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RESEARCH PAPER

Species and functional responses of ants to inter-row tillage and vegetation in organic Mediterranean vineyards

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Abstract

Ants are arthropods providing crucial ecosystem services such as soil structuring, nutrient cycling, seed dispersal and pest predation. Thus, their abundance and diversity need to be considered in approaches to improve sustainability of land use such as Mediterranean viticulture. In our study, we tested whether (1) inter-row vegetation and the absence of tillage increase the species richness and/or functional diversity of ants in vineyards and (2) ground cover vegetation drives ant species composition. We included 23 Mediterranean organic vineyards in our analyses and distinguished three types of inter-row management: all inter-rows tilled, half of the inter-rows tilled, and all inter-rows are untilled and covered by vegetation. The occurrence of ant species was analysed in six pitfall traps per vineyard. Around each trap, the floristic composition of inter-row vegetation was analysed in 2×2 m^2 plots. We found that inter-row tillage significantly affected ant species richness, being higher in partially than in fully tilled vineyards whereas untilled vineyards were not different from the other tillage types. Grass cover and the perennial/annual rate were positively correlated with ant species richness. Ant functional diversity and the frequency of most predatory ants were not correlated neither with plant functional groups nor with tillage type. In conclusion, ant communities benefit from inter-row vegetation and/or absence of soil disturbance but partial inter-row tillage of vineyards may be tolerated and even benefit several species. In particular, grasses and perennial plant species favour ants in our system and need to be considered in inter-row sowing.

Keywords: Ants, Agroecology; Community ecology; Functional traits

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Introduction

Agricultural intensification has resulted in a loss of biodiversity and related ecosystem services. This loss of ecosystem services is often compensated by an increased use of agrochemicals such as pesticides. Approaches to improve the sustainability of agriculture need thus to consider biodiversity and ecosystem services (Tscharntke et al., 2012). Invertebrates are key organisms that provide services in agroecosystems (Saunders, 2018). They contribute to the decomposition of organic matter (Bagyaraj, Nethravathi & Nitin, 2016), to the improvement of soil porosity, mineralisation and aeration (Culliney, 2013), to pollination (Ollerton, Winfree & Tarrant, 2011) and to biological pest control (Flint, Dreistadt & Clark, 1998). The restoration of invertebrate habitats in field margins and/or within fields is increasingly advocated as a measure to improve ecosystem services (Cahenzli et al., 2019).

In perennial crops such as vineyards, the restoration or creation of inter-row vegetation may contribute to the

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improvement of invertebrate habitats (Blaise et al., 2022; Carpio, Castro & Tortosa, 2019). Inter-row vegetation is known to provide habitat functions to pollinators and predators of pest insects and to improve soil structure (Holland, 2004; Klein et al., 2012; Pollier, Guillomo, Tricault, Plantegenest & Bischoff, 2018). Furthermore, non-crop vegetation of inter-rows may attract alternative prey required to maintain pest predator populations in agroecosystems (Bischoff et al., 2016; Griffiths, Holland, Bailey & Thomas, 2008). Flowering plants are key components of non-crop habitats providing resources (pollen and nectar) to several arthropod groups (Blaise et al., 2022; Puig-Montserrat et al., 2017; Rusch, Beaumelle, Giffard & Alonso Ugaglia, 2021). Inter-row vegetation also reduces soil erosion, the impact of agricultural machinery, and may be beneficial to ground- and canopy-dwelling arthropods (Blaise et al., 2022; Chen, Li, Xiao, Ning & Tang, 2021; Winter et al., 2018). Despite these multiple services provided by inter-row vegetation, winegrowers in the French Mediterranean are still reluctant to adopt this practice because of competition for water. However, in contrast to annual crops, in which crop plants are in strong competition with non-crop species (Schenk & Jackson, 2002), grapevine may tolerate inter-row vegetation due to its deeper root system (Winter et al., 2018).

