



Local management and landscape composition affect predatory mites in European wine-growing regions

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ABSTRACT

Sustainable land use in agricultural landscapes is essential to counteract the global decline of biodiversity, as well to ensure ecosystem services like natural pest control. Phytoseiid mites are key natural enemies of pest mites in vineyards but how local management and landscape context affect phytoseiid mites remains poorly known. In this study, we examined the effects of farming systems, inter-row management and landscape composition on phytoseiid mite communities in 156 vineyards across five European wine-growing regions. Our results showed that phytoseiid communities were mainly dominated by one or two phytoseiid species across Europe and that local management was a major factor affecting population densities. According to the wine-growing regions, phytoseiid mite densities benefited from integrated pest management or conventional farming compared to organic farming and from spontaneous vegetation cover compared to seeded cover crops. Moreover, mite densities benefited from increasing proportions of vineyards at the landscape scale. The farming systems effects were most likely related to the positive impact of the lower pesticide use in integrated and conventional vineyards. The positive effect of spontaneous vegetation cover could be related to a better supply of nutritive pollen as food resource compared to seeded cover crops, which depends on the plant species in the inter-row. Our findings indicated accordingly that a reduced pesticide use, and inter-row management are crucial factors for promoting pest control by predatory mites in European vineyards. Moreover, the proportion of viticultural area in the landscape is a considerable factor to retain stable phytoseiid mite populations.

1. Introduction

Agricultural intensification through habitat losses, landscape homogenization, or high levels of pesticides use contribute to biodiversity loss across the world (Sánchez-Bayo and Wyckhuys, 2019). Thus, sustainable land use is essential for biodiversity conservation and the

provision of ecosystem services in agricultural landscapes (Bianchi et al., 2006; Gurr et al., 2003). Natural pest control, an important ecosystem service that can contribute to limit pesticide use, is influenced by habitat and resource management through farming practices (González-Chang et al., 2019; Landis et al., 2000) and through the landscape structure (Chaplin-Kramer et al., 2011; Karp et al., 2018).

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At the field scale, the use of pesticides has been shown to have devastating impacts on many natural enemy communities (Geiger et al., 2010; Pimentel et al., 1992). These effects might interact with other farming practices such as intensive soil tillage which decreases plant diversity (Rusch et al., 2010; Sáenz-Romo et al., 2019b; Winter et al., 2018). Organic farming has been shown to benefit biodiversity and pest control but that effect varies greatly depending on the organism group and crop type (Bengtsson et al., 2005; Mureret et al., 2018). At the landscape scale, maintaining semi-natural habitats such as grasslands, forests or hedgerows are known in many cases to benefit natural pest control services (Martin et al., 2019; Rusch et al., 2016). Nevertheless, the negative effect of a high pesticide use, can hamper the positive effect of semi-natural habitats, highlighting the need for a multiscale management perspective (Ricci et al., 2019). Knowledge on how local and landscape-scale factors interact to shape natural pest control services would be helpful considering the two major targets in the European Union (EU) farm to fork strategy of 50 % reduction of pesticide use and the goal to reach a 25 % share of the agricultural land under organic farming by 2030 (European Commission, 2020).

In vineyards, the intensive use of pesticides may affect pest control services (Nash et al., 2010; Ostandie et al., 2021; Pennington et al., 2018). The type of farming system strongly influences pesticide use, as in conventional viticulture a broader range of synthetic and inorganic pesticides are allowed compared to organic viticulture, where only inorganic and bio-pesticides are permitted in the EU (European Parliament, Council of the European Union, 2018). Furthermore, habitat quality which is an important factor for biodiversity and biological pest control services, is strongly affected by the management of vineyard inter-rows, differing in respect to vegetation cover, floral resources and plant community composition (Burgio et al., 2016; Kehinde and Samways, 2014; Winter et al., 2018). Especially the maintenance of the vegetation through cover crops or spontaneous vegetation can increase the abundance of natural enemy communities in vineyards like spiders, ants, earwigs, parasitoid wasps or predatory mites and may therefore increase the biological control potential of viticultural pests (Beaumelle et al., 2021; Burgio et al., 2016; Sáenz-Romo et al., 2019b). This beneficial effect of vegetation covers is mediated by the provision of alternative prey, host and food resource (e.g. pollen, floral nectar), as well as shelter for overwintering (Landis et al., 2000). Furthermore, diverse landscapes with high proportions of non-crop habitats may benefit pest control services of the grape berry moth in vineyards (Paredes et al., 2020; Rusch et al., 2017). The effect of landscape composition on biological pest control highly depends on the taxonomic group, their traits (e.g. dispersal abilities, diet breadth) as well as the habitat composition (Martin et al., 2019; Sentenac et al., 2018). For instance, Judt et al. (2019) found in vineyards a lower abundance of parasitoids in landscapes with high proportion of vineyards, while more spiders were found in landscapes harbouring more non-flowering crops. However, the combined effects of local pesticide management, plant diversity and landscape composition for most natural enemies operating in vineyard landscapes remain poorly investigated (but see Beaumelle et al., 2021).

Phytoseiid mites (Acari: Phytoseiidae) are important predators in vineyards. Small populations or the absence of these predatory mites can lead to serious reductions of grape yield and quality, through damages by pest mites like eriophyid (Acari: Eriophyidae) and spider mites (Acari: Tetranychidae) (Duso et al., 2012). Besides the effects of climatic conditions (Montserrat et al., 2013) and leaf hair characteristics of different grape varieties (Duso and Vettorazzo, 1999; English-Loeb et al., 2002; Tixier et al., 2005, 2015), one key point is the use of pesticides (Duso et al., 2012), which can have detrimental effects on phytoseiid mites (Gadino et al., 2011; Kemmitt et al., 2015). Phytoseiid mites on vines (Tixier et al., 2013) are mainly generalists, which feed on pest mites and other mites like tydeid mites (Acari: Tydeidae), fungi and pollen (McMurtry et al., 2013). Tydeid mites do not only serve as alternative food for phytoseiid mites, the tydeid species *Tydeus goetzi* Schruft and *Tydeus caudatus* Dugés, also prey on eriophyid mites in

vineyards (Camporese and Duso, 1995; Ferragut et al., 2008; Schruft, 1972). The accessibility of various food resources is important for the sustainable establishment of phytoseiid populations in vineyards (Duso et al., 2012). Pollen provision through the vineyard inter-row vegetation or the surrounding landscape can maintain their populations (Duso et al., 2004, 2002; Kreiter et al., 2017; Malagnini et al., 2022; Möth et al., 2021; Wiedmer and Boller, 1990). In general, seeded cover crops or spontaneous vegetation in vineyard inter-rows can increase phytoseiid mite densities on vines (Burgio et al., 2016; Castagnoli et al., 1999; de Villiers and Pringle, 2011; Sáenz-Romo et al., 2019a; Tixier, 2018; Vogelweith and Thiéry, 2017). Semi-natural habitats like hedges at the landscape scale may also act as phytoseiid mite reservoir (Duso et al., 2004; Gavinelli et al., 2020; Tixier et al., 2005, 2000a, 1998; Tixier, 2018), where they can spill-over in adjacent vineyards through wind dispersal (Tixier et al., 1998).

In this study, we investigated phytoseiid mite communities in five different wine-growing regions across Europe, considering the relative effects of local management, i.e., pesticide use (according to the farming system) and ground cover management in interaction with landscape composition (defined here as the amount of semi-natural habitats at the landscape scale) on their populations. We hypothesized that (i) local management would strongly affect phytoseiid mite populations due to their low dispersal abilities and that (ii) surrounding semi-natural habitats of vineyards can mitigate the negative effects of local pesticide use on phytoseiid mites.

2. Material and methods

2.1. Study sites and design

The study was conducted in five European wine-growing regions (Fig. 1) ranging from: (i) Târnave in Romania (RO) with a snow climate, fully humid and warm summers (Köppen-Geiger climate classification: Dfb), (ii) Leithaberg in Austria (AT), (iii) Palatinate in Germany (DE), (iv) Bordeaux in France (FR), with a warm temperate climate, fully humid and warm summers (Cfb) and (v) PDO (protected designation of origin) Montilla-Moriles in Spain (ES) with a warm temperate climate, dry and hot summers (Csa) (Kottek et al., 2006). At each study site, the landscape was mainly characterised through a mix of vineyards, other types of agricultural land use (e.g. pastures, orchards and arable crops) and semi-natural habitats (e.g. hedgerows, solitary trees, woodlands and grasslands). All study sites were commercial vineyards and planted with a range of different *Vitis vinifera* L. ssp. *vinifera* grape varieties (see supplemental material Table S1), mainly trained in trellis system (except for six vineyards in goblet system in PDO Montilla-Moriles).

