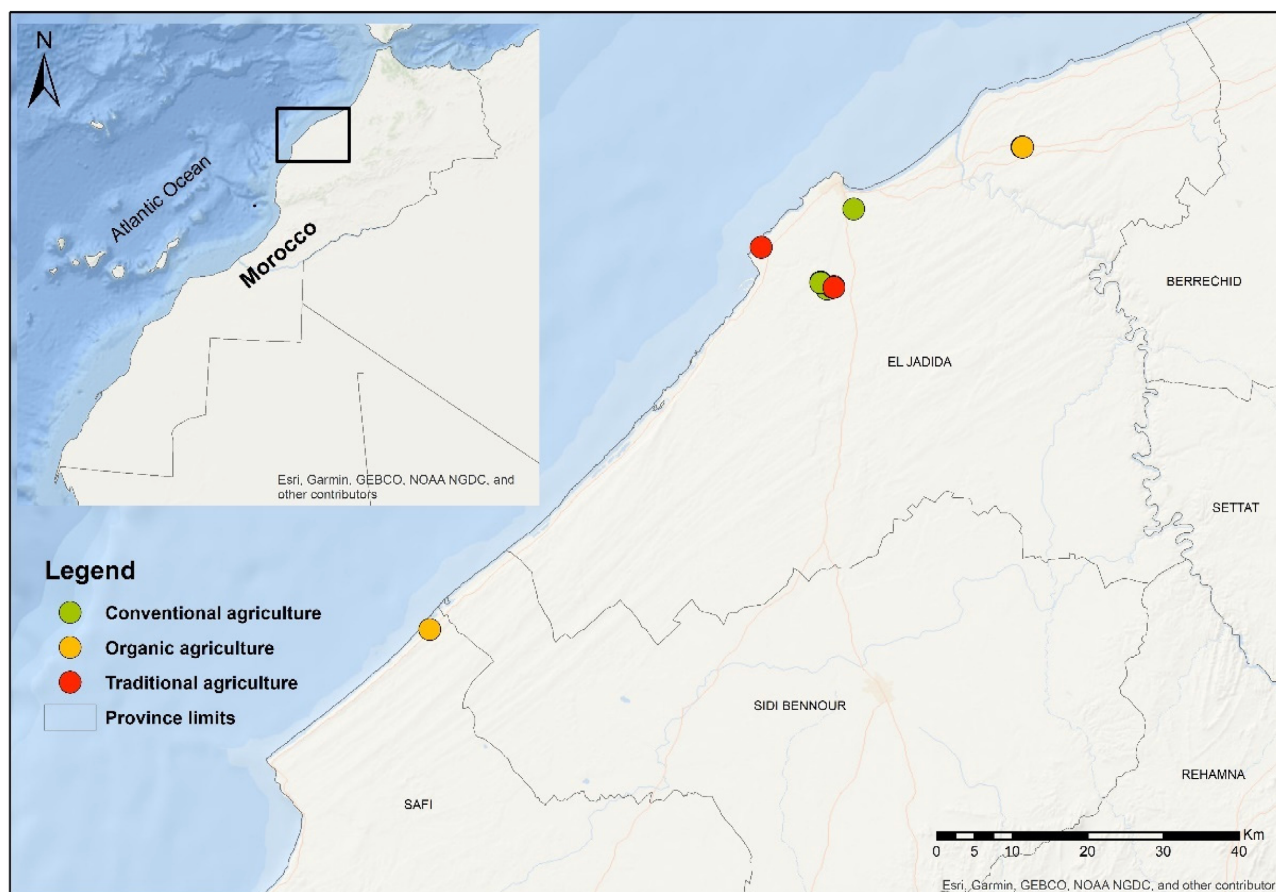


Fig. 1. Geographical location of the study area.

hance biodiversity and reduce pest pressure. Each site comprised several agricultural fields. Although the total field areas differ, the sampling effort via pitfall traps was standardised across all fields to allow comparable biodiversity assessments. Detailed information about these locations and crops is available in the Table S1.