Ants are arthropods that benefit from both resources of inter-row vegetation and the absence of soil tillage (Blaise et al., 2021). They participate in soil structuring (Cammeraat & Risch, 2008) and nutrient recycling (De Almeida et al., 2020) by nest building and caring. A high diversity of ant species may improve soil porosity because different ant species build their nests in soil layers of different depth. By foraging, ants also contribute to the dispersal of plant species (Arnan, Molowny-Horas, Rodrigo & Retana, 2012). This is particularly true for granivorous ants that have been recently described as ecosystem engineers with major effects on soil chemistry, above- and below-ground fauna and vegetation (De Almeida et al., 2020). Granivorous ants improve soil fertility, increase and diversify the soil seed bank and increase plant biomass, species richness and spatial heterogeneity (De Almeida et al., 2020). These activities may be important in maintaining a stable level of floristic diversity and thus enhance the stability of ecological niches. Ants further participate in the control of pest insects (Offenberg, 2015). Although often considered as pests due to their mutualistic relationship with aphids (Albert, Franck, Gilles & Plantegenest, 2017) or by reducing the efficiency of biocontrol against mealybugs (Mansour et al., 2012), there is increasing evidence that ants can also contribute to pest regulation, particularly in Mediterranean vineyards (Blaise et al., 2021; Reiff et al., 2021).

As many insects, ants are affected by farming practices. Pesticides were found to have a strong negative effect on alpha and beta diversity of ant communities in Italian vineyards, with a greater ant diversity in organic vineyards (Masoni et al., 2017). Soil mechanical disturbance such as tillage may destroy nests and reduce population densities (Santos, Bischoff & Fernandes, 2018). Predatory ants involved in pest insect regulation do not directly use plant resources but may still depend on vegetation providing alternative prey, while granivorous species of the *Messor* genus, known as key ecosystem engineers in open Mediterranean habitats, may directly benefit from seeds produced by inter-row vegetation. Ants may also benefit from the floral nectar as a nutritional resource (Haber, Frankie, Baker, Baker & Koptur, 1981). Floral resources further indirectly influence ants by favouring prey or honeydew production of aphids often colonising inflorescences (Bischoff & Trémulot, 2011; Goggin, 2007). However, vegetation characteristics do not always affect ant communities, and vegetation effects may be the result of habitat openness effects (Andersen, 2019). Thus, the specific and functional responses of ant communities to soil tillage and inter-row vegetation characteristics in vineyards are still not well known (Chong, Thomson & Hoffmann, 2011; Mugnai et al., 2021).

Using Mediterranean vineyards of the Luberon region as a model system, we analysed interactions between ant communities and inter-row vegetation in addressing the following research questions for the whole ant community and more specifically for ant species that may deliver ecosystem services to the grapevine (predatory and granivorous ants): (1) Do inter-row vegetation and the absence of soil tillage increase the species richness and/or functional diversity of ants in vineyards? (2) Do vegetation characteristics (plant functional groups, diversity, cover) drive ant species composition? We hypothesise that predatory ant species benefit from an increase in prey associated with inter-row vegetation, that granivorous species are directly favoured by resources provided by inter-row vegetation (seeds), and that tillage negatively affects the specific and functional richness of ants.

Materials and methods

Study sites

We analysed 23 organic vineyards in the southern Luberon Mountains, in south-eastern France (Appendix C: Fig. 1). The study area is characterised by a Mediterranean climate, hot and dry summers, mild winters and maximum rainfall in spring and autumn (700 mm per year, 1991−2020, Pertuis meteorological station). Grapevine varieties were Grenache or Syrah. Many vineyards are still under soil tillage to control weeds that are considered strong competitors for water. Partial tillage (half of the inter-rows) is also common whereas no-tillage is rare. Usually, tillage is shallow to 10 cm depth using rotary tillers or harrows. In order to represent the major management types of the study area, we included three types of inter-row tillage in our study: (i) all inter-rows tilled ($N = 7$); (ii) half of the inter-rows tilled, the other half with vegetation cover ($N = 8$); (iii) no tillage and all inter-rows covered by vegetation ($N = 8$). Average tillage frequency of (i) and (ii) was 4 to 5 times a