In each wine-growing region, we selected pairs of vineyards to investigate the effects of (i) the farming system and (ii) inter-row vegetation along a (iii) landscape composition gradient (proportion of semi-natural habitats and vineyards in a 500 m buffer). Depending on the region, we investigated the effects of organic farming compared to integrated pest management or conventional farming (Leithaberg, Bordeaux, PDO Montilla-Moriles; in Palatinate all vineyards were organic, whereas in Târnave all were conventional differing in respect to pesticide use). Inter-row vegetation types were either: sown cover crop mixtures with a high diversity (20–34 species), poor diversity (4–9 species), spontaneous vegetation cover (no cover crops were sown) or bare soil (see Table 1). Additionally, in Palatinate, vineyard pairs were selected to evaluate the presence or absence of a neighbouring hedge in about 15 m distance to the vineyard. Overall, 156 vineyards were sampled.

Detailed information on viticultural practices (e.g., pesticide applications, grape variety) in each vineyard was gathered through personal interviews with the winemakers based on a structured questionnaire. Pesticide use was determined by the total amount of applications, fungicide and insecticide applications (one application consists mostly out of a spray mixture of several pesticides). Furthermore, an area-

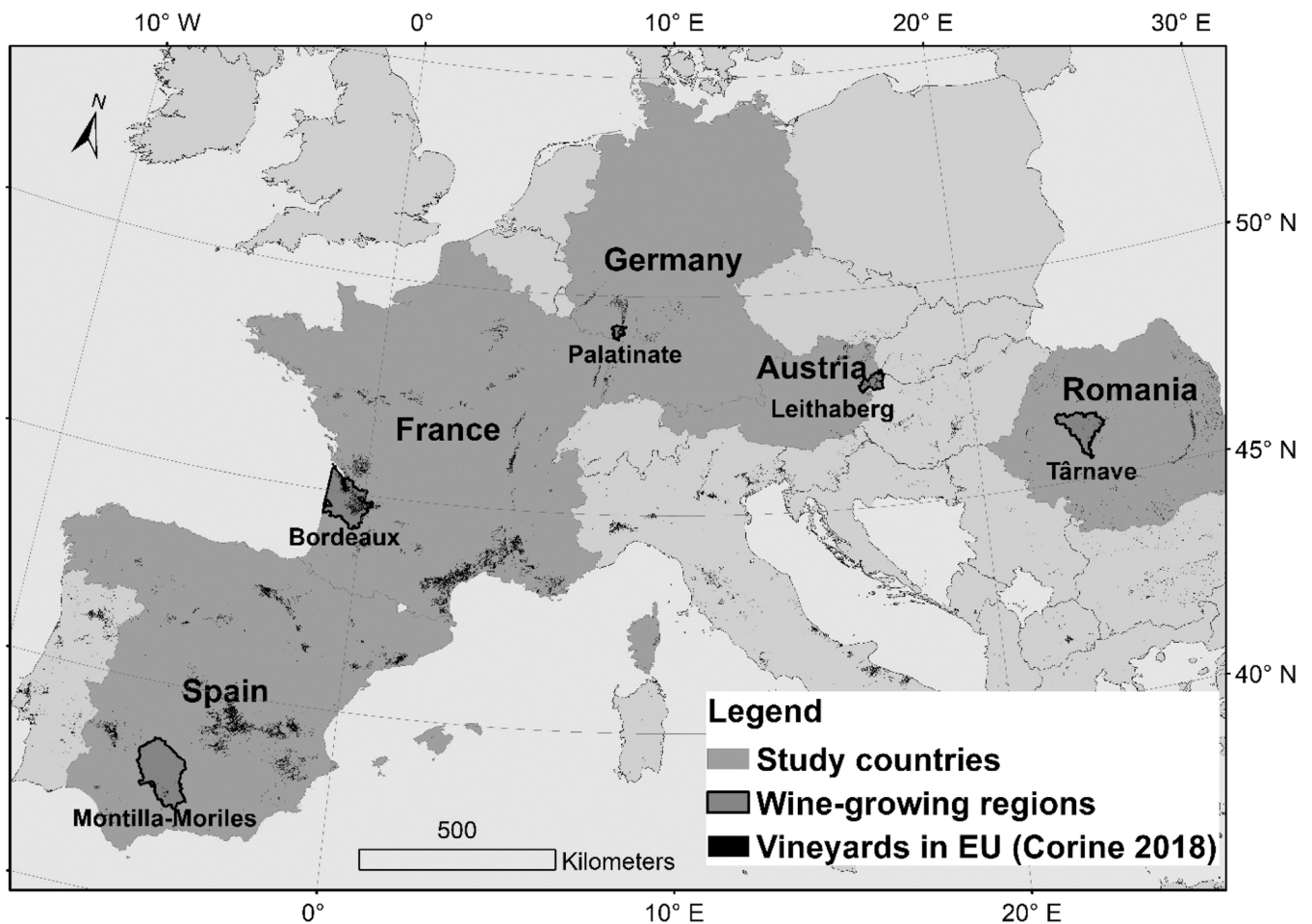


Fig. 1. Location of the studied wine-growing regions across Europe. The black line marks the border of each wine-growing region. The marked region Montilla-Moriles shows the Córdoba province and PDO Montilla-Moriles, whereby the latter is in the south of it. The viticultural area in Europe is illustrated with black spots according to the Corine land cover 2018 (Corine, 2018).

Table 1

Geographical coordinates, information on the regional study design (farming system and vegetation type with the particular number of vineyards in parentheses), study year and number of sampled vineyards from the five European wine-growing regions.

Wine-growing region (country)	GPS coordinates of the wine-growing region	Study year	Total number of sampled vineyards	Farming system	Vegetation type
Târnave (Romania)	46°10'N, 23°54'E	2019	24	Conventional with high (17) /low pesticide input (7)	Spontaneous vegetation (13) /bare soil (11)
Târnave (Romania)	46°10'N, 23°54'E	2020	26	Conventional with high (17) /low pesticide input (9)	Spontaneous vegetation (15) /bare soil (11)
Leithaberg (Austria)	47°53'N, 16°39'E	2020	32	Organic (16) /integrated (16)	Spontaneous vegetation (6) / species -rich cover crops (14) /species-poor cover crops (12)
Palatinate (Germany) †	49°12'N, 8°02'E	2019	32	Organic (32)	Spontaneous vegetation (16) / species -rich cover crops (16)
Bordeaux (France)	44°53'N, 0°09'W	2020	36	Organic (18) /conventional (18)	Spontaneous vegetation (36)
PDO Montilla-Moriles (Spain)	37°33'N, 4°40'W	2021	30	Organic (12) /conventional (18)	Spontaneous vegetation (10) /bare soil (20)

† The second factor in Palatinate was the presence (16 vineyards) or absence (16 vineyards) of a nearby hedge.

related acute pesticide contact toxicity loading index (aAPTLC) based on the honeybee LD₅₀ contact lethal doses (Lewis et al., 2016) was additionally calculated for each vineyard, according to Möth et al. (2021). Unfortunately, due to missing information of the spraying regime we could not calculate the aAPTLC for the vineyards in PDO Montilla-Moriles. Detailed information on the pesticide use of fungicides (including applied sulphur as additional information), insecticides and aAPTLC, among the farming systems and wine-growing regions can be seen in Table S2.

2.2. Mite sampling

Mites from vine leaves were sampled four times during the vegetation season in each vineyard after the BBCH scale coding system for vines (Lorenz et al., 1994): (i) 60–65: beginning of flowering – full flowering, (ii) 75–77: berries pea sized – berry touch, (iii) 81: berries begin to brighten in colour and (iv) 85–89: softening of the berries – ripe for harvest. Sampling took place during one vegetation season in all wine-growing regions between 2019 and 2021, except for two seasons in

Tárnave (Table 1, for sampling dates see Table S3). For each sample, 25 vine leaves were collected randomly from the whole canopy along a 30 m transect per vineyard. The soaking-checking-washing filtering protocol from Boller (1984) and Hill and Schlamp (1984) was used with a 63 µm mesh sieve for phytoseiid, tydeid and spider mites and a 32 µm mesh sieve for eriophyid mites. Samples were afterwards stored at -20 °C. The Li-COR Modell 3000, 3100 or 3050 A area meter (Lincoln, NE, USA) was used after the extraction of the mites, to measure the total vine leaf area for each sample to calculate mite densities per 100 cm² leaf area. Only in Tárnave, the smartphone application Easy Leaf Area (Eason and Bloom, 2014) was used for this purpose. Moreover, the vineyards in Tárnave were heavily infested with mildew, which resulted in necrotic old leaves and probably a higher proportion of newly developed young leaves during the vegetation season. The necrotic leaves were not sampled, therefore more young leaves without necrotic spots but with a considerably lower leaf area were chosen.

