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ORIGINAL ARTICLE

Effect of fungicide sprays on spiders in vineyards

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Abstract. Spiders are the most abundant naturally occurring predators in vineyards and play a crucial role in natural pest control. However, vineyards are frequently sprayed with fungicides, which can harm spider communities. Fungus-resistant grape varieties can drastically reduce this fungicide input. The spiders on grape vines that were sprayed with a variable number of fungicide applications in 32 vineyards in different landscapes in Southwestern Germany were recorded. Vineyards received between 0 and 14 fungicidal sprays of varying toxicity (cumulated hazard quotients for honeybee up to 6). The majority of spiders benefited from a reduction in the number fungicide sprays, particularly Dictynidae, Philodromidae, Theridiidae and Thomisidae. Overall, space web weavers, orb web weavers and ambush hunters were most strongly affected by the frequency and toxicity of fungicide applications. The response of spiders to the landscape were highly variable and included both positive and negative effects of the percentage cover of woodland. In conclusion, reducing the cumulative hazard of fungicides by reducing the number of fungicide applications is a key element in fostering spiders in vineyards.

1. INTRODUCTION

Spiders are very abundant naturally occurring predators in agroecosystems and are a crucial component of natural pest control (Cahenzli et al., 2017). Although most spiders are generalists, their hunting strategies differ greatly (Cardoso et al., 2011). For instance, ambush hunters catch mainly Hymenoptera while orb web weavers catch mainly Diptera (Michalko & Pekár, 2016). Furthermore, even within the same family of web-building spiders, prey preferences vary (Birkhofer et al., 2017). This indicates their potential in terms of pest control, and that the targeting of various pest species and life stages is enhanced by a high spider biodiversity.

However, agroecosystems are characterized by frequent disturbances such as tillage and pesticide treatments (Landis et al., 2000). In particular, the application of pesticides can have detrimental effects on spiders. In laboratory experiments some insecticides, acaricides and fungicides are lethal for some single species of spiders (Mansour & Nentwig, 1988; Pekár, 2002). In addition, web building behaviour, such as web size, frequency of web renewal and accuracy of web construction can be affected by pesticides (Samu & Vollrath, 1992; Benamú et al., 2013). In the field, it is mainly insecticides, but also some fungicides, that affect the abundance of spiders in orchards, vineyards and cereal fields (Bostanian et al., 1984; Wisniewska & Prokopy, 1997; Holland et al., 2005; Thomson & Hoffmann, 2006; Markó et al., 2010; Marliac et al., 2016). Although the majority of fungicides appear to be harmless to spiders, at least under field conditions (Pekár, 2012), there is evidence that frequent applications of fungicides can have detrimental effects on arthropod communities, including spiders (Nash et al., 2010; Michalko & Košulič, 2020).

Vineyards are among the most pesticide dependent crops worldwide. Grapes are highly susceptible to several fungal diseases, which can result in 12–15 fungicide sprays per year (Pertot et al., 2017). A frequent use of fungicides is further related to increased accumulated toxicity and thus poses great hazard for non-target organisms (Möth et al., 2023). Organic farming is often said to use less pesticide of lower toxicity which in turn promotes arthropod diversity and natural pest control (Bengtsson et al., 2005; Muneret et al., 2018). However, pesticide applications in viticulture are similar or even higher under organic compared to conventional management (Reiff et al., 2021b; Beaumelle et al., 2023; Kaczmarek et al., 2023). Fungus-resistant grape varieties can reduce this fungicide input on average by 80% (Thiollet-Scholtus et al., 2021) and consequently fosters natural enemies (Pennington et al., 2017, 2018; Reiff et al., 2021a, 2023).

In addition to local factors, spiders are known to be greatly influenced by the composition of the agricultural landscapes (Schmidt et al., 2008; Chaplin-Kramer et al., 2011). Usually natural habitats harbour a greater arthropod richness and abundance, particularly of predators, than intensive agriculture (Attwood et al., 2008; Mestre et al., 2018). Accordingly, natural pest control is promoted in complex landscapes (Bianchi et al., 2006; Veres et al., 2013). The efficacy of spiders in natural pest control can vary over time and depends on factors such as the species, their ability to disperse and structure of non-crop habitats in the agricultural landscape (Öberg et al., 2008; Picchi et al., 2016; Schirmel et al., 2016; Munévar et al., 2018; Michalko & Birkhofer, 2021). Effects of landscape composition on vineyard arthropods in general are highly variable, and may be less pronounced than in annual crops (Thomson et al., 2010; Wilson et al., 2015; González et al., 2017; Judt et al., 2019; Papura et al., 2020; Möth et al., 2021; Kaczmarek et al., 2023). Previous studies on the effect of landscape on spiders in vineyards focused on ground-dwelling species (Kolb et al., 2020). Thus, there is a lack of research on how spiders on grape vines are affected by the landscape.