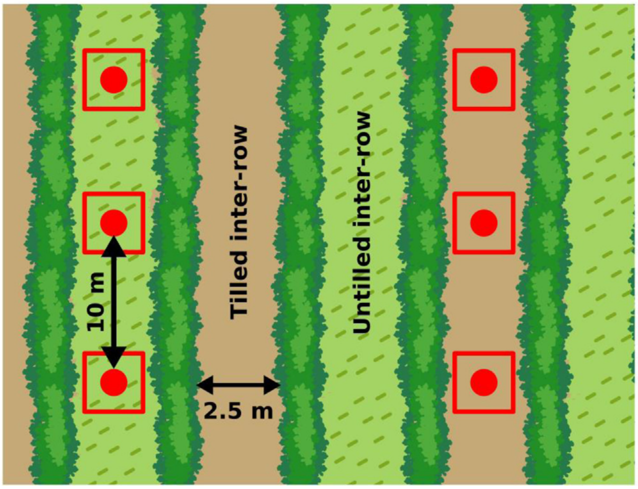

Fig. 1. Experimental design: position of pitfall traps (red spots) and vegetation quadrats (red squares) in a vineyard tilled in one out of two rows (1/2).

year. The selected vineyards had an average size of 7008 ± 746 m^2 representative of the study region and were dispersed over an area of 20 × 6 km^2. The landscape is dominated by vineyards with a low proportion of other crops such as orchards (cherry, apple, olives), durum wheat and lavender as well as small-sized semi-natural habitats such as herbaceous margin vegetation and woodlands.

Ant sampling

Six pitfall traps per vineyard were placed in May 2018 and June 2018 to capture ants in the inter-rows of the central part of each vineyard. They were buried up to the rim and filled with propylene glycol to a quarter of the depth. The six traps were assigned to two inter-rows in the centre of each vineyard (Fig. 1). In 1/2 tilled vineyards, three traps were placed in tilled and three traps in untilled inter-rows. The distance between traps was 5 m. All ants were identified to genus and most of them to species level using the key of Blatrix, Galkowski, Lebas and Wegnez (2013). According to Blaise et al. (2021), *Camponotus vagus, Cataglyphis cursor, Crematogaster scutellaris, Pheidole pallidula, Tapinoma nigerrimum* complex were considered as predatory ant species. They were all identified as main predators in vineyards. *Messor structor* was the only strictly granivorous ant. Because abundance in traps may be biased by distance from a nest or ant trail, we instead considered the frequency of occurrence of ant species (Gotelli, Ellison, Dunn & Sanders, 2011; Greenslade, 1973).

Floristic surveys

The floristic composition of the vegetation was analysed in 2 × 2 m^2 quadrats. The quadrats were placed at the sampling points of pitfall traps resulting in six quadrats per vineyard and a total of 138 traps (Fig. 1). In each quadrat, all vascular plant species were identified. The cover of each species was visually estimated, and it was recorded whether a species was flowering. Plant cover was estimated as the vertical projection of above-ground plant organs on the ground. Additionally, total flower cover of nectariferous species was estimated in each quadrat.

Using these floristic surveys, we were able to select different characteristics of the vegetation that are important for ants such as: (i) total cover in order to analyse whether vegetation in general provides resources that benefit ants, (ii) flower cover to analyse specific effects of floral resources, (iii) plant species richness to evaluate the role of resource diversity, (iv) proportion of Poaceae (grass cover) often dominating in vineyard inter-rows, (v) proportion of Fabaceae increasing nitrogen availability and productivity and thus often used in seed mixtures sown by winegrowers, (vi) Bray-Curtis dissimilarity index (at vineyards scale) to analyse the role of habitat diversity, and (vii) the ratio of perennial to annual plants as a long-term soil disturbance indicator with high values indicating low disturbance.

Ant community assessment

Six response variables were selected to characterise ant communities: (i) ant species richness per trap, (ii) frequency of occurrence (hereafter briefly “occurrence”) of the eight most common species (*Cataglyphis cursor, Crematogaster scutellaris, Messor structor, Pheidole pallidula, Plagiolepis pygmaea, Tapinoma nigerrimum* complex, *Tapinoma madeirense and Solenopsis* sp.), (iii) occurrence of predatory species across all vineyards, (iv) functional richness index (FRic), (v) average colony size and (vi) average worker size. Occurrence and species richness were calculated at trap level in order to establish a direct link with the vegetation survey conducted around each sample (Fig. 1).