Sampling method

Ant sampling method was conducted using ground pitfall traps (Agosti et al., 2000; Sankovitz et al., 2024). These traps offer ease of operation and demonstrate the ability to capture a broad spectrum of myrmecofauna, making them highly suitable for conducting comparative analyses across diverse ecological settings. This technique has been employed in other similar research examining the interactions between ants and agricultural systems, such as Underwood & Fisher (2006), De Bruyn (1999) and Philpott et al. (2009). The pitfall traps we used were 150 cm³ plastic containers, with a diameter of 5.5 cm and a depth of 7 cm. We filled them to 75% of their capacity with a detergent-based mixture (Fairy® detergent diluted with salt and water). The traps were then embedded into the soil to ensure they were flush with the surface, preventing insects from walking around the traps due to gaps in the soil. The experimental protocol stipulated that the traps remain deployed for a period of 24 h (Agosti et al., 2000). We placed 10 pitfall traps arranged in a straight line, spaced 10 m apart, covering a total length of 100 m. The transect was positioned at a 30° angle relative to the field boundary (Fig. S1). A total of 60 pitfall traps were used across all fields.

Data analysis

To analyse and compare ant diversity across the three agricultural systems (Table 1), we calculated species richness (the

total number of species), relative abundance (the proportion of individuals per species), and the Shannon diversity index (which accounts for both species richness and evenness) for each system (Magurran, 2013). We also plotted rarefaction curves (Fig. 2) to assess sampling effort and constructed boxplots to illustrate variation in abundance (Fig. 3) and Shannon index (Fig. 4) values among the systems. To test for statistically significant differences in Shannon diversity between systems, we used Hutcheson's t-test, which compares Shannon indices while accounting for sample size (Zar, 1999), implemented in R using the *ecolTest* package. Species composition differences were tested using PERMANOVA, a non-parametric multivariate variance analysis based on Bray-Curtis distances (Anderson, 2001). Indicator species analysis (IndVal; Dufrêne & Legendre, 1997) was performed for each agricultural system (formerly called "field type" for consistency) to identify species characteristic of specific management practices. Finally, linear discriminant analysis (LDA) was applied to explore how ant species composition differed between systems, highlighting potential bioindicators of agricultural practices. Data analyses were conducted using R software version 4.4.0 (R Core Team, 2024), and IndVal analyses were performed with PAST software version 4.16 (Hammer et al., 2001).

The analytical framework adopted in this study was designed to match the scale and structure of the data. Given the balanced sampling effort and the independence of transects across agricultural systems, univariate diversity metrics were compared using Hutcheson's t-test, which adequately accounts for sample size effects on Shannon indices. More complex mixed models were not required, as the main objective was to characterise overall patterns of alpha- and beta-diversity rather than to model nested random effects.

Table 1. Species captured in the prospected sites: Organic Agriculture (OA), Conventional Agricultural (CA), Traditional Agricultural (TA), Total number of individuals (N), Relative abundances (RA), and Invasive alien species (*).

Species	OA		CA		TA	
	N	RA %	N	RA %	N	RA %
<i>Aphaenogaster senilis</i> Mayr, 1853	64	6.72	0	0	10	1.48
<i>Camponotus spissinodis</i> Forel, 1909	0	0	0	0	1	0.15
<i>Cardiocandyla mauritanica</i> Forel, 1890	71	7.45	0	0	0	0
<i>Cataglyphis theryi</i> Santschi, 1921	2	0.21	0	0	0	0
<i>Cataglyphis otini</i> Santschi, 1929	1	0.10	0	0	0	0
<i>Cataglyphis vaucheri</i> (Emery, 1906)	34	3.57	6	3.11	0	0
<i>Cataglyphis viatica</i> (Fabricius, 1787)	75	7.87	0	0	0	0
<i>Crematogaster auberti</i> Emery, 1869	2	0.21	0	0	0	0
<i>Dorylus fulvus</i> (Westwood, 1839)	1	0.10	0	0	0	0
<i>Lasius grandis</i> Forel, 1909	18	1.89	1	0.52	38	5.61
<i>Messor barbarus</i> (Linnaeus, 1767)	0	0.00	39	20.21	126	18.61
<i>Messor foreli</i> Santschi, 1923	3	0.31	0	0	0	0
<i>Messor maroccanus</i> Santschi, 1927	3	0.31	16	8.29	1	0.15
<i>Monomorium salomonis</i> (Linnaeus, 1758)	201	21.09	63	32.64	35	5.17
<i>Monomorium subopacum</i> (Smaaihi, F., 1858)	17	1.78	0	0	0	0
* <i>Nylanderia jaegerskioeldi</i> (Mayr, 1904)	9	0.94	0	0	1	0.15
* <i>Paratrechina longicornis</i> (Latreille, 1802)	158	16.58	0	0	136	20.09
<i>Pheidole pallidula</i> (Nylander, 1849)	0	0	0	0	30	4.43
<i>Tapinoma simrothi</i> Krausse, 1911	25	2.62	48	24.87	229	33.83
<i>Tetramorium alternans</i> Santschi, 1929	27	2.83	20	10.36	70	10.34
* <i>Tetramorium caldarium</i> (Roger, 1857)	242	25.39	0	0	0	0