Spiders are the most abundant naturally occurring predators in the macrofauna on grape vines (Costello & Daane, 1999; Reiff et al., 2023), which makes them key species for natural pest control. For instance, spiders have been observed attacking larvae and pupae of lepidopteran grapevine pests (Marchesini & Dalla Montà, 1994; Frank et al., 2007; Reiff et al., 2021b). Furthermore, web building spiders play an important role in capturing flying adults of pests of grape vines (Michalko et al., 2019). Preserving a diverse spider community comprised of species with different hunting strategies may be crucial for suppressing the different life stages of vineyard pests.

Here, we studied how spiders on grape vines in vineyards are affected by the number of fungicide applications and the composition of the landscape in 32 vineyards in Southwestern Germany. Currently, negative effects of frequent fungicide application are reported for two of the four analysed dominant spider families (Reiff et al., 2023). In this paper, the same samples as those used in Reiff et al. (2023) were used, but the taxonomic coverage was extended to include all of the spiders, their trait composition and diversity at various taxonomic levels was assessed, and analyses of landscape effects were incorporated. It was hypothesized that the frequency of fungicide treatments and the overall toxicity of applications has a marked negative effect on spider abundance and diversity. Secondly, a higher spider diversity is predicted in landscapes with a high cover of semi-natural habitats.

2. MATERIAL AND METHODS

2.1. Study sites

Thirty-two vineyards in the Palatinate region of Germany (between 49°16′41.034″N, 8°5′13.412″E and 49°8′22.787″N, 8°9′56.581″E) were studied. These vineyards belonged to 16 winegrowers, who managed them either conventionally or organically (no synthetic fertilisers or pesticides). Each winegrower provided one pair of vineyards, one of which was planted with fungus-resistant varieties and the other with susceptible grape varieties. These four combinations resulted in a highly variable plant protection regime, including different frequencies of fungicide treatments and hazard quotients of the products applied. No insecticides were used in the vineyards studied, with the exception of one application each in two conventionally managed vineyards. Hazard quotients were calculated by summing the quotients based on the application rates and contact LD_{50} values for honeybees for all fungicides and insecticides applied (Reiff et al., 2023). The half-lives of pesticides were not considered, as it was assumed the direct effects were on the grape vines, which were sprayed and where the spiders were sampled, and as persistent pesticides such as copper would influence disproportionally the calculated hazard quotient (a non-degradable heavy metal cannot be included in an index where degradability is relevant). While organic sprays are mainly copper, sulphur and potassium bicarbonate, the conventional vineyards were sprayed with a total of 35 different products containing 33 distinct active ingredients. The most frequently applied were sulphur (in both organic and conventional vineyards), Folpet, Metiram, and Ametoctradin.

In addition, the cover of woody semi-natural habitats (mainly hedgerows, woodlands and forest) within circular landscape sectors were analysed. A 500 m radius around the vineyards was chosen, since this spatial scale best explained differences in species richness in both univariate and multivariate analyses (Drapela et al., 2008) and is used in several other studies (Clough et al., 2005; Öberg et al., 2008; Schirmel et al., 2016). Using QGIS (QGIS Development Team, 2016) and satellite images obtained from Landesamt für Vermessung und Geobasisinformation Rheinland-Pfalz, Koblenz, 2014, patches of woody semi-natural habitats were identified and their percentage surface area calculated.

2.2. Spider sampling

Spiders were sampled from grape vines where the effect of fungicide applications is expected to be highest. Sampling took place during the vegetation period from the end of May to mid-October 2018 on six occasions. On average, each vineyard was sampled every 23 ± 7 days. However, sampling intervals varied due to vineyard management by the winegrowers. Accordingly, there was not a standardised period between fungicide application and spider sampling. Each time 30 randomly selected grape vines per vineyard were sampled by placing a 72 cm diameter beating tray (Dynort, bioform Dr. J. Schmidl e.K., Nürnberg, Germany) underneath the canopy and then shaking the grape vines vigorously for approximately 5 s. Spiders falling on to the tray were collected and stored in 70% ethanol. Adult spiders were identified to species and juvenile spiders to family level. Several juveniles with a unique habitus were further identified to genus level.