Functional traits of ant species to characterise the functional response of ant communities and predatory ants were obtained from the database “matrix sppx traits” (Arnan, Cerdá & Retana, 2014). We considered the following traits: worker size, worker polymorphism, colony size, nutrition (seed, insect, liquid food), independent colony foundation, polygyny (two or more queens contribute to egg-laying), polydomy (ant colony occupies two or more spatially separated nests), strictly diurnal, dominant, foraging type (individual or collective), nest location (dead wood, soil or mixed). These traits were used to calculate three functional indexes: (i) the functional richness (calculated using R “FD” package, (Laliberté, Legendre & Shipley, 2014)), (ii) the average colony size in each trap and (iii) the average body size of the different worker species found in each trap. Colony sizes were log-transformed prior to analysis to avoid bias generated by large colonies. The same set of explanatory variables and the same model structure were applied as in the analysis of the six response variables above.

Data analysis

Generalized linear mixed-effects models (GLMMs) were computed using R (version 4.1.1, R Development Core Team, 2011) to explore the effects of tillage and vegetation characteristics on the six response variables mentioned above. The effects of the three tillage management types and the seven vegetation characteristics were tested in different models. To check the correlations between vegetation characteristics, a correlation matrix was calculated and a threshold of $R = 0.5$ was established to eliminate correlated variables. A Poisson distribution with log link function was applied to response variables not showing over-dispersion. A negative binomial error distribution was used for over-dispersed data. Occurrence at trap level was coded binary and binomial distribution with logit link function was fitted to occurrence data. No overdispersion was detected in these binary coded data. In order to avoid over-parametrisation in tests including vegetation characteristics, we selected the best fitting model using the stepwise backward procedure of the dredge function (R package: MuMIn). Starting from a full model, the dredge function eliminates in each step the one explanatory variable that provides the highest AIC (Akaike Information Criterion) when fitted to the model. In the case of a significant tillage management type effect, post-hoc Tukey tests were performed to compare the three treatment levels.

Two multivariate analyses were performed: (i) NMDS (non-metric multidimensional scaling) based on Bray-Curtis dissimilarity was carried out to analyse links between ant community composition and inter-row tillage. Non-parametric permutational multivariate analysis (R function Anosim, R package: Vegan) was used to detect differences in ant community composition; (ii) Redundancy analysis (RDA) was applied in order to analyse the influence of vegetation on ant community composition. Both RDA and NMDS were run at vineyard level using the sum of occurrences for each species across the two trapping campaigns ($N = 12$ traps). Permutational multivariate analysis was used to detect differences in ant community composition. To characterise the vegetation, we used the seven vegetation characteristics mentioned above as explanatory variables. Explanatory Variables were log-transformed to homogenise variances and to obtain similar scales. NMDS and RDA analyses were performed using the R package "vegan" (Oksanen et al., 2016).

Results

In total, we found 26 ant species belonging to 14 genera and four subfamilies (Appendix A: Table 1) with an average

Table 1. Effect of inter-row tillage and vegetation characteristics on total ant richness and occurrence of the eight most common ant species. Estimates (± SE) and significance of variables selected by the "dredge" function. Differences between inter-row tillage were evaluated using post-hoc Tukey tests. Significant effects are indicated: . = $P < 0.1$* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.005$.