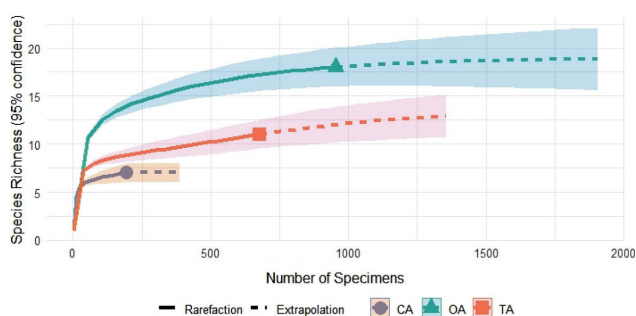
RESULTS

A total of 1,823 ant workers were collected across the studied agricultural systems, representing 4 subfamilies, 14 genera, and 21 species (Table 1). *Myrmicinae* was the most dominant subfamily, with 7 genera and 11 species, followed by *Formicinae* with 4 genera and 7 species. *Dolichoderinae* and *Dorylinae* were the least represented, each comprising a single genus and species. Organic farming hosted the highest number of species (17), followed by traditional agriculture (11), and conventional farming with only 8 species. Notably, no species were found exclusively in conventional agriculture – its species were all shared with at least one of the other systems. In contrast, 51% of the species recorded in organic fields were unique to that system.

Before 2021, the *Formicidae* catalogue of the El-Jadi-da region included only seven species: *Dorylus fulvus* (Westwood, 1839), *Aphaenogaster theryi* Santschi, 1923, *Linepithema humile* (Mayr, 1868), *Tetramorium bicarinatum* (Nylander, 1846), *T. caldarium*, *P. longicornis*, and *Cataglyphis vaucheri* (Emery, 1906) (Cagniant, 2006, 2009; Taheri & Reyes-López, 2018). This study has enriched the catalogue with 18 new species, raising the total to 25 species in the province. Of the seven species previously recorded, only *D. fulvus*, *C. vaucheri*, and *P. longicornis* were captured in this study.

The analysis of the relative abundance of the 21 recorded *Formicidae* species across the three agricultural systems (Table 1) revealed clear dominance patterns. In organic fields, *Tetramorium caldarium* (Roger, 1857) was the most abundant, accounting for 25.31%, followed by *Monomorium salomonis* (Linnaeus, 1758) with 20.09%, and *Paratrechina longicornis* (Latreille, 1802) at 16.58%. In traditional fields, *Tapinoma simrothi* Krausse, 1911 ranked first with 229 individuals (33.83%), followed by *P. longicornis*

(20.09%) and *Messor barbarus* (Linnaeus, 1767) with 18.61%. In conventional fields, *M. salomonis* dominated (32.64%), followed by *T. simrothi* (24.87%) and *M. barbarus* (20.21%). These patterns are visually summarised in Fig. 3 through a boxplot showing the distribution of relative abundances by agricultural system. Notably, three invasive alien ant species were found exclusively in organic and traditional systems: *Nylanderia jaegerskioeldi* (Mayr, 1904), *P. longicornis*, and *T. caldarium*, and were absent in conventional fields. The analysis of the cumulative species richness rarefaction curve (Fig. 2) indicated adequate sampling effort across the three agricultural systems: organic (OA), traditional (TA), and conventional (CA). The curve also revealed clear differences in species richness: the OA system exhibited the highest cumulative richness (17 spp.), followed by the TA system (11 spp.), and finally the CA system (8 spp.). This confirms that OA supports the richest species pool, although it does not account for how evenly those species are distributed. Regarding species abundance, the box plot (Fig. 3) illustrates marked differences among the systems. The abundance values were standard-

**Fig. 2.** Rarefaction curves of ant species across different agricultural systems. OA – Organic Farming, TA – Traditional Agriculture, and CA – Conventional Agriculture.