Spider and eriophyid mite identification was based on knowledge of their incidence in each studied wine-growing region, limiting the range of possible species. The number of all phytoseiid and tydeid mites were counted at family level and spider mites at species level at 25x magnification. Eriophyid mites were counted with a 50x magnification at species level, carried out with a stereomicroscope (Leica M80, Wetzlar, Germany). Hoyer's medium (Walter and Krantz, 2009) was used to mount all phytoseiid and tydeid mites, for species identification with appropriate species-specific keys for tydeid mites (Da Silva et al., 2016), female phytoseiid mites (Tixier et al., 2013) and a light microscope at 200x and 400x magnification with phase contrast (Zeiss Axioplan 2 imaging, Oberkochen, Germany).

We calculated Shannon's diversity index (H) (Shannon, 1948) of phytoseiid mite communities and Pielou's evenness index (J') (with the implementation of the Shannon's diversity index) (Pielou, 1966), to compare the phytoseiid mite species diversity and evenness between the five wine-growing regions.

2.3. Vine leaf hairiness index

An index for the leaf hairiness of the different grape varieties was used to consider its possible effect on phytoseiid mite densities (Schmidt, 2014). The nine-step scale of leaf hairiness (descriptor prostrate hairs) on the underside of the leaf according to the International Organisation of Vine and Wine (OIV) (2009) was merged into four categories (1 = absent, 2 = weak, 3 = medium and 4 = dense hairiness) to categorize all sampled varieties. Missing data in the OIV (2009) was complemented by various descriptive grape variety lists which described their leaf underside hairiness in broader categories than the OIV (Höhere Bundeslehranstalt und Bundesamt für Wein- und Obstbau, 2022; IFV, INRAE, l'Institut Agro, 2022; Popescu et al., 2015) (Table S4).

2.4. Landscape survey

Landscape mapping was done within a 500 m buffer around each vineyard based on field mapping and available base maps for each country. This spatial extent was chosen as it is often found to fall within the range of relevant spatial extent for natural enemies (Chaplin-Kramer et al., 2011; Jackson and Fahrig, 2015; Redlich et al., 2018) and on the known dispersal distances of phytoseiid mites ranging from 10 to 200 m (Hoy et al., 1985; Jung and Croft, 2001). Land use was categorized after the EUNIS habitat type classification scheme (European Environment Agency (EEA), 2016), digitized with ArcGIS (Environmental System Research Institute, 2008) or QGIS (QGIS Development Team, 2019). The proportion of semi-natural habitats (including the habitat types: hedgerow, solitary tree, tree row, woodland, fallow, grassland, and grass strip from field margins) and proportion of vineyard cover were then analysed and used as explanatory variable in our statistical models (Table S5).

2.5. Data analyses

All the data visualization and statistical analysis were done with R Version 4.1.2 (R Core Team, 2021) and RStudio (RStudio Team, 2021) including the R packages "lme4" (Bates et al., 2015), "MuMIn" (Bartoń, 2020), "car" (Fox and Weisberg, 2019), "dplyr" (Wickham et al., 2020), "AICcmodavg" (Mazerolle, 2020), "effects" (Fox, 2003; Fox and Weisberg, 2019), "lattice" (Sarkar, 2008), "corrplot" (Wei and Simko, 2017) and "ggplot2" (Wickham, 2016). The landscape analysis was done with the package "landscapemetrics" (Hesselbarth et al., 2019) and the Shannon's diversity index of phytoseiid mite communities and Pielou's evenness index were calculated with the package "vegan" (Oksanen et al., 2019).

Data exploration (e.g. outliers, distribution of the response variable, variance homogeneity) was done following Zuur et al. (2010). Statistical modelling was performed for the phytoseiid mite datasets from Bordeaux, Palatinate, Leithaberg and Tárnave (corresponding dataset from 2020, Tárnave 2020 from here on). The phytoseiid dataset from Tárnave (corresponding dataset from 2019, Tárnave 2019 from here on) contained too many missing values and the phytoseiid dataset PDO Montilla-Moriles from 2021 too many zero counts with a very low population density overall, and therefore these datasets were not modelled, to avoid possible misinterpretations (Zuur et al., 2010).

The response variable, phytoseiid mite densities per 100 cm² vine leaf area, was transformed with $\log_{10}(\log_{10}(y + 1))$ (Curran-Everett, 2018; O'Hara and Kotze, 2010) for fitting linear mixed models (LMM) and linear models (LM), to use Gaussian distribution and not violate the model assumption of normal distributed residuals (Zuur et al., 2009). LMM were used for the phytoseiid data from Bordeaux with the paired vineyards nested within the landscape as random effect. LM were used for the other phytoseiid datasets from Leithaberg, Palatinate, Tárnave 2020 due to a very low variance of the random effect estimated at zero, leading to boundary issues (Bolker et al., 2013). We analysed the effect on the response variable through the following explanatory variables: farming system, vegetation type (with the exception of Bordeaux, see Table 1), date (i.e., sampling date), aAPTLC, proportion of semi-natural habitats cover and vineyard cover. For Palatinate, the additional landscape variable with or without hedge was added. The vine leaf hairiness index was added as explanatory variable for Leithaberg and Tárnave 2020. This variable could not be used for modelling the data from Palatinate and Bordeaux because in each region only one vineyard had a different leaf hairiness index (Table S4). Furthermore, we also added an interaction between farming system and date, in accordance with the wine-growing regions. Collinear explanatory variables with $\text{cor} \geq \pm 0.5$ were not included in the same models. This was only the case for the proportion of semi-natural habitats cover versus vineyard cover in Bordeaux ($\text{cor} = -0.81$) and Palatinate ($\text{cor} = -0.68$) and farming system versus aAPTLC in Tárnave 2020 ($\text{cor} = -0.7$). The variance inflation factor (VIF) of 2 was additionally used as criterion for exclusion of explanatory variables in the models (Zuur et al., 2010). Accordingly, global models were computed (Bartoń, 2020; Burnham and Anderson, 2002) for the phytoseiid datasets from Bordeaux, Palatinate, Leithaberg and Tárnave 2020 with all possible combinations of the explanatory variables that passed the above mentioned criteria. The most parsimonious models were selected based on the second-order Akaike's Information Criterion corrected for small sample size (AIC_c) with a minimum difference of Δi of 2 between the most parsimonious models (Burnham and Anderson, 2002). Model validations were performed graphical to ensure no violation of the model assumptions (Zuur et al., 2009).

3. Results

3.1. Phytoseiid mites across European wine-growing regions

We found phytoseiid mites in all investigated wine-growing regions, even though they were absent in some vineyards, especially in PDO

Montilla-Moriles. The highest phytoseiid mite densities across our survey were found in Târnavă 2019, followed by Leithaberg, Târnavă 2020, Bordeaux and Palatinate, whereas the lowest densities were found in PDO Montilla-Moriles (Table 2, Figure S1). Despite the high mite densities in Târnavă, the vineyards in this region also showed the lowest measured leaf areas, which were three to four times lower compared to the other wine-growing regions.

We identified 9 different phytoseiid mite species across the investigated wine-growing regions (Table 3). *Typhlodromus pyri* Scheuten was the dominant species in Bordeaux, Palatinate and Leithaberg. In PDO Montilla-Moriles, the main species was *Typhlodromus exilaratus* Ragusa. *T. pyri* and *Amblyseius andersoni* (Chant) were the most abundant species in Târnavă. The Shannon's diversity index showed a very low diversity of phytoseiid mite communities in Bordeaux, Palatinate, Leithaberg and PDO Montilla-Moriles. Only Târnavă had a higher Shannon's diversity and Pielou's evenness index, which is related to the dominance of two phytoseiid species in vineyards in this wine-growing region (Table S6).

3.2. Local and landscape effects on phytoseiid mite densities across European wine-growing regions

In general, the most parsimonious models in the Δi range from Târnavă 2020, Leithaberg, Palatinate and Bordeaux showed that phytoseiid mite densities were influenced by local and landscape variables in these wine-growing regions (Table 4). The influence of the sampling date was also consistent in all parsimonious models but affected phytoseiid mites differently in each region. Their populations increased during the vegetation season in Târnavă 2020, decreased in Palatinate and fluctuated in Leithaberg and Bordeaux (see effect plots for Târnavă 2020 Fig. 2, Leithaberg Fig. 3, Palatinate Fig. 4, Bordeaux Fig. 5). The effect of the farming system in the most parsimonious models in Leithaberg and Bordeaux showed that phytoseiid mite densities in integrated or conventional vineyards, respectively, were higher compared to the organic vineyards in those regions. This is in line with the application intensity and aAPTLC value, which was lower in integrated vineyards in Leithaberg and conventional vineyards in Bordeaux compared to the organic ones (Table S2). The negative effect of higher pesticide use measured by the aAPTLC was also visible in Palatinate where an increasing aAPTLC decreased the phytoseiid mite densities. In contrast, a high aAPTLC increased phytoseiid mite densities in Leithaberg. This could be related to applications of the active ingredient spinosad in three integrated vineyards, which lead to an increased aATPLC in those vineyards, despite high phytoseiid mite densities. In Târnavă 2020 phytoseiid mite densities seemed to slightly benefit from a higher pesticide input in the conventional vineyards.