dependant variables	inter-row management			vegetation cover	plant richness	flower cover	Bray-Curtis dissimilarity	fabacae cover	grass cover	perennials/annuals
	0/2 - 1/2	0/2 - 2/2	1/2 - 2/2							
Species richness	−0.25 ± 0.09*	−0.12 ± 0.09	0.13 ± 0.08	–	–	–	–	–	4e-3 ± 2e-2*	0.16 ± 0.06*
C. cursor	0.16 ± 0.24	−0.27 ± 0.22	−0.44 ± 0.22	–	–	–	–	–	–	–
C. scutellaris	0.35 ± 0.057	1.59 ± 0.7 .	1.94 ± 0.68*	–	–	–	–	–	0.02 ± 0.01	–
M. structor	−0.46 ± 0.23	−0.37 ± 0.22	0.13 ± 0.20	–	–	–	–	–	0.02 ± 0.01	–
P. pallidula	0.02 ± 0.17	−0.17 ± 0.16	−0.19 ± 0.15	–	–	–	–	–	–	–
P. pygmaea	−0.49 ± 0.27	−0.38 ± 0.27	0.11 ± 0.24	–	–	–	–	0.03 ± 0.02*	0.03 ± 0.01*	2.54 ± 0.63***
T. madeirense	−0.29 ± 0.53	2.48 ± 1.10 .	2.77 ± 1.10*	–	–	–	–	–	–	–
T. grp. nig.	−0.38 ± 0.47	0.44 ± 0.50	0.82 ± 0.47	–	–	−0.23 ± 0.12 .	–	–	0.03 ± 0.01**	–
Solenopsis sp.	−0.66 ± 0.41	−0.96 ± 0.39*	−0.30 ± 0.33	–	–	–	–	–	–	–

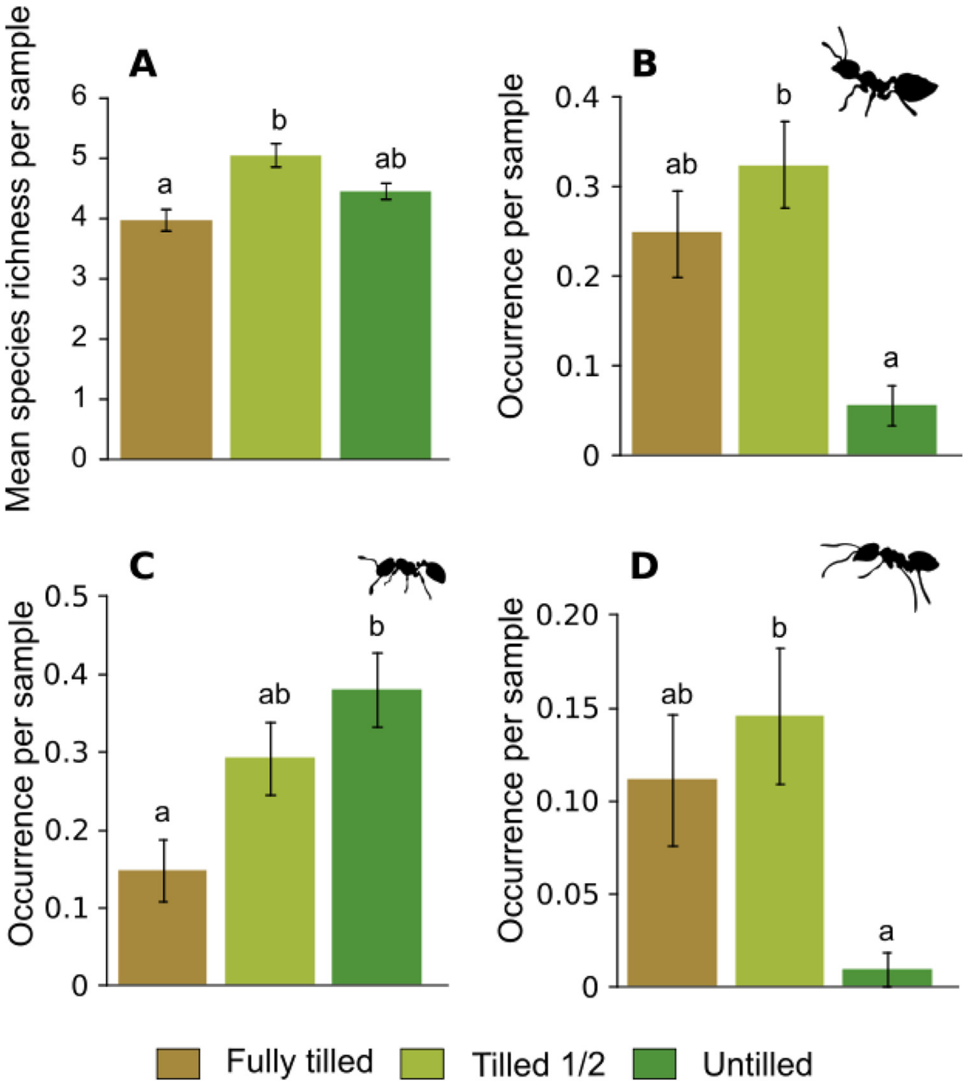

Fig. 2. Effect of inter-row tillage on (A) mean ant species richness per trap (+/- SE), (B,C,D) the occurrence per trap of the three ant species that respond significantly to tillage (means ± SE). (B) *Crematogaster scutellaris*; (C) *Solenopsis sp.*; (D) *Tapinoma madeirense*. Letters indicate significant differences between management types ($P < 0.05$).