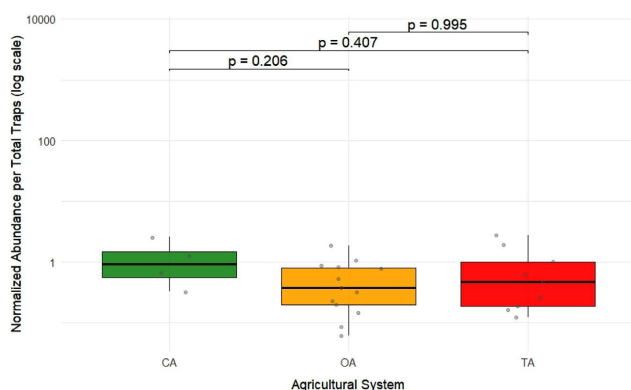


Fig. 3. Normalized ant abundance per total traps across agricultural systems (CA, OA, TA), on a logarithmic scale. Median values are shown with boxplots ($IQR \pm 1.5 \times IQR$), and individual transect data are represented as grey dots. No significant differences were detected (Kruskal-Wallis, $p > 0.05$); post-hoc Dunn's tests with Bonferroni correction are indicated.

ised based on the total number of traps in each system and plotted on a logarithmic scale to improve visual clarity. The CA system displayed the highest median abundance, followed by the OA system. The TA system showed a median abundance similar to that of the OA system but with greater variability. It is worth noting that while cumulative species richness was highest in OA, the median Shannon diversity index (representing species evenness) was highest in CA (Fig. 4), suggesting a more uniform distribution of individuals across species in conventional fields.

The boxplots (Fig. 4) show that the Shannon diversity index is highest in CA, followed by OA, and lowest in TA. These values describe how evenly ant individuals are distributed among species within each system, with higher values reflecting more even communities. However, Shannon diversity is a measure of alpha diversity; it does not capture variability across transects (i.e., beta diversity), which was not the focus of this analysis. OA exhibits slightly lower median Shannon diversity but higher variability, while TA displays both the lowest median and greatest variation. To statistically compare the Shannon diversity index between systems, Hutcheson's t-test was applied (though not shown in the Methods, this should be added). The test revealed significant differences between all three systems: CA had significantly higher Shannon diversity than TA ($p = 0.007$), while OA differed significantly from both systems CA ($p < 0.001$) and TA ($p < 0.001$). Although CA exhibited the highest median Shannon index, the rarefaction analysis (Fig. 2) confirmed that OA had the highest species richness. These differences highlight how diversity indices and species richness may capture different aspects of community composition.

A PERMANOVA analysis based on a Bray-Curtis distance matrix revealed significant differences in the composition of ant communities among the three agricultural systems: organic (OA), conventional (CA), and traditional (TA) ($F = 3.16$, $p = 0.001$). This variation, explaining 21.54% of the model, highlights the influence of agricultural practices on ant community structure. Complementing this, the IndVal analysis identified species significantly

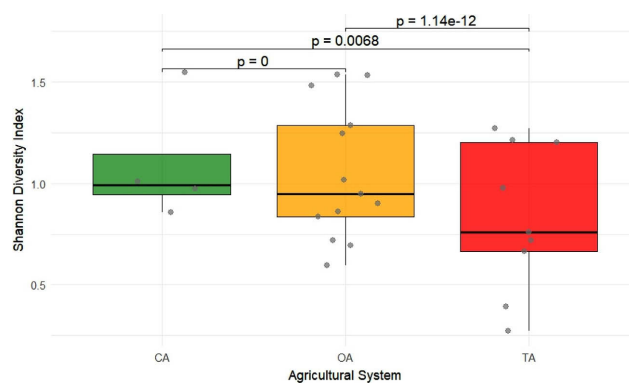


Fig. 4. Shannon diversity index of ant communities across the three agricultural systems studied: conventional (CA), organic (OA), and traditional (TA). Boxplots display the distribution of Shannon diversity values per transect. Each box represents the interquartile range (IQR), with the horizontal line indicating the median; whiskers extend to the minimum and maximum values excluding outliers. Black dots represent individual transect-level observations (raw data). Pairwise comparisons were assessed using Hutcheson's t-test; t and p-values are shown on the graph. Significant differences were found between all systems (CA vs. OA: $t = 5.32$, $p < 0.0001$; CA vs. TA: $t = 3.14$, $p = 0.0068$; OA vs. TA: $t = 7.11$, $p < 0.0001$).