2.3. Data analyses

To take into account the design of the study and reduce seasonal effects, the total number of spiders collected from the end of May to mid-October was recorded for each vineyard. All statistical analyses were done using R version 3.6.3 (R Development Core Team, 2015). Individuals were classified into guilds according to their hunting strategy described in Cardoso et al. (2011). In addition, all guilds, families and genera that were sufficiently abundant were also analysed statistically.

The distribution of the response and predictor variables were checked visually using ‘qqp’ (R package car; Fox & Weisberg, 2019) using either Gaussian or negative binomial distributions (see Table 1). Several (generalized) linear mixed-effect models containing “site” as a random factor were fitted with the functions ‘lmer’ or ‘glmer.nb’ (R package lme4; Bates et al., 2015). A separate lmer with “spraying frequency” as explanatory and “hazard quotient” as a response variable was run to test for their relation-

Table 1. Family distribution and model output for two explanatory and 32 tested response variables. Model predicted effect sizes for hazard quotients (from 0 to 6) and percentage of semi-natural habitats (SNH, from 0 to 45%) are given as percentage increase or decrease. Significant P-values (α = 0.05) are highlighted in bold.

Response variable	Family distribution	Hazard quotient			% woody SNH		
		X^2	P	%	X^2	P	%
spider abundance	Gaussian	13.263	**<0.001**	–48.65	0.020	0.888	+4.67
family richness	Gaussian	0.295	0.530	–4.78	1.846	0.174	+16.99
genus richness	Gaussian	2.082	0.149	–11.23	6.318	**0.012**	+28.32
species richness	Gaussian	7.761	**0.005**	–42.73	0.084	0.772	+7.38
abundance of orb web weavers	Gaussian	4.758	**0.029**	–40.89	0.428	0.513	–26.66
abundance of other hunters	Gaussian	3.833	0.050	–42.93	1.708	0.191	+55.93
abundance of sheet web weavers	negative binomial	0.266	0.606	–20.74	0.015	0.902	+8.21
abundance of space web weavers	negative binomial	31.910	**<0.001**	–61.35	0.715	0.398	–29.79
abundance of ambush hunters / Thomisidae	Gaussian	5.112	**0.024**	–62.61	0.009	0.924	+5.53
abundance of Araneidae	Gaussian	3.671	0.055	–37.21	0.651	0.420	–31.36
abundance of Dictynidae	negative binomial	7.818	**0.005**	–84.41	12.103	**<0.001**	–97.56
abundance of Linyphiidae	negative binomial	0.429	0.513	–24.86	0.001	0.982	+1.92
abundance of Philodromidae	negative binomial	4.461	**0.035**	–52.57	2.979	0.084	+122.49
abundance of Salticidae	Gaussian	0.020	0.889	–4.53	1.942	0.163	–66.47
abundance of Tetragnathidae	negative binomial	3.561	0.059	–65.43	0.022	0.881	–13.40
abundance of Theridiidae	Gaussian	8.731	**0.003**	–52.86	0.353	0.552	+73.20
Araneus sp.	negative binomial	0.009	0.923	+6.70	0.114	0.736	+30.88
Araniella sp.	negative binomial	5.324	**0.021**	–59.98	0.008	0.928	–4.28
Dictyna sp.	negative binomial	4.668	**0.031**	–77.14	13.149	**<0.001**	–99.67
Heliophanus sp.	negative binomial	2.302	0.129	–62.45	0.566	0.452	–40.33
Mangora sp.	Gaussian	0.562	0.453	–26.56	3.473	0.062	–68.72
Marpissa sp.	negative binomial	0.141	0.707	+37.44	5.782	**0.016**	–97.72
Misumena sp.	negative binomial	3.814	0.051	–70.68	11.060	**<0.001**	+883.72
Neottiura sp.	negative binomial	1.842	0.175	–45.42	0.443	0.506	–33.20
Philodromus sp.	negative binomial	2.302	0.129	–41.26	5.779	**0.016**	+201.05
Phylloneta sp.	negative binomial	2.481	0.115	–45.98	0.139	0.709	–15.58
Salticus sp.	negative binomial	0.022	0.881	–6.25	4.739	**0.029**	–72.35
Synageles sp.	negative binomial	0.567	0.452	–38.07	0.007	0.934	–7.43
Theridion sp.	negative binomial	2.373	0.123	–61.46	0.026	0.873	–13.44
Tenuiphantes sp.	negative binomial	0.757	0.384	–50.23	0.493	0.483	–42.92
Tetragnatha sp.	negative binomial	2.180	0.140	–66.78	0.042	0.837	–18.05
Xysticus sp.	negative binomial	0.921	0.337	–30.37	0.033	0.856	–9.05