of five species per vineyard. We identified 181 vascular plants with an average species richness of 17 per quadrat of 4m^2.

Effect of inter-row tillage

Inter-row tillage of vineyards significantly influenced ant specific richness ($p = 0.012$). We found more species in the 1/2 tilled vineyards than in fully tilled vineyards, whereas the difference between untilled and fully tilled vineyards was not significant (Fig. 2A, Table 1). On average species richness was 25% higher in 1/2 tilled vineyards than in fully tilled vineyards. Ant community composition did not show any response to inter-row tillage (NMDS, ANOSIM: $p = 0.081$, stress: 0.195; Appendix D: Fig. 1). Functional richness, worker and colony size, and the global occurrence of predatory ants were also not affected by inter-row tillage ($p = 0.535$, Table 2).

Within the predatory ant group, only the occurrence of *Crematogaster scutellaris* was affected by inter-row tillage being highest in 1/2 tilled vineyards ($p = 0.015$, Fig. 2B). The omnivorous *Tapinoma madeirense* followed the same pattern ($p = 0.037$, Fig. 2D). On the contrary, the omnivorous *Solenopsis sp.* was more frequent in fully vegetated vineyards ($p = 0.052$, Fig. 2C). All other ant species including the granivorous ant *Messor structor* did not show any significant response to inter-row tillage (Table 1).

Effects of vegetation characteristics

Grass cover and the ratio of perennial to annual plants were positively correlated with ant species richness (Fig. 3;

Table 2. Effect of inter-row tillage and vegetation characteristics on (i) the functional richness; (ii) ant species size and (iii) the colony size. Estimates (± SE) and p-values of the variables selected by the "dredge" function. Differences between inter-row tillage were evaluated using post-hoc Tukey tests.

dependant variables	inter-row management			vegetation cover	plant richness	flower cover	Bray-Curtis dissimilarity	fabacae cover	grass cover	perennials/annuals
	0/2 - 1/2	0/2 - 2/2	1/2 - 2/2							
Funcional richness	0.19 ± 0.25	−0.08 ± 0.23	−0.27 ± 0.25	–	–	–	–	–	–	–
Worker size	0.26 ± 0.29	0.19 ± 0.28	−0.08 ± 0.27	–	–	–	−0.64 ± 0.92	–	–	–
Colony size	0.04 ± 0.05	−0.01 ± 0.05	−0.05 ± 0.05	–	–	–	–	–	–	–

Table 1). The redundancy analysis did not reveal significant relationships between vegetation and ant community composition (PERMANOVA: $p = 0.105$; Appendix E: Fig. 2), and the RDA axis explained a very small proportion of total variance (only 10% for the first axis and 9% for the second).

The global occurrence of predatory ants was not affected by vegetation characteristics. amongst functional indexes, the size of colonies was positively influenced (marginally significant) by the Bray-Curtis dissimilarity index of plant species composition (Table 2). Functional richness of ants was not related to plant functional groups (Table 2).

Within the predatory ant group, only the occurrence of the *Tapinoma nigerrinum* complex was positively correlated to grass cover but was negatively correlated to flower cover (Table 1). The occurrence of *Plagiolepis pygmaea* was positively correlated to the cover of both legumes (Fabaceae) and grasses, as well as to the ratio of perennial to annual plants.