associated with the agricultural systems (Fig. 5): *Cataglyphis viatica* with OA (IndVal = 0.734, $p = 0.045$), *Pheidole pallidula* with TA (IndVal = 0.882, $p = 0.005$), and *Tapinoma simrothi* with both CA and TA (IndVal = 0.975, $p = 0.005$). No species were significantly associated with CA.

The results of the Linear Discriminant Analysis reveal a clear and statistically significant separation of ant communities among the three agricultural systems. The low Wilks' Lambda value ($\lambda = 6.76 \times 10^{-5}$) and highly significant p-value ($p = 5.56 \times 10^{-7}$) indicate substantial differences in species composition between the groups. Although the low Wilks' Lambda value indicates a strong group separation, this Linear Discriminant Analysis was used as an explora-

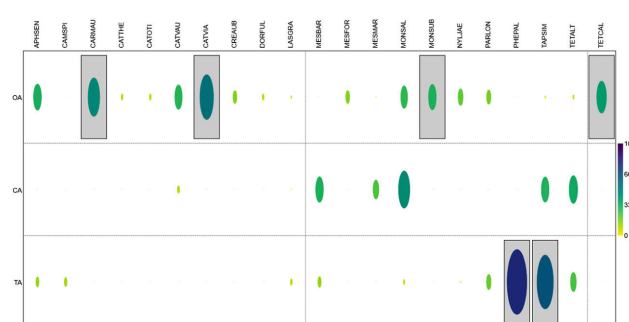


Fig. 5. IndVal analysis unveiling systems specific ant communities in three studied agricultural systems: OA – Organic Farming, TA – Traditional Agriculture, and CA – Conventional Agriculture. $p < 0.05$ boxed. Species abbreviations – APHSEN: *Aphaenogaster senilis*, CAMSPI: *Camponotus spissinodis*, CARMAU: *Cardiocondyla mauritanica*, CATTHE: *Cataglyphis theryi*, CATOTI: *Cataglyphis otini*, CATVAU: *Cataglyphis vaucheri*, CATVIA: *Cataglyphis viatica*, CREAUB: *Crematogaster auberti*, DORFUL: *Dorylus fulvus*, LASGRA: *Lasius grandis*, MESBAR: *Messor barbarus*, MESFOR: *Messor foreli*, MESMAR: *Messor maroccanus*, MONSAL: *Monomorium salomonis*, MONSUB: *Monomorium subopacum*, NYLJAE: *Nylanderia jaegerskioeldi*, PARLON: *Paratrechina longicornis*, PHEPAL: *Pheidole pallidula*, TAPSIMR: *Tapinoma simrothi*, TETALT: *Tetramorium alternans*, TETCAL: *Tetramorium caldarium*.

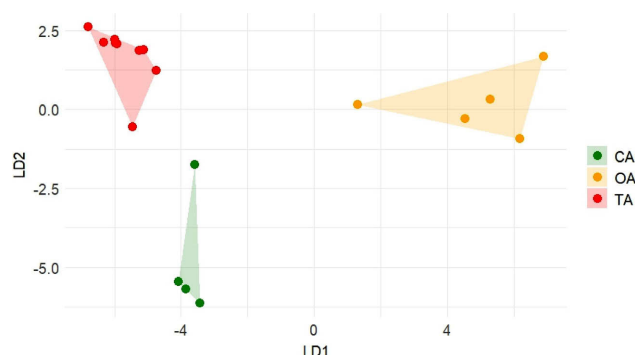


Fig. 6. Linear Discriminant Analysis (LDA) of log-transformed ant species assemblages across the three studied agricultural systems: OA (Organic Farming), TA (Traditional Agriculture), and CA (Conventional Agriculture). Convex polygons represent group clustering. The analysis reveals a clear separation between systems (Wilks' Lambda = 6.76×10^{-5} ; $p = 5.56 \times 10^{-7}$).