The vegetation type in the most parsimonious models showed that phytoseiid mite densities benefited most from spontaneous vegetation cover in the inter-rows compared to bare soil in Târnavă 2020 and seeded cover crops in Palatinate and Leithaberg.

A higher vine leaf hairiness index increased phytoseiid mite densities in the most parsimonious models in Târnavă 2020 and Leithaberg (with the exception of a single vineyard in Leithaberg with a dense leaf hairiness index).

Considering the landscape variables, several most parsimonious models from Târnavă 2020, Leithaberg and Bordeaux showed that an increasing proportion of vineyards in the landscape increased phytoseiid mite densities. The opposite trend showed a higher proportion of semi-natural habitats, which decreased phytoseiid mite densities in those regions. In contrast, the most parsimonious models (15 different models in total) from Palatinate showed the opposite trend with increasing phytoseiid mite densities with higher proportions of semi-natural habitats and hedges nearby the vineyards. Furthermore, an increasing proportion of vineyards in the landscape decreased mite densities there. Even though half of the vineyards were chosen with a nearby hedge in Palatinate, the proportion of semi-natural habitats was more than two times lower compared to Târnavă, Leithaberg and Bordeaux. In addition, Palatinate landscapes were characterised by the highest proportion of vineyards at the landscape scale compared to the other wine-growing regions (Table S5).

3.3. Tydeid and pest mite communities across European wine-growing regions

Tydeid mites were found in all investigated wine-growing regions (Table 2). Nevertheless, they were absent in some vineyards in Târnavă and very scarce in PDO Montilla-Moriles with only few individuals in three vineyards. *T. goetzi* was the only identified species in Leithaberg and Palatinate (respectively 1760 and 739 identified individuals). In Bordeaux, *T. goetzi* was the most abundant species, followed by *Tydeus kochi* Oudemans (respectively 541 and 46 identified individuals). Species identification was not possible in Târnavă in both years and PDO Montilla-Moriles due to low numbers of shrivelled individuals.

Spider mites as known phytophagous mites in vineyards were absent in most vineyards and in general rare across our survey regions (Table 2). The vineyards in Târnavă showed the overall highest spider mite densities with the most abundant species *Panonychus ulmi* (Koch) (1746 individuals in 2019, 346 in 2020) followed by *Tetranychus urticae* Koch (50 individuals in 2019, 27 in 2020). Spider mites were absent in Leithaberg and only a few *P. ulmi* (25 individuals) were found in the Palatinate vineyards. Only a few vineyards were infested with spider mites in Bordeaux with mainly *P. ulmi* (76 individuals) and a few *T. urticae* (12 individuals). In PDO Montilla-Moriles, the main species was *Eotetranychus carpini* (Oudemans) (87 individuals), followed by *T. urticae* (2 individuals).

The two phytophagous eriophyid mite species *Colomerus vitis* (Pagenstecher) and *Calepitrimerus vitis* (Nalepa) were present in all wine-growing regions (Table 2). The lowest densities were found in Palatinate, Bordeaux and Leithaberg, followed by PDO Montilla-Moriles and Târnavă 2020. The high mean densities in Târnavă 2019 were associated to few vineyards (planted with the varieties Feteasca Regala, Feteasca Neagra and Sauvignon Blanc), which reached very high densities of eriophyid mites with up to 1502 eriophyid mites per 100 cm² vine leaf area. *Cal. vitis* was the dominant eriophyid species across our survey.

Table 2

Densities of the different mite communities in vineyards (mean \pm standard deviation) from each wine-growing region.

Wine-growing region (country)	Year	Mean \pm standard deviation of mite densities per 100 cm ² vine leaf area			
		Phytoseiid	Tydeid	Tetranychid	Eriophyid
Târnavă (Romania)	2019	3.09 \pm 4.95	0.63 \pm 3.63	2.6 \pm 6.95	31.65 \pm 161.46
	2020	1.83 \pm 2.36	0.19 \pm 0.92	0.45 \pm 1.57	3.28 \pm 12.22
Leithaberg (Austria)	2020	2.19 \pm 1.72	1.79 \pm 3.97	0 \pm 0	0.34 \pm 0.47
Palatinate (Germany)	2019	1.07 \pm 1.19	0.62 \pm 1.24	0.01 \pm 0.02 †	0.22 \pm 0.19
Bordeaux (France)	2020	1.42 \pm 1.03	0.97 \pm 1.72	0.02 \pm 0.07 †	0.33 \pm 0.57
PDO Montilla-Moriles (Spain)	2021	0.05 \pm 0.08	0.00 \pm 0.03 †	0.02 \pm 0.09 †	2.09 \pm 8.9

† Only a few individuals were found in some vineyards

Table 3

List of identified Phytoseiidae species from the whole survey with the number of identified specimens from each wine-growing region.

Phytoseiidae species	Number of specimens of each wine-growing region (country)					
	Tárnave 2019 (Romania)	Tárnave 2020 (Romania)	Leithaberg (Austria)	Palatinate (Germany)	Bordeaux (France)	PDO Montilla-Moriles (Spain)
<i>Amblyseius andersoni</i> (Chant)	309	208	0	0	1	0
<i>Amblyseius rademacheri</i> Dosse	2	0	0	0	0	0
<i>Euseius finlandicus</i> (Oudemans)	2	0	50	9	2	2
<i>Kampimodromus aberrans</i> (Oudemans)	0	0	0	0	1	0
<i>Paraseiulus talbii</i> (Athias-Henriot)	0	0	49	24	12	0
<i>Phytoseius macropilis</i> (Banks)	4	0	0	0	0	0
<i>Typhlodromus exhilaratus</i> Ragusa	0	0	0	0	0	82
<i>Typhlodromus pyri</i> Scheuten	245	281	3284	1617	2540	0
<i>Typhlodromus (Anthoseius) rhenanus</i> (Oudemans)	1	2	3	0	52	0
Total identified specimens	563	491	3368	1650	2608	84

Table 4Summary of the AIC_c (second-order Akaike's Information Criterion) values used for the selection of the most parsimonious models of the response variable phytoseiid mite density, with Δ_i as difference between the AIC_c values to the best model of the global models from the Linear models (LM) for Palatinate, Leithaberg and Tárnave as well from the Linear mixed models (LMM) for Bordeaux.

Wine-growing region	Most parsimonious models	AIC _c	Δ_i	Adjusted R ²	Marginal R ² _m	Conditional R ² _c
Tárnave 2020 (Romania)	Null model	27.08	–	–		
	Date + proportion of semi-natural habitat	-10.25	0.0	0.35		
	Date + proportion of semi-natural habitat + proportion of vineyards	-9.48	0.77	0.36		
	Date + vegetation type + proportion of semi-natural habitat	-8.35	1.90	0.35		
	Date + farming system + proportion of semi-natural habitat	-8.35	1.90	0.35		
	Date + vine leaf hairiness index + proportion of semi-natural habitat	-8.27	1.98	0.36		
	Date + aAPTLC + proportion of semi-natural habitat	-7.95	2.30	0.35		
Leithaberg (Austria)	Null model	-54.13	–	–		
	Date + aAPTLC + farming system + vegetation type + vine leaf hairiness index + proportion of semi-natural habitat + proportion of vineyards	-107.71	0.0	0.41		
	Date + aAPTLC + farming system + vegetation type + vine leaf hairiness index + proportion of semi-natural habitat	-107.07	0.64	0.41		
	Date + farming system + vegetation type + vine leaf hairiness index + proportion of semi-natural habitat + proportion of vineyards	106.08	1.63	0.39		
	Date + aAPTLC + farming system + vegetation type + proportion of semi-natural habitat	-105.51	2.2	0.38		
Palatinate (Germany)	Null model	-54.68	–	–		
	Date + proportion of semi-natural habitat	-91.34	0.0	0.28		
	Date + aAPTLC	-91.31	0.03	0.27		
	Date	-91.26	0.08	0.27		
	Date + aAPTLC + with or without hedge	-90.91	0.43	0.28		
	Date + aAPTLC + proportion of semi-natural habitat	-90.79	0.55	0.28		
	Date + with or without hedge	-90.66	0.68	0.27		
	Date + aAPTLC + proportion of vineyards	-90.26	1.08	0.28		
	Date + vegetation type + proportion of semi-natural habitat	-90.22	1.12	0.28		
	Date + aAPTLC + vegetation type	-90.19	1.15	0.28		
	Date + vegetation type	-90.17	1.17	0.27		
	Date + aAPTLC + vegetation type + with or without hedge	-89.77	1.57	0.28		
	Date + aAPTLC + vegetation type + proportion of semi-natural habitat	-89.65	1.69	0.28		
	Date + aAPTLC + with or without hedge + proportion of vineyards	-89.62	1.72	0.28		
	Date + vegetation type + with or without hedge	-89.54	1.80	0.27		
Date + proportion of vineyards	-89.45	1.89	0.26			
Date + aAPTLC + vegetation type + proportion of vineyards	-89.12	2.22	0.28			
Bordeaux (France)	Null model: circle/vineyard	-103.46	–	–	0	0.27
	Date + farming system	-147.13	0.0		0.25	0.53
	Date + farming system + proportion of vineyards	-146.18	0.95		0.27	0.53
	Date + farming system + proportion of semi-natural habitat	-145.58	1.55		0.26	0.53
	Date + farming system + aAPTLC	-144.86	2.27		0.25	0.53