ship (see Fig. 1). To calculate the R^2-value for this relationship the function ‘rsquare’ (R package modelr; Wickham, 2023) was used (see Fig. 1). Due to the strong dependency of the two explanatory variables “spraying frequency” and “hazard quotient”, “spraying frequency” was not included in subsequent analyses. Models contained “% woody semi-natural habitat” and “hazard quotient” as explanatory variables and the different abundances of spiders (total, guilds, families, genera) as a response variable (see Table 1). No correction for multiple testing was done (see Moran, 2003).

Effects on the composition of families, genera, species and guilds were analysed using the R package vegan (Oksanen et al., 2018). Partial distance-based redundancy analysis (dbRDA) using Bray-Curtis distance as a dissimilarity measure was used with the function ‘capscale’ (Oksanen et al., 2018). To account for the pairwise design of this study, a permutation design based on “site” and 9999 permutations was used and “site” was added as a conditional term in the dbRDA. To reduce the influence of dominant families, genera and guilds, community data were log10 (x + 1) transformed. The dbRDA was fitted with “% woody semi-natural habitat” and “hazard quotient”. Cook’s Distance was used to check for outliers. Assumptions were checked for all models using graphical validation procedures (Zuur et al., 2009).

3. RESULTS

The number of fungicide sprays and their hazard quotient were strongly correlated and 57% lower for fungus-

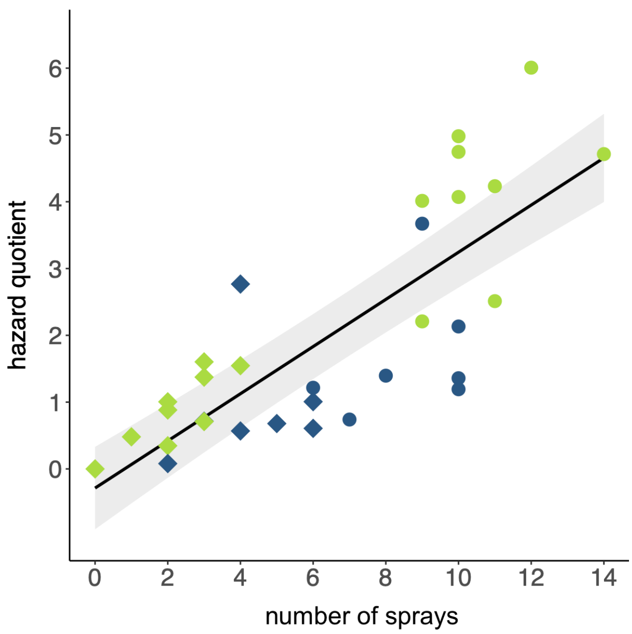

Fig. 1. Relationship between hazard quotients of applied pesticides with the actual number of applications in 32 vineyards: P ≤ 0.001 (X^2 = 137.54; df = 1); R^2 = 0.924. Displayed are the results for both organic (green) and conventional (blue) vineyards as well as fungus-resistant (diamonds) and susceptible (circle) grape varieties.