tory tool to visualise compositional patterns already supported by PERMANOVA. Given the ratio between the number of species and samples, the results should be interpreted with caution. The graphical representation (Fig. 6) shows distinct, non-overlapping clusters for each system, confirming that the ant communities associated with conventional (CA), traditional (TA), and organic (OA) agriculture are compositionally distinct. This distinct clustering means that each agricultural system hosts a unique ant community, with little species composition overlap, highlighting the strong influence of agricultural management on community structure. The separation suggests that differences in farming practices create environmental conditions favouring particular ant assemblages, which could serve as bioindicators of agricultural impact. Rather than emphasizing axis directionality, we note that the lack of overlap across the three groups along the discriminant axes reflects strong ecological separation in community structure.

DISCUSSION

This study considerably enriched the Formicidae catalogue of the El Jadida region, increasing the number of recorded species from 7 to 25. Interestingly, only 3 of the 7 previously reported species were recorded in our study, indicating notable changes in community composition. Among the newly recorded taxa, we found three exotic species: *Nylanderia jaegerskioeldi*, *Paratrechina longicornis*, and *Tetramorium caldarium*. These species were previously documented primarily in parks and public gardens (Taheri & Reyes-López, 2018), and their presence in traditional and organic farms may reflect increased connectivity or dispersal from nearby human-influenced habitats. Although distance from human settlements was not measured in this study, the detection of exotic species in less intensively managed systems raises questions about the role of landscape context and anthropogenic pressures in shaping ant communities. Human activities and land-use patterns are known to facilitate the spread of non-native

species, as noted in the studies by Didham et al. (2005) and Perfecto & Vandermeer (2008). Future research could further clarify these patterns by incorporating spatial data.

Our findings reinforce the ecological importance of ant communities in agricultural ecosystems, particularly their roles in pest regulation and maintaining biodiversity, as noted by previous studies (Drummond & Choate, 2011; Martínez-Núñez et al., 2021). The observed decline in Formicidae diversity from organic crops (17 species, $H' = 2.13$) to traditional (11 species, $H' = 1.78$) and conventional systems (8 species, $H' = 1.61$) supports evidence that land use and management practices directly influence ant foraging behaviour and community composition (Curry et al., 2023). Conventional agricultural systems are expected to have the lowest ant diversity due to factors such as intensive chemical use (pesticides and fertilisers), frequent soil disturbance (e.g., tillage), habitat simplification, and reduced vegetation cover, and our findings align with this expectation. These changes likely reflect the sensitivity of ant communities to habitat structure. Furthermore, the presence of functionally diverse ants across systems may enhance nutrient cycling and soil structure through organic matter redistribution, contributing to improved plant health (Griffiths et al., 2018). The observed decline in diversity may be attributed to specific factors, including soil compaction and fertility, vegetation cover and heterogeneity, the frequency and intensity of tillage, and the application of synthetic inputs such as pesticides and fertilisers (Andersen, 2000). Moreover, previous studies have shown that organic farming, through reduced agrochemical inputs and enhanced plant diversity, promotes more stable and diverse ant assemblages (Helms et al., 2021). The higher species richness and diversity indices observed in organic crops compared to traditional and conventional systems highlight the positive influence of organic practices on ant communities. These findings are consistent with previous studies demonstrating that organic farming promotes greater ant diversity due to the use of organic fertilisers, increased vegetation complexity, and reduced pesticide application (Helms et al., 2021). Such patterns also support Andersen's (2000) framework, which emphasises the role of environmental and management-related factors: such as soil characteristics and disturbance regimes, in shaping ant assemblages. While traditional systems are often thought to support ant diversity due to lower disturbance (Helms et al., 2021), our cumulative species richness data showed fewer species in traditional crops compared to organic systems. This result may reflect factors such as inconsistent management and the use of pesticides (Dudley & Alexander, 2017). Although conventional agriculture showed high Shannon diversity at the replicate level (as seen in Fig. 4), it had the lowest total species richness across all samples. This suggests that despite locally diverse communities, the overall community was more homogeneous and possibly dominated by a few adaptable species (Folgarait, 1998). The variation in ant species richness across different agricultural systems highlights the significant impacts of farming practices (Bisseleua et al., 2009). Organic farms, which