4. Discussion

Our results highlight that field- and landscape-scale parameters affect the European phytoseiid mite species in vineyards. Overall, phytoseiid mites benefited most from integrated and conventional farming, spontaneous vegetation cover in the inter-row and from a higher proportion of vineyards in the surrounding landscape. The stable, effective phytoseiid populations combined with mostly low pest mite densities below economic thresholds (Duso and De Lillo, 1996; Isaacs et al., 2012) in Bordeaux, Palatinate, Leithaberg and Tárnave suggest that these natural enemies are able to provide biological control of pest mites in the

investigated vineyards across Europe. Only the vineyards in PDO Montilla-Moriles showed very low phytoseiid populations, which could be possibly due to the unfavourable dry and hot climate conditions for some phytoseiid species (Montserrat et al., 2013) and/or unfavourable local management practices (bare soil management and/or use of toxic pesticides for phytoseiid mites) (Duso et al., 2012). Furthermore, Pedro Ximénez is the main grape variety planted in PDO Montilla-Moriles and it has none to very weak pubescent leaves (International Organisation of Vine and Wine (OIV), 2009), which is probably not suitable enough for phytoseiid mite species which prefer pubescent leaves (Duso and Vectorazzo, 1999; English-Loeb et al., 2002; Schmidt, 2014; Tixier et al.,

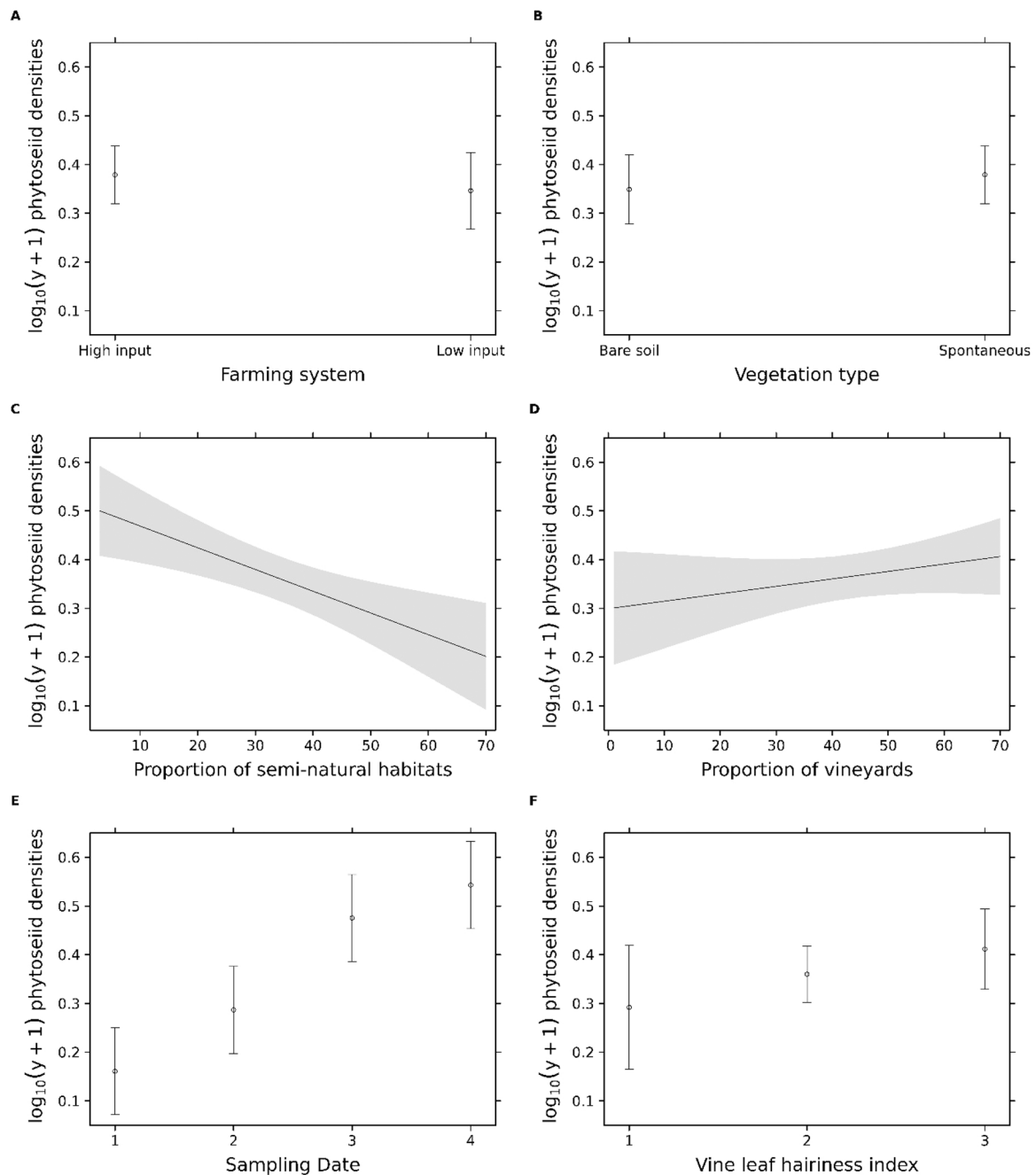


Fig. 2. Effect plots of the transformed phytoseiid mite densities per 100 cm² vine leaf area in Tärnave 2020. Response according to the five most parsimonious LMs: (A) farming system, (B) vegetation type, (C) proportion of semi-natural habitats in the landscape, (D) proportion of vineyards in the landscape, (E) sampling date in 2020 (1 = 15 June, 2 = 20 July, 3 = 24 and 25 August, 4 = 20, 25 September, and 5 October) and (F) vine leaf hairiness index (1 = absent, 2 = weak, 3 = medium hairiness). Grey shading/error bars indicate 0.95 confidence intervals.

2005). Beside phytoseiid mites, the occurrence of the tydeid species *T. goetzi* in Leithaberg, Bordeaux and Palatinat could possibly be an additional natural enemy, because this species was reported to feed on eriophyid mites on vines (Schruff, 1972).

4.1. Phytoseiid mite communities in European vineyards

Overall, the low phytoseiid species diversity in Leithaberg, Palatinat, Bordeaux and PDO Montilla-Moriles was mainly attributed to the dominance of *T. pyri* in the former three wine-growing regions and *T. exhilaratus* in the latter. The higher diversity in Tärnave was based on the co-occurrence of *T. pyri* and *A. andersoni* in similar proportions. The

dominance of *T. pyri* was already shown in Bordeaux (Kreiter et al., 2000), Palatinat (Reiff et al., 2021) and Leithaberg (Möth et al., 2021). Pesticide applications as well as a species- or strain-specific pesticide resistance of phytoseiid mites (Duso et al., 2020) are often mentioned as two factors out of several which can cause the dominance of a single or few species (Kreiter et al., 2000; Sabbatini Peverieri et al., 2009; Tixier et al., 2013). The resistance to some pesticides is already well known for *T. pyri* (Hluchý et al., 1991) and *A. andersoni* (Bonafos et al., 2007) in vineyards. Also, intraguild predation among phytoseiid species can lead to a shift in their dominance ranking. For example, *A. andersoni* is known as an aggressive intraguild predator (Walzer and Schausberger, 2011) which could be an advantage for its dominance together with *T. pyri* in