Discussion

Tillage negatively affects ground-dwelling arthropods including ants through soil disturbance and destruction of vegetation (Blaise et al., 2022; Holland, 2004; Santos et al., 2018). In our study, however, such a negative tillage effect was only apparent on the occurrence of one species. Interestingly, ant species richness and the occurrence of two abundant species were highest in 1/2 tilled vineyards whereas differences between fully and untilled vineyards were not significant. The global occurrence of predatory ants was not negatively affected by tillage, and *Crematogaster scutellaris* showed an even positive response to 1/2 tillage compared with untilled vineyards. Inter-row vegetation, in particular grasses and the ratio of perennials to annuals had a positive influence on ant diversity and the frequency of several species whereas flowering nectariferous species had no effect. We did not detect a significant influence of inter-row tillage and vegetation on ant functional traits or community composition.

The particularly positive effect of 1/2 tillage on ant diversity may be explained by a higher habitat diversity allowing species of bare soil and vegetated habitats to co-exist in the same vineyard. Habitat heterogeneity has already been identified as an important factor driving ant diversity (Gaston, 2000). Sites with heterogeneous habitats provide a higher number of niches resulting in a higher ant species richness (Lassau & Hochuli, 2004).

The response of different ant species to inter-row tillage was heterogeneous. The differences in ant response to inter-row management may be explained by differences in their ecology. The two species particularly favoured by 1/2 tillage, the predatory *Crematogaster scutellaris* and the omnivorous *Tapinoma madeirense,* are known to maintain their populations in disturbed habitats (Blatrix et al., 2013), but disturbance level of our fully tilled vineyards may have been

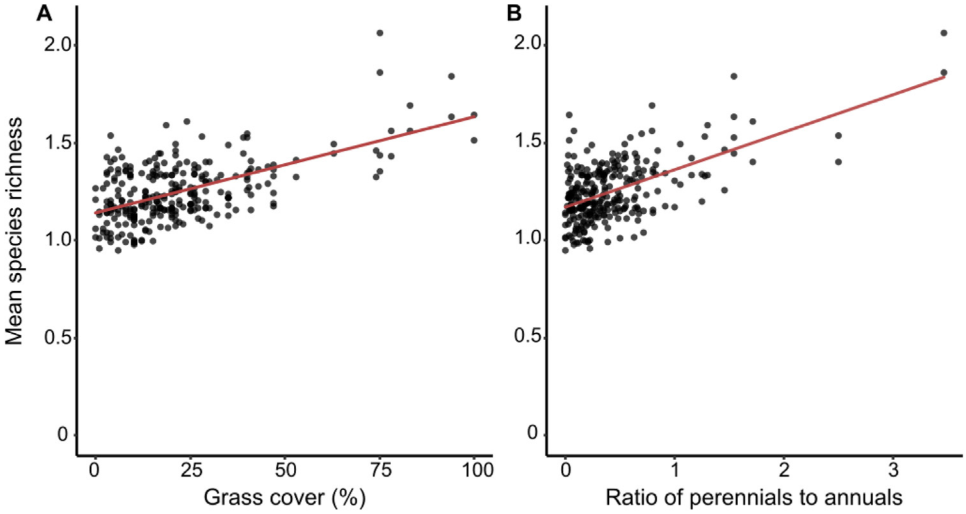

Fig. 3. Relationship between ant species richness (fitted values) and (A) grass cover per trap (r^2=0.34), (B) the ratio of perennials to annuals (r^2=0.33). For estimates and p-values, see table 1.

too high. In contrast, species of the genus *Solenopsis* live in nests close to the soil surface which may explain their higher vulnerability to tillage. The granivorous species, *M. structor* that is known for its contribution to soil structuring and seed dispersal (Schlick-Steiner, Steiner, Stauffer & Buschinger, 2005) and the other predatory ants were not affected by tillage. These species build deep nests in the soil, which may allow them to escape tillage. The sampling method used might also explain some of the differences we recorded between species. Indeed, habitat complexity may affect the probability of capture, often decreasing with increasing vegetation cover (Melbourne, 1999). Therefore, the method may have underestimated the positive effect of fully vegetated inter-row on the presence of certain species, in particular on those ants that feed on plants such as *Crematogaster scutellaris*, or *Camponotus* and *Tapinoma* species.