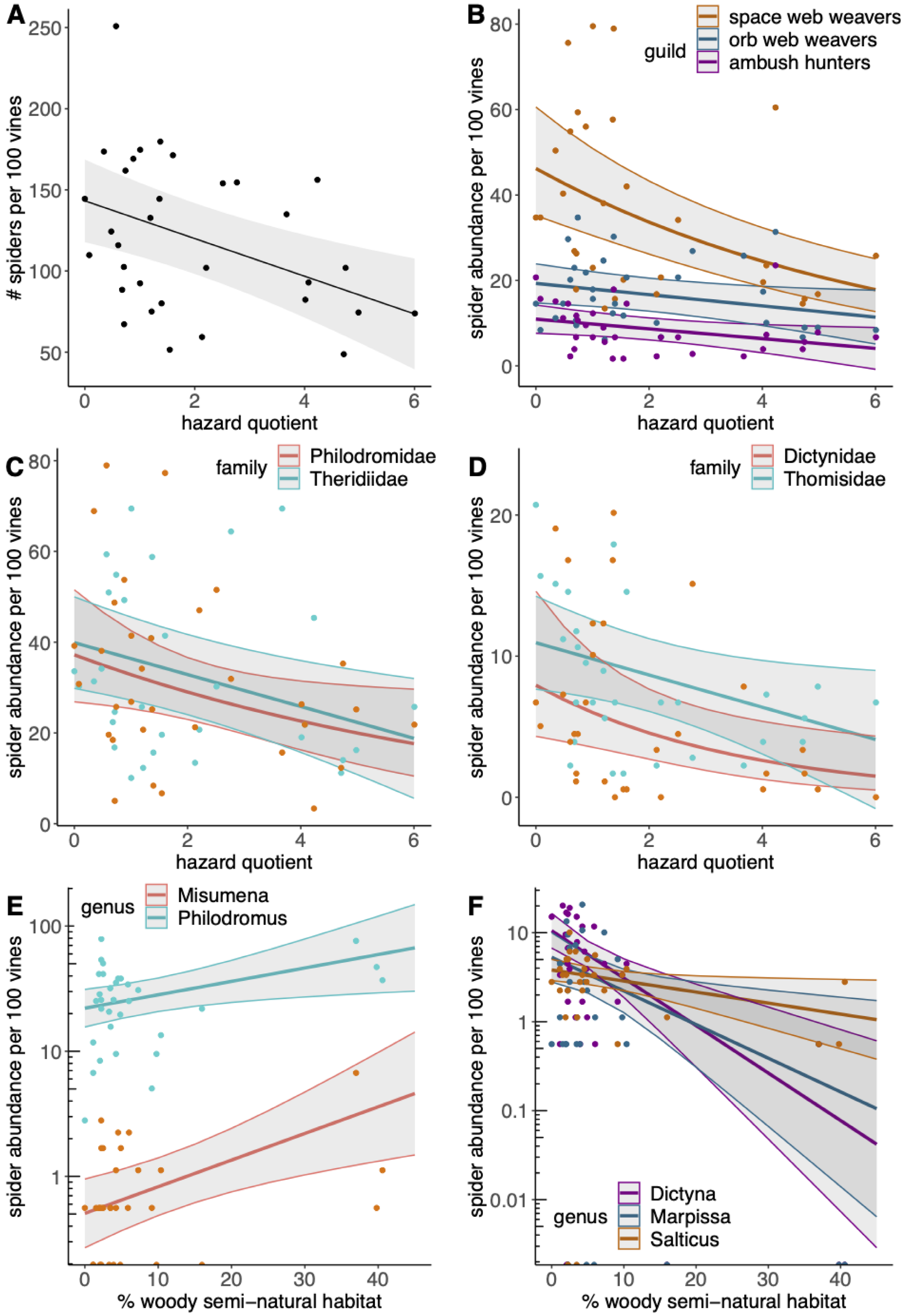

Fig. 2. Relationships between increasing hazard quotients of applied pesticides and the abundances of (A) all spiders, (B) three guilds, (C) and (D) for four families, and (E) and (F) the effects of landscape composition within a radius of 500 m for five genera. Displayed are model-predicted abundances and corresponding 95%-confidence-intervals.

Table 2. Model output of redundancy analyses for two explanatory and four tested response variables. Significant P-values are highlighted in bold.

	Hazard quotient		% woody SNH	
	F	P	F	P
family composition	3.457	**0.014**	1.025	0.806
genus composition	1.905	**0.013**	1.340	0.653
species composition	0.783	0.542	0.919	0.730
guild composition	3.675	**0.009**	0.599	0.919

resistant than susceptible varieties of grapes (Fig. 1). Reductions in fungicide sprays were more pronounced for fungus-resistant varieties of grapes under organic management, but overall hazard quotients of the sprays were lower under conventional management. Sulphur in particular is highly toxic for honeybees (see Pesticide Properties DataBase, Lewis & Tzilivakis, 2019). As a consequence, the greater frequency of sulphur sprays in organic vineyards led to higher hazard quotients compared to those in conventional vineyards.

A total of 6867 spiders were identified of which 5% were adult. The dominant spider guilds were other hunters (38.91%), space web weavers (32.52%) and orb web weavers (13.89%). With 27% each, Theridiidae and Philodromidae were the most abundant families, followed by Araneidae (13%) and Salticidae (11%; Table 3). The genus *Philodromus* dominated with almost 24% amongst different genera. Spider communities included 21 families, 63 genera, 34 species, and 8 different guilds of hunting strategies (Table 3). Family, genus, and guild composition were clearly associated with cumulated hazard quotients of pesticide applications, but did not respond to different percentages of woody semi-natural habitats (Fig. 3, Table 2). Although species composition was similar, species richness decreased by 43% with increase in pesticide applications (increase in hazard quotient from 0 to 6; Tables 1, 2). Neither family richness nor genus richness were significantly associated with the number of pesticide sprays. An increased percentage of woody semi-natural habitats from 0% to 45% was associated with a 28% increase in genus richness (Table 1). Neither family richness nor species richness are associated with landscape composition.