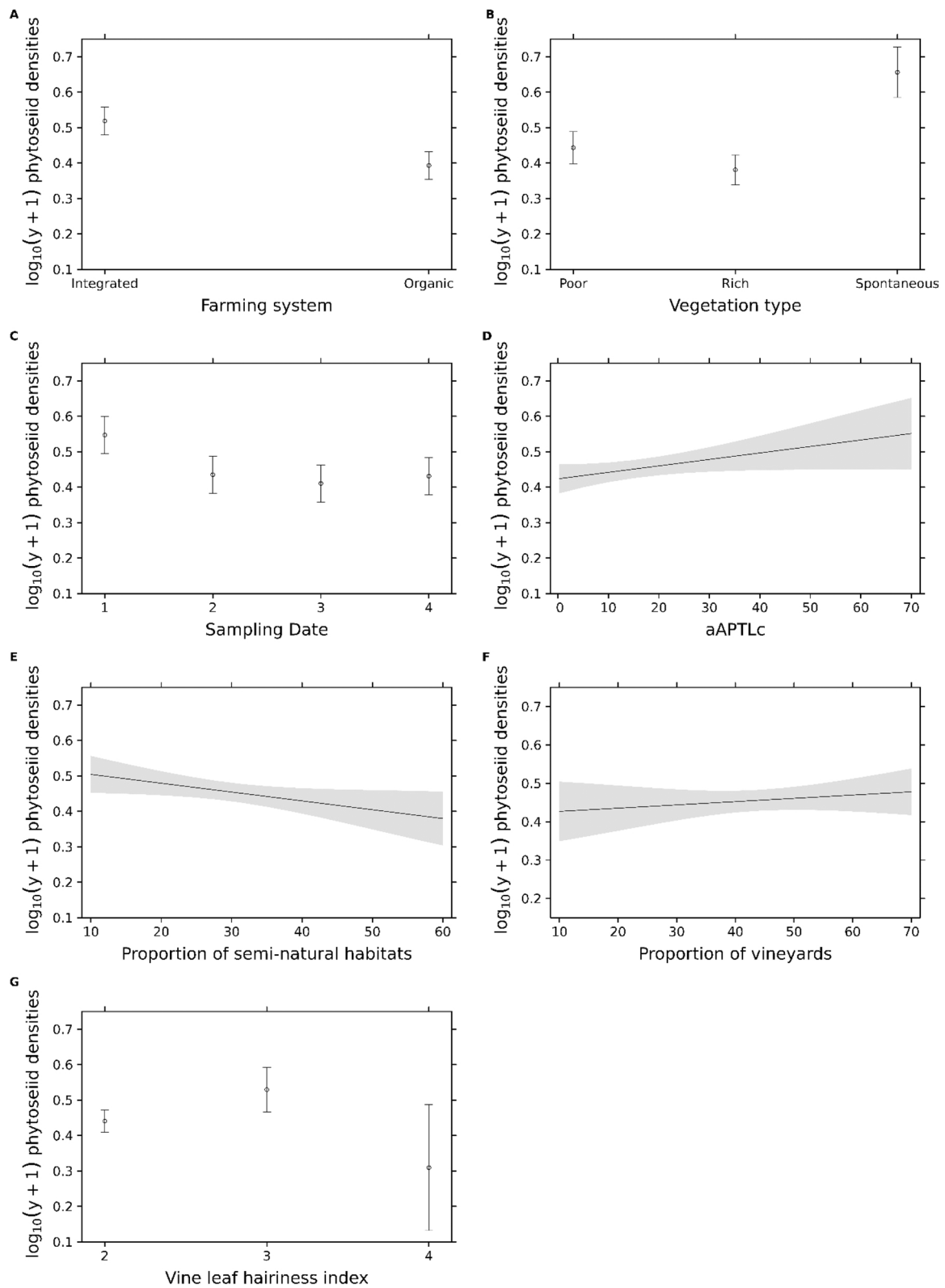


Fig. 3. Effect plots of the transformed phytoseiid mite densities per 100 cm² vine leaf area in Leithaberg. Response according to the two most parsimonious LMs: (A) farming system, (B) vegetation type, (C) sampling date in 2020 (1 = 8 June, 2 = 6 July, 3 = 3 August, 4 = 31 August), (D) area-related acute pesticide contact toxicity loading index (aAPTLC), (E) proportion of semi-natural habitats in the landscape, (F) proportion of vineyards in the landscape and (G) vine leaf hairiness index (2 = weak, 3 = medium and 4 = dense hairiness). Grey shading/error bars indicate 0.95 confidence intervals.

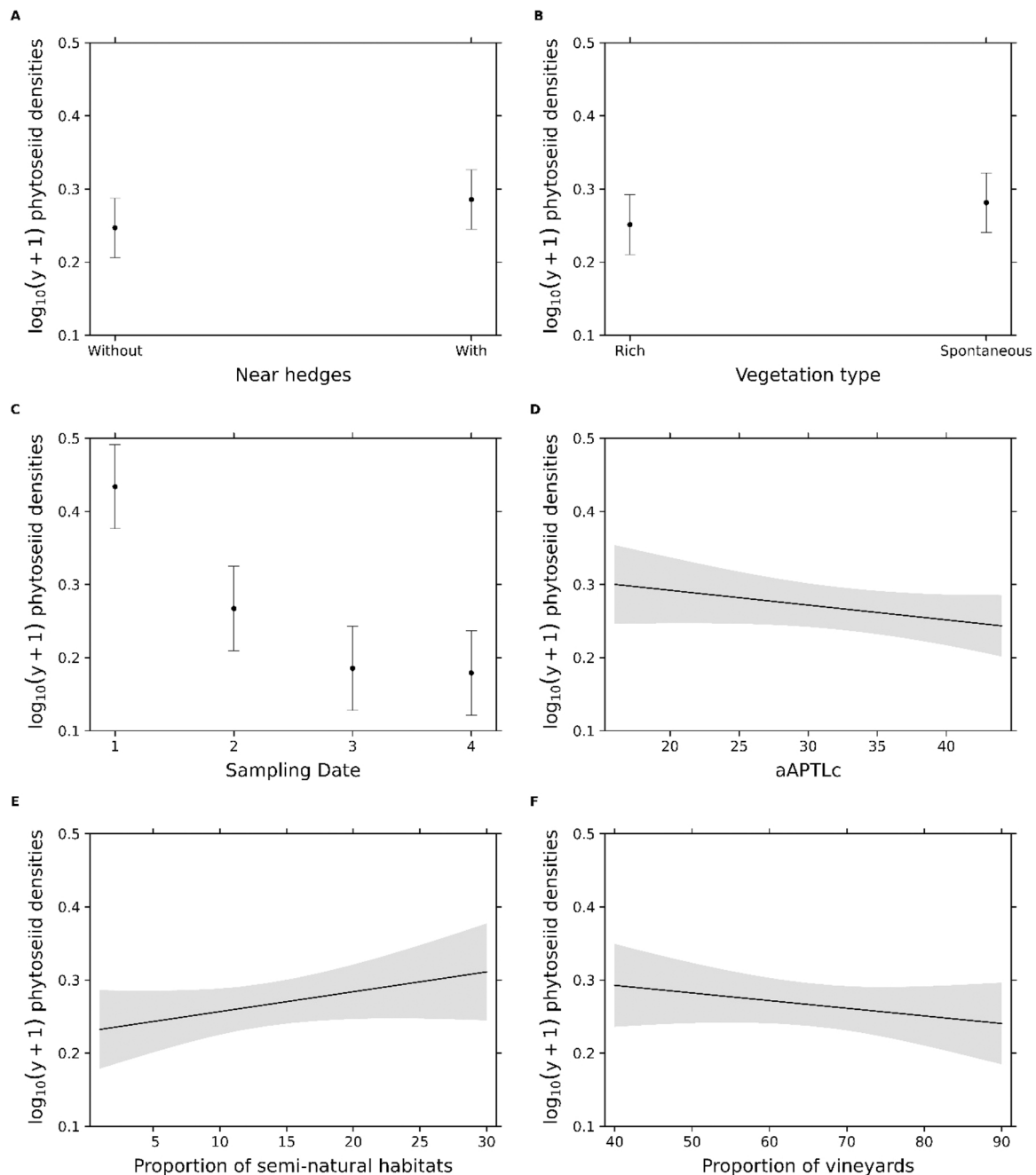


Fig. 4. Effect plots of the transformed phytoseiid mite densities per 100 cm² vine leaf area in Palatinat. Response according to five most parsimonious LMs out of 15: (A) hedges near the vineyard, (B) vegetation type, (C) sampling date in 2019 (1 = 3 June, 2 = 11 July, 3 = 15 August, 4 = 10 September), (D) area-related acute pesticide contact toxicity loading index (aAPTLC), (E) proportion of semi-natural habitats in the landscape and (F) proportion of vineyards in the landscape. Grey shading/error bars indicate 0.95 confidence intervals.