minimise or eliminate pesticide use, tend to support more diverse ant communities (Helms et al., 2021). In contrast, conventional and traditional farms that rely heavily on pesticides can harm ant habitats (Badji et al., 2006). Habitat complexity is also vital; organic farms typically offer diverse vegetation and complex structures, which are conducive to a broader range of species (Albrecht et al., 2020; Vandermeer & Perfecto, 2007). Conversely, the simpler environments associated with conventional agriculture restrict species diversity (Meyer, 2013; Albrecht et al., 2020). Habitat fragmentation, prevalent in conventional and traditional fields, further reduces the diversity of available habitats, particularly for ants inhabiting underground colonies (Armbrecht et al., 2006; De La Mora & Philpott, 2010). Soil health and management practices also significantly influence ant diversity. Higher levels of organic matter, food availability, and microbial diversity in organic farming create favourable conditions for diverse ant populations (De La Mora & Philpott, 2010). In contrast, the intensive use of chemical fertilisers in conventional and traditional fields degrades soil quality and diminishes biodiversity (Gabriel et al., 2006; Padmavathy & Poyyamoli, 2013).

Our results highlight a clear spatial separation in ant diversity across the three agricultural systems studied, confirming the influence of agricultural practices on community structure. While cumulative species richness was highest in organic farms, the Shannon diversity index revealed the highest median diversity values in conventional systems (Fig. 4). However, Hutcheson's t-test indicated significant differences in diversity between the systems, suggesting that both species abundance and evenness were influenced by the farming practices. The higher median Shannon index observed in conventional systems likely reflects more even distributions among fewer dominant species, consistent with community homogenisation. These findings align with previous studies suggesting that specific agricultural inputs and habitat structure can shape ant community composition (Henckel et al., 2015; Hamza et al., 2023). The relatively higher species abundance and consistent Shannon diversity observed in conventional systems may be attributed to environmental homogenisation, favouring a few dominant, disturbance-tolerant ant species. In contrast, the variability seen in organic systems suggests that organic practices create more heterogeneous microhabitats, which can support a wider range of ecological niches and transient species dynamics (Philpott et al., 2008). The distinct community structures observed across farming systems, as revealed by PERMANOVA, emphasise how agricultural intensification reshapes species assemblages. These findings underscore the ecological importance of organic management in preserving functional diversity and promoting complex, resilient ant communities in agroecosystems.

The Indicator Species Analysis (IndVal) analysis highlights the ecological value of organic and traditional agricultural systems in supporting unique ant communities, with both benefiting from habitat heterogeneity. Organic systems, in particular, were associated with four indicator species (*C. mauritanica*, *C. viatica*, *M. subopacum*, and *T.*

caldarium), reflecting habitat complexity, environmental quality, and low-input management practices. These species are known to prefer heterogeneous microhabitats and are sensitive to high levels of chemical inputs, which supports their role as indicators of organic agricultural habitats. In contrast, traditional systems were associated with only two more generalist species (*P. pallidula* and *T. simrothi*), reflecting a less diverse but still distinct community. Despite this, traditional systems provide specific microhabitats; such as increased ground vegetation cover, organic residues, and heterogeneous soil structure that support these species, a result of the unique conditions generated by their diversified and low-input practices (Perfecto & Snelling, 1995; Dias et al., 2015; Muhammad et al., 2022; Pushnya et al., 2023). The absence of specialist species in conventional systems reflects the homogenizing effect of intensive practices on landscape structure, which limits ecological niches and reduces community specialisation. These findings emphasise the critical role of diversified agricultural practices, particularly organic and traditional systems, in preserving biodiversity and maintaining ecological functions (Perfecto & Snelling, 1995; Myllemn-gap, 2021; Kurmi et al., 2022).