The effects of tillage on the frequency of different ant species were not strong enough to result in significant effects in ant species and trait composition. The most abundant ant species are widespread generalists that tolerate disturbance but also occur in undisturbed habitats resulting in weak tillage effects. *Pheidole pallidula* is for example one of the most common species in disturbed areas of the Mediterranean region (Carpintero & Reyes-López, 2014). Similarly, *M. structor* colonises disturbed open habitats as well as the desert ant *C. cursor* (Blatrix et al., 2013). Several ant species build their nests in great soil depth, sometimes several meters, avoiding tillage effects (MacKay, 1981). This avoidance strategy of frequent ant species including predatory ants may explain why the tillage effect was less strong than in a previous study on ground-dwelling arthropods including the same vineyards (Blaise et al., 2022). In a study on *Lucilia* sp. (Diptera) larvae predation, the same authors found that ant predation decreases with disturbance by tillage (Blaise et al., 2021). Soil disturbance may thus affect ecosystem services without affecting ant species composition (Andersen, 2019) by reducing for example the number of colonies per species.

In several studies, plant species composition had only a small influence on ant communities and such vegetation effects were finally mediated by habitat openness (Andersen, 2019). Habitat openness is a key driver of variation in the composition of ant communities along gradients from open habitats (e.g. grasslands, savannahs) to forests (Dalle Laste, Durigan & Andersen, 2019; Solar et al., 2016). In our study, we still identified two plant functional groups affecting ant species richness and frequency, grass cover and the perennial to annual ratio. Grass cover is well known to favour ground-dwelling arthropods (Al Hassan et al., 2013; Collins, Boatman, Wilcox, Holland & Chaney, 2002; Marshall & Moonen, 2002). Grasses often represent a large part of total vegetation cover directly related to habitat openness, improve protection against natural enemies and may provide food resources. Although the specific effect of grasses on Mediterranean ant species is less well-known similar functions of grass cover can be assumed. The perennial to annual ratio may be an indicator of long-term disturbance. Annual plant species are adapted to higher soil disturbance because they survive as seeds in the soil whereas above- and belowground plant organs of perennials are mostly destroyed by soil tillage (Nabe-Nielsen, Reddersen & Nabe-Nielsen, 2021). Thus, annual plant species are usually replaced by perennials in the course of plant succession following disturbance (Bischoff, 2002; Kiehl, Kirmer, Donath, Rasran & Hölzel, 2010). Although we did not find a strong negative tillage effect on ant communities, the correlation with the perennial to annual ratio still suggests a sensitivity of ants to soil disturbance in our vineyards. The perennial to annual ratio may better reflect past disturbance intensity than the current inter-row tillage. Increasing the abundance of floral resources (nectar, pollen) was found to be favourable to several arthropod groups even to those that do not directly depend on nectar (Griffiths et al., 2008; Pollier et al., 2018). The effect on ant diversity and frequency was, however, not significant or even negative in our study, suggesting that ants of our Mediterranean vineyards do not use floral resources and do not feed on prey that depend on floral resources.

Conclusions

Tillage effects on ant communities in Mediterranean vineyards of our study zone were smaller than expected. Interestingly, 1/2 tilled vineyards showed the highest richness and occurrence of one predatory species (*C. scutellaris*) indicating that full vegetation cover may not be required to protect ant species and related ecosystem services. Intensive use of tillage is not desirable for the establishment of ants but removing inter-row vegetation in a part of the vineyards may even be beneficial. Two vegetation traits or functional groups were identified that favour ant species. Grasses and perennial species were positively related to ant richness and frequency of several species. Whereas perennial plant abundance may be an indicator of long-term disturbance level, grasses provide important habitat functions (Collins et al., 2002). Approaches to improve ecosystem services of inter-row vegetation by sowing should thus not only focus on flowering nectariferous species but also include grasses.

Author contribution statement

L Rocher: Validation, Ant identifications, Formal analysis, Writing - original draft. R. Blaya: Ant identifications, Writing - review & editing. C. Blaise: Conceptualization, Validation. A. Bischoff: Conceptualization, Validation, Writing - review & editing. O. Blight: Conceptualization, Validation, Investigation, Formal analysis, Writing - original draft, Writing - review & editing.

Declaration of competing interest

The authors have no conflict of interest to declare.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2022.11.009.

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