Tárnave. The community composition of phytoseiid mites depends also on leaf traits such as leaf hairiness or domatia formation (Duso, 1992; Kreiter et al., 2002; Roda et al., 2003; Schmidt, 2014; Tixier et al., 2005). The most parsimonious models in Leithaberg and Tárnave showed that phytoseiid mite densities were the highest on grape varieties with a medium leaf hairiness index but only slightly lower on grape varieties with a weak leaf hairiness. *T. pyri* prefers pubescent leaves, whereas *A. andersoni* tends to prefer glabrous or slightly pubescent leaves (Duso and Vettorazzo, 1999). The grape varieties in Bordeaux, Palatinat, Leithaberg and Tárnave showed a weak and medium vine leaf hairiness index and were therefore suitable for *T. pyri* (e.g. Feteasca regala, Grüner Veltliner, Merlot, Müller-Thurgau, Riesling, Sauvignon Blanc and

Zweigelt). Nevertheless, the co-dominance of *T. pyri* and *A. andersoni* in Tárnave may only be partly connected with the leaf hairiness index as only a few sampled vineyards planted with the varieties Palatina, Muscat Ottonel and Feteasca alba had glabrous leaves. Moreover, *A. andersoni* was also dominant on the cultivar Sauvignon Blanc with a medium leaf hairiness index.

The consequences of climate warming (Jia et al., 2019), region-specific temperatures and relative humidity conditions may have also influenced the phytoseiid species composition (Montserrat et al., 2013; Tixier et al., 2013; Warburg et al., 2019) or caused a shift in the dominance of one species (Guzmán et al., 2016). This could be another possible factor for the co-dominance of *T. pyri* and *A. andersoni* in

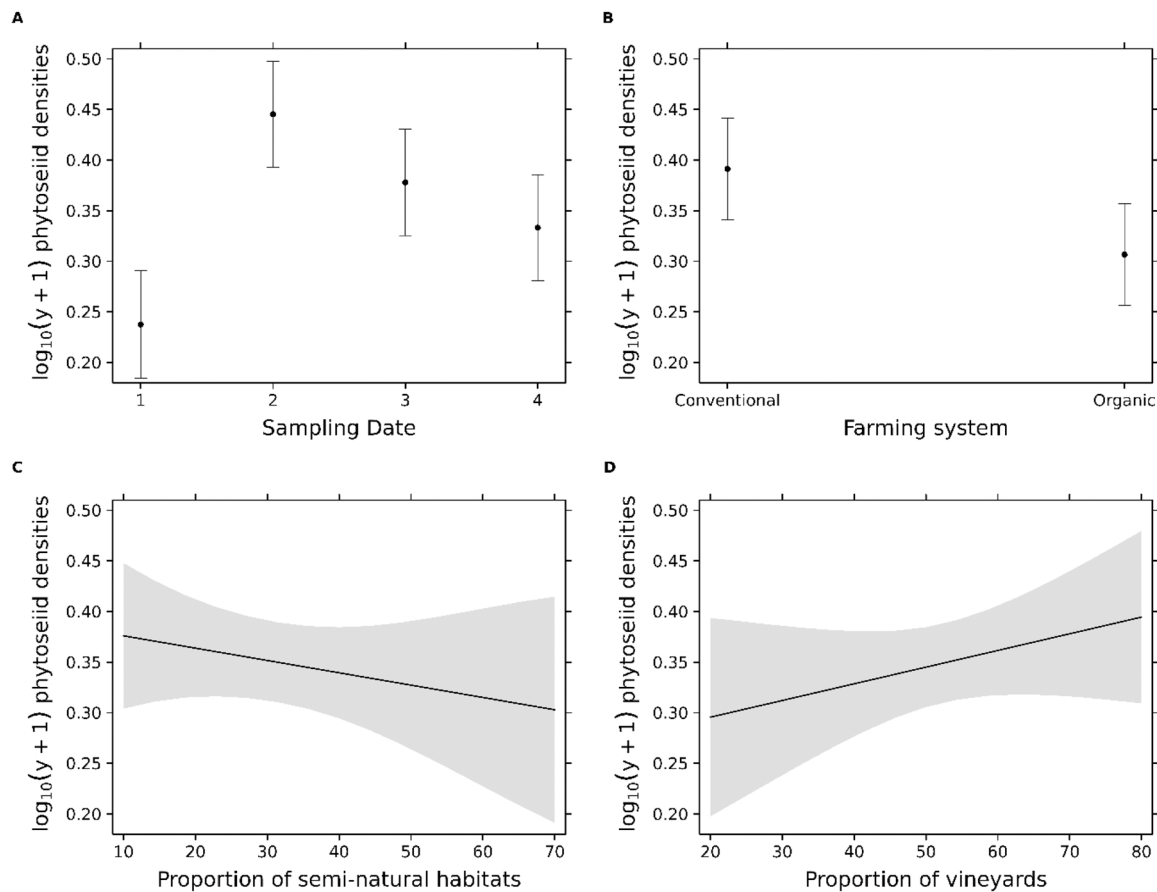


Fig. 5. Effect plots of the transformed phytoseiid mite densities per 100 cm² vine leaf area in Bordeaux. Response according to the three most parsimonious LMMs: (A) sampling date in 2020 (1 = 2 June, 2 = 29 June, 3 = 10 August, 4 = 7 September), (B) farming system, (C) proportion of semi-natural habitats in the landscape and (D) proportion of vineyards in the landscape. Grey shading/error bars indicate 0.95 confidence intervals.

Tárnave because [Duso and Pasqualetto \(1993\)](#) showed that *A. andersoni* populations did not decline drastically during a summer with high temperatures and low relative humidity compared to *T. pyri* populations in an experimental vineyard in Italy. [Karg \(1993\)](#) suggested that relative humidity may be the main limiting factor for phytoseiid species. Such effects could explain the dominance of *T. exhilaratus* in PDO Montilla-Moriles, because this species has a high tolerance against dry and hot conditions ([Liguori and Guidi, 1995](#)). Accordingly, the influence of the region-specific weather conditions could be already seen by the different phytoseiid populations dynamics in each wine-growing region, indicated through the sampling date effects. Summing up, evidence for a mono-causal explanation of the dominance of a single species in the wine-growing regions could not be determined. Nevertheless, we also point out that the very low phytoseiid diversity across European wine-growing regions could be problematic due to climate change. Accordingly, the dependency on a single taxon or even strain could result in a dominance shift of predatory mite communities ([Yachi and Loreau, 1999](#)).

4.2. Effect of the farming system and pesticide use on phytoseiid mites

Our findings showed that the farming system was one major variable, which affected phytoseiid mite densities in vineyards. Surprisingly, organic vineyards exhibited lower mite densities in comparison to integrated (Leithaberg) or conventional (Bordeaux) ones. Studies from Switzerland and Germany also found that phytoseiid mite densities were lower in organic compared to conventional farming ([Linder et al., 2006](#); [Reiff et al., 2021](#)). Contrary, beneficial effects of organic farming for phytoseiid mites were observed in Italy and Portugal ([Sabbatini](#)

[Peveieri et al., 2009](#); [Silva et al., 2019](#)). The most plausible reason for our observed negative effect of organic management could be associated to the pesticide use in these vineyards. It is known that some active ingredients such as mancozeb, metiram, paraffinic oil, sulphur are harmful for phytoseiid mites ([Gadino et al., 2011](#); [Kemmitt et al., 2015](#); [Pozzebon et al., 2002](#); [Schruff et al., 1992](#)), especially when they are applied several times ([Schruff et al., 1992](#)). Studies showed accordingly that phytoseiid mites benefited from lower pesticide applications ([Blümel et al., 1997](#); [Pennington et al., 2017](#); [Reiff et al., 2021](#); [Schruff et al., 1992](#)). Nevertheless, phytoseiid mite species could have developed specific pesticide resistance, e.g. *T. pyri* and its resistance to pyrethroid and organophosphate insecticides ([Bonafos et al., 2007](#); [Hluchý et al., 1991](#)). The higher toxicity load index and frequency of applied pesticides in organic, compared to conventional or integrated vineyards, reflects this negative effect of the relative intensive use of the fungicides sulphur and copper in that farming system. The negative effect of sulphur on phytoseiid mites ([Gadino et al., 2011](#); [Schruff et al., 1992](#)) is of special interest, because of its frequent applications in organic vineyards. This was also shown in Palatinate (only organic vineyards) where the phytoseiid mites benefited from a lower aAPTLC (this explanatory variable was present in more than 50 % of the most parsimonious models). However, in Leithaberg, a higher aAPTLC seemed to be associated with higher phytoseiid mite densities, which could be due to the used insecticide with the active ingredient spinosad in three integrated vineyards with high phytoseiid mite densities in this survey region. Spinosad is highly toxic to bees, but not to phytoseiid mites ([Bundesamt für Verbraucherschutz und Lebensmittelsicherheit, 2021](#); [Lewis et al., 2016](#)), which resulted in a high aAPTLC reflecting the toxicity for bees but not for phytoseiid mites. Nevertheless, a recent study showed that

the aAPTLc correlates moderately with a categorial toxicity rating for phytoseiid mites (Möth et al., 2021). In Palatinate, no insecticides were used, and all investigated vineyards applied only sulphur, copper, and other organic-certified fungicides. Despite the disadvantage of the taxon-specific toxicity of this index, the aAPTLc was useful to show differences in the pesticide input between farming systems.