Total spider abundance was 49% higher when the cumulated hazard quotient of pesticide applications was low (0 compared to 6; Table 1, Fig. 2A). Reduced hazard quotients of pesticide applications were also associated with an increase in the abundance of the families Dictynidae (84%), Philodromidae (54%), Theridiidae (53%) and Thomisidae (58%), the abundance of the genus *Araniella* (69%) and *Dictyna* (77%), and abundance of the other hunters (44%), orb web weavers (41%), space web weavers (61%) and ambush hunters guilds (54%, Table 1, Fig. 2B, C, D). Including non-significant relationships, spider abundance and richness decreased with increase in pesticide applications in 30 of 32 investigated response variables (Table 1). In landscapes with a high percentage of woody semi-natural habitats (45% compared to 0%) the abundances of the genera *Philodromus* and *Misumena* were 67%, and 90% higher, respectively, but abundance

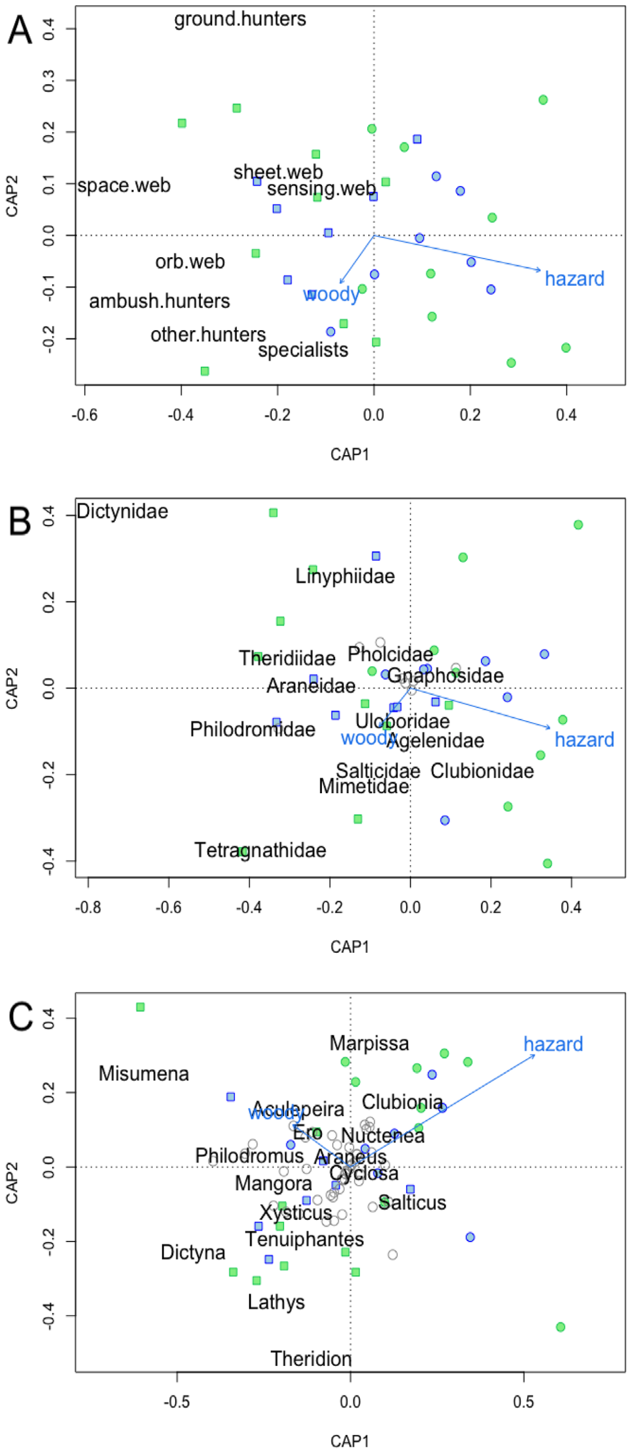

Fig. 3. Ordination diagrams of spiders with hazard quotients of applied pesticides and landscape complexity within a radius of 500 m analysed using dbRDA with Bray-Curtis distance as the dissimilarity measure. Spiders are grouped by A) different hunting strategies, and communities at B) family level and C) genus level. Blue symbols represent conventional and green symbols organic vineyards, while circles represent susceptible and squares resistant varieties respectively. If there were overlapping labels, more common species were displayed as text and less common species as small grey surrounded dots.

of Dictynidae decreased by 98%, as well as those of the genera *Dictyna* (99%), *Marpissa* (98%) and *Salticus* (72%, Table 1, Fig. 2E, F). Spider abundances increased with increase in the percentage of woody semi-natural habitats for 13 of the 32 spider taxa investigated (Table 1).