To further explore how ant communities differ among systems, we used Linear Discriminant Analysis (LDA), a method that separates groups based on their species composition. The LDA showed a clear separation of ant communities linked to different farming practices. The spatial separation of ant communities observed through Linear Discriminant Analysis highlights how distinct management regimes shape community assembly. Organic systems were strongly associated with one axis, indicating that their low-input, biodiversity-friendly management fosters more diverse and specialised communities. Traditional systems separated along another axis, suggesting an intermediate or transitional state, where management practices may not consistently support either native species diversity or stable ant assemblages. Conventional systems clustered separately and negatively, which could reflect more homogenised conditions resulting from intensive practices. However, further analyses are needed to identify the specific ecological drivers behind these patterns. These results underline how farming practices act as ecological filters, favouring ants with specific traits and shaping overall community structure. The presence of invasive alien ant species within organic agricultural systems may confound community patterns, as these species can alternative assemblages and disrupt ecosystem functions. Future studies should consider their influence to better assess the effects of organic management on native ant diversity. This presence of these invasive ants in organic farms may be facilitated by increased habitat heterogeneity and resource availability, which unintentionally provide niches for non-native species to colonise (Suarez et al., 2001; Holway et al., 2002). Invasive ants can outcompete native species, leading to reduced native ant diversity and altered community dynamics (Bertelsmeier et al., 2015). This underscores the importance of monitoring and implementing control

measures to mitigate their impact and preserve local native species diversity in all agricultural systems, including those managed organically.

In conclusion, this study demonstrates that organic and traditional agricultural systems play a crucial role in maintaining higher native ant diversity and more specialised communities compared to conventional systems. At the same time, the presence of invasive alien ant species, particularly within organic systems, poses a significant threat that could compromise these biodiversity benefits. To promote sustainable agricultural landscapes, it is essential to combine biodiversity-friendly farming practices with targeted invasive species management. Such integrated strategies will help preserve native ant diversity and ensure ecological resilience across different agricultural systems.

ACKNOWLEDGEMENTS. We would like to express our gratitude to the companies and farm owners who allowed us to conduct our study on their land. We also thank the CNRST (Morocco) for awarding A. Fernane the Excellence Research PhD-Associate Scholarship as part of their doctoral work at the Faculty of Sciences of El Jadida. We are grateful to two anonymous reviewers whose constructive comments improved the clarity of the manuscript.

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Received December 17, 2024; revised and accepted January 7, 2026
Published online February 3, 2026

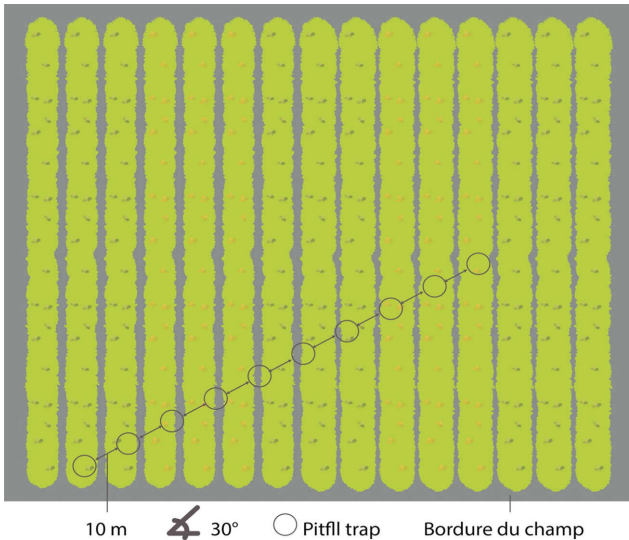


Fig. S1. Sampling plan.

Table S1. Studied agricultural fields.

Province	Site	Geographic coordinates	Sampling date	Farm					
				Traditional	Conventional		Organic		
				N	Farming	N	Farming	N	Farming
El Jadida	Dr krada	33.0737, -8.3106	17/5/2022	1	Corn	5	Corn, potato, tomato, parsley, turnip	—	—
El Jadida	Alentours de la ville	33.1323, -8.2901	17/5/2022	—	—	1	Cucumber	—	—
Azemmour	Sidi Ali Ben Hamdouche	33.1810, -8.1451	23/6/2022	—	—	—	—	8	Cabbage, salad, turnip, zucchini, tomato, corn, cucumber, coriander
El Jadida	Moulay Abdallah Amaghar	33.1027, -8.3647	4/6/2022	9	Parsley, coriander, zucchini, leek, salad, cabbage, radish, corn	—	—	—	—
El Oualidia	El Oualidia	32.4221, -9.0350	5/9/2022	—	—	—	—	6	Salad, passion fruit, tomato, menthe, melissa