Surprisingly, phytoseiid mite densities from Tärnave in 2020 were slightly higher under high pesticide input in comparison to low pesticide input (all vineyards under conventional farming). However, this response was rather weak with a high variation. It is also important to mention that those vineyards had a high disease pressure due to mildew infections. Mycelium and spores from grape powdery mildew and grape downy mildew are suitable alternative food resources for *A. andersoni* and *T. pyri* (Pozzebon et al., 2009; Pozzebon and Duso, 2008), which therefore could have contributed to an increase of their populations.

In summary, the use of pesticides which are harmful for phytoseiid mites, especially sulphur (Gadino et al., 2011; Schruft et al., 1992) in organic vineyards, is a crucial factor for phytoseiid mite densities in vineyards. The reduction of these harmful pesticides has beneficial effects for predatory mites (Pennington et al., 2017; Reiff et al., 2021; Schruft et al., 1992) and contributes to the European Union policy goal of halving the use of pesticides by 2030 (European Commission, 2020).

4.3. Beneficial impact of inter-row vegetation as food resource for phytoseiid mites

Our statistical analysis suggests that phytoseiid mite populations in vineyards benefited from spontaneous vegetation cover in the inter-rows in Palatinate, Leithaberg and Tärnave. This could be related to the beneficial effect of pollen on vine leaves from flowering plants in the vineyard inter-rows (Duso et al., 2002; Möth et al., 2021; Wiedmer and Boller, 1990), because pollen is a key food resource for phytoseiid mites (Boller and Frey, 1990; Engel and Ohnesorge, 1994; McMurtry et al., 2013). Previous studies showed that spontaneous vegetation cover compared to bare soil, significantly increased phytoseiid mite populations in vineyards (Castagnoli et al., 1999; Sáenz-Romo et al., 2019a; Vogelweith and Thiéry, 2017) which complies with our results in Tärnave. Vegetation cover generally increase phytoseiid mite densities in vineyards (Burgio et al., 2016; Castagnoli et al., 1999; de Villiers and Pringle, 2011; Sáenz-Romo et al., 2019a; Vogelweith and Thiéry, 2017; Zanettin et al., 2021). However, according to our results from Palatinate and Leithaberg, spontaneous vegetation resulted in higher mite densities compared to seeded cover crops (see also Möth et al., 2021). This could be related to the type of plants and thus to the type of pollen provided by spontaneous vegetation versus seeded cover crops (Möth et al., 2021), as the nutritive value for development and reproduction of phytoseiid mites vary between different plant species (Engel and Ohnesorge, 1994). Further research investigating pollen composition on vine leaves would be required to confirm our hypothesis across different wine-growing regions.

4.4. Effects of the landscape structure on phytoseiid mites

Our results from Bordeaux, Leithaberg and Tärnave showed that phytoseiid mite densities benefited from a higher proportion of vineyards and that populations decreased with a higher proportion of semi-natural habitats in the surrounding landscape. This suggests lower spill-over from semi-natural habitats, which can therefore hardly mitigate negative effects through pesticides. This is in contrast to the study from Judt et al. (2019) which showed that a higher proportion of vineyards decreased parasitoids. Moreover, semi-natural habitats could promote biological pest control of grape berry moth delivered by its natural enemies in vineyards (Paredes et al., 2020; Rusch et al., 2017). Semi-natural habitats may be the source for phytoseiid mite dispersal into vineyards (Duso et al., 2004; Hill and Schlamp, 1986; Tixier et al., 2006, 2000a, 1998). Nevertheless, vineyards and viticultural areas in a

broader sense also act as reservoirs for phytoseiid mites and favour their dispersal in neighbouring vineyards, if they already contain well established and high populations (Hill and Schlamp, 1986; Tixier et al., 1998). As a result, the proportion of vineyards are probably more important for phytoseiid mite dispersal within a viticultural area at the landscape scale. This is in line with a recent French study, which confirmed the missing positive effect of semi-natural habitats for phytoseiid mites in vineyards (Kreiter et al., 2017). Furthermore, dominant phytoseiid species in vineyards were mostly adapted to viticultural practices, e.g. *T. pyri* and its pesticide resistance (Camporese and Duso, 1996; Kreiter et al., 2017; Tixier et al., 2000b). This could be an advantage for those phytoseiid species and their dispersal ability, considering possible side effects of pesticides on phytoseiid mites through spray drift (Fornasiero et al., 2017; Otto et al., 2013). Therefore, we suggest that neighbouring vineyards are more favourable to mitigate possible phytoseiid population declines through the negative effect of harmful pesticides than semi-natural habitats.

The results from Palatinate are contrastive to the other wine-growing regions, because phytoseiid mite densities benefited from a higher proportion of semi-natural habitats but decreased with a higher proportion of vineyards at the landscape scale. This could be related to the much lower proportion of semi-natural habitats at the landscape scale and the study design, where half of the sampled vineyards were chosen based on their proximity to a nearby hedge. This positive influence of the nearby hedge was recognizable in the slightly higher phytoseiid mite densities in those vineyards. This was also the case in a French experimental vineyard where Tixier et al. (2000a) showed that trees and hedges strongly impacted mite densities, especially in a short distance to vineyards. This could have masked the dispersal effect of the surrounding vineyards (Hill and Schlamp, 1986; Tixier et al., 1998). Moreover, it is possible that the influence of semi-natural habitats is an important factor for vineyards with low phytoseiid mite populations, while in vineyards with high and stable phytoseiid mite densities, the dispersal effect in vineyards from semi-natural habitats is less significant. Therefore, the deviating results in Palatinate could be associated with the low phytoseiid mite densities in those organic vineyards, compared to Bordeaux and Leithaberg.

5. Conclusion

In all investigated wine-growing regions except for PDO Montilla-Moriles, the low densities of eriophyid and tetranychid mites suggested that phytoseiid populations were able to provide effective biological control of these pest mites. Phytoseiid mite populations were influenced by local viticultural practices and landscape composition in the wine-growing regions in Europe we investigated. Our results showed that lower applications of fungicides and insecticides, a reduced use of active ingredients harmful to phytoseiid mites, inter-row spontaneous vegetation as well as high proportions of vineyards in the landscape benefited phytoseiid mites. Pesticide use at the local scale seems to be a major factor for these natural enemies, while we suppose that pollen supply provided by spontaneous vegetation may have enhanced phytoseiid mite densities more than seeded cover crops or bare soil inter-rows. Surprisingly, our results showed that in most cases vineyards act as source of phytoseiid mites for other vineyards in the landscape. Phytoseiid diversity was very low across all investigated wine growing regions highlighting the need to further studies how such species-poorly communities might resist to global change impacts. Future studies exploring an even larger set of vineyards with different grape varieties covering the whole range of the leaf hairiness index would be needed to explore the mutual effects of the landscape, vineyard management and leaf hairiness on phytoseiid mites. Furthermore, there is still a lack of knowledge how other natural enemy communities in vineyard landscapes may be affected through the investigated factors.

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Author contributions

Conceptualization, S.W., A.W., and S.M.; methodology, C.H., S.W., S.M.; mite sampling S.R.-C., J.R., S.K., D.P., M.C., R.H.A., S.M.; species determination, S.M.; data analysis and validation, S.M. and S.W.; investigation, S.M.; resources, S.W.; data curation, S.M.; writing—original draft preparation, S.M.; writing—review and editing, S.W., A.W., C.H. J.R., S.K., D.P., M.C., R.H.A., A.R., P.T. S.R.-C.; visualization, S.M.; supervision, S.W. and A.W.; project administration, S.W.; funding acquisition, S.W. All authors have read and agreed to the published version of the manuscript.

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.

Data Availability

The data presented in this study are openly available in Zenodo at: <https://doi.org/10.5281/zenodo.7096327>.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2022.108292](https://doi.org/10.1016/j.agee.2022.108292).

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