Table 3. Abundances of spider taxa and their relative percentages ordered by family.

Taxon	No. of individuals	Percentage [%]	Guild
Agelenidae	1	0.01	sheet web weaver
Amaurobiidae	1	0.01	sheet web weaver
Amaurobius sp.	1	0.01	
Anyphaenidae	30	0.44	other hunter
Anyphaena sp.	30	0.44	
Araneidae	870	12.67	orb web weaver
Aculepeira sp.	20	0.29	
Araneus sp.	87	1.27	
Araniella sp.	239	3.48	
Araniella opistographa	2	0.03	
Cyclosa sp.	4	0.06	
Gibbaranea sp.	2	0.03	
Lariniodes sp.	4	0.06	
Mangora sp.	466	6.79	
Mangora acalypha	3	0.04	
Metellina sp.	1	0.01	
Nuctenea sp.	28	0.41	
Nuctenea umbratica	2	0.03	
Zygiella sp.	3	0.04	
Zygiella x-notata	1	0.01	
Cheiracanthiidae	13	0.19	other hunter
Cheiracanthium sp.	13	0.19	
Clubionidae	23	0.33	other hunter
Clubiona sp.	18	0.26	
Dictynidae	380	5.53	
Dictyna sp.	334	4.86	space web weaver
Dictyna uncinata	12	0.17	space web weaver
Lathys sp.	14	0.20	ground hunter
Nigma sp.	4	0.06	space web weaver
Nigma puella	1	0.01	space web weaver
Gnaphosidae	12	0.17	ground hunter
Drassodes sp.	2	0.03	
Scotophaeus sp.	2	0.03	
Linyphiidae	397	5.78	
Agyneta fuscipalpa	3	0.04	sheet web weaver
Agyneta rurestris	24	0.35	sheet web weaver
Araeoncus humilis	1	0.01	other hunter
Erigone atra	2	0.03	other hunter
Erigone dentipalpis	1	0.01	other hunter
Frontinellina sp.	1	0.01	sheet web weaver
Linyphia sp.	1	0.01	sheet web weaver
Mermessus trilobatus	1	0.01	sheet web weaver
Microlyniphia sp.	2	0.03	sheet web weaver
Neriene sp.	7	0.10	sheet web weaver
Porrhomma microphthalmum	1	0.01	sheet web weaver
Tenuiphantes sp.	240	3.49	sheet web weaver
Tenuiphantes tenuis	47	0.68	sheet web weaver
Lycosidae	11	0.16	ground hunter
Mimetidae	6	0.09	specialist
Ero aphana	1	0.01	
Philodromidae	1821	26.52	other hunter
Philodromus sp.	1623	23.63	
Philodromus cespitum	41	0.60	
Tibellus sp.	13	0.19	
Tibellus oblongus	1	0.01	
Pholcidae	1	0.01	space web weaver
Pholcus opilionoides	1	0.01	
Pisauridae	3	0.04	sheet web weaver
Pisaura sp.	3	0.04	
Salticidae	773	11.26	other hunter
Ballus sp.	3	0.04	
Euophrys sp.	4	0.06	
Evarcha sp.	3	0.04	
Evarcha arcuata	1	0.01	
Heliophanus sp.	190	2.77	
Heliophanus auratus	49	0.71	
Leptorchestes beroliensis	1	0.01	
Marpissa sp.	162	2.36	
Marpissa muscosa	29	0.42	
Salticus sp.	158	2.30	
Salticus scenicus	24	0.35	
Synageles sp.	77	1.12	
Synageles venator	58	0.84	
Segestriidae	2	0.03	sensing web weaver
Segestria sp.	2	0.03	
Sparassidae	3	0.04	other hunter
Micrommata sp.	1	0.01	
Tetragnathidae	83	1.21	orb web weaver
Meta sp.	2	0.03	
Tetragnatha sp.	81	1.18	
Theridiidae	1881	27.39	space web weaver
Anelosimus sp.	3	0.04	
Dipoena sp.	18	0.26	
Enoplognatha sp.	2	0.03	
Enoplognatha latimana	8	0.12	
Neottiura sp.	322	4.69	
Neottiura bimaculata	5	0.07	
Paidiscura sp.	8	0.12	
Paidiscura pallens	5	0.07	
Phylloneta sp.	367	5.34	
Phylloneta impressa	9	0.13	
Platnickina sp.	5	0.07	
Platnickina tincta	1	0.01	
Rugathodes sp.	1	0.01	
Simitidion sp.	1	0.01	
Theridion sp.	599	8.72	
Theridion boesenbergii	2	0.03	
Theridion mystaceum	1	0.01	
Theridion varians	1	0.01	
Thomisidae	501	7.30	ambush hunter
Diaea sp.	2	0.03	
Misumena sp.	45	0.66	
Misumena vatia	9	0.13	
Ozyptila praticola	1	0.01	
Runcinia sp.	2	0.03	
Synema sp.	7	0.10	
Tmarus sp.	2	0.03	
Xysticus sp.	427	6.22	
Uloboridae	1	0.01	orb web weaver
unidentified spiderlings	54	0.79	
Total	6867	100	

4. DISCUSSION

Overall spider abundance was affected by the cumulated hazard quotients of fungicide applications. Given that the abundances of the most dominant families, Philodromidae and Theridiidae as well as the abundant Thomisidae, were significantly lower when fungicides were frequently applied, it is likely that this shaped the overall patterns. However, the abundances of the equally abundant families, Salticidae and Araneidae, did not change significantly when fungicides were frequently applied. Pekár (2012) proposes that some pesticides have guild-specific effects. Hunting spiders appear to be more susceptible to pesticide treatments than web building spiders (Bostanian et al., 1984; Pekár & Haddad, 2005). Nevertheless, some web building species are highly susceptible to insecticides (Dinter & Phoeling 1995; Benamú et al., 2013). It is unknown whether webs protect spiders from contact with pesticides or even accumulate them to lethal levels (Samu et al., 1992; Pekár, 1999). In the current study families with both, hunters and web builders, were affected by fungicide applications to variable extent.

Although the effects were only significant for some of the spider taxa investigated, abundances of almost all them were negatively associated with the hazard quotient of fungicide applications. For instance, abundances of *Heliophanus*, *Philodromus*, *Tetragnatha* and *Theridion* were much lower, although not significantly so. For some taxa their vulnerability to fungicides is already documented. For instance, Theridiidae benefited from reduced fungicide applications in previous studies (Wisniewska & Prokopy, 1997; Pennington et al., 2019). Likewise, *Phylloneta* is reported to be susceptible to one fungicide (Pekár, 2002). Further, the abundance of *Araniella* in pear orchards decreased after sulphur applications (Clymans et al., 2015). In contrast, *Philodromus* is reported to be relatively unsusceptible to fungicides (Mansour & Nentwig, 1988). In addition, Philodromidae were unaffected by a reduction in fungicide applications (Wisniewska & Prokopy, 1997; Pennington et al., 2019). In contrast, pesticide free orchards harbour significantly more hunting spiders (mainly *Philodromus*) than those treated with fungicides (Michalko & Košulič, 2020). Similarly, the current study revealed pronounced effects of fungicide applications on Philodromidae. In summary, it is concluded that the majority of spiders are negatively affected by fungicides. However, Salticidae, particularly *Salticus* and *Marpissa,* appear to be relatively unaffected. Nevertheless, the decrease in the abundances of *Heliophanus* and *Synageles* with increase in the hazard quotients of pesticide applications, although not significant, indicate that the responses of species in same family and with similar hunting strategies vary. This variability indicates that the revealed effects on spiders can neither be fully explained by phylogenetic relatedness or ecological traits such as foraging behaviour (Duque et al., 2024). Future studies are needed on the phylogenetic and ecological patterns in spider pesticide sensitivity.

Landscape complexity had different effects, particularly at the genus level. However, neither overall abundance nor spider guilds were affected by increased percentages of semi-natural habitats in the landscape. Similarly, spider abundance and species richness are not reported to be affected by the surrounding landscape or even promoted by increased percentages of agricultural areas in other grape vine growing regions (Caprio et al., 2015; Judt et al., 2019; Kolb et al., 2020). Nevertheless, ambush hunters, such as *Misumena,* and *Philodromus* strongly benefited from higher percentages of woody semi-natural habitats. Similar patterns are associated with higher percentages or the proximity of woodland habitats in Italian orchards and vineyards (Isaia et al., 2006; Picchi et al., 2020). Shrubs and trees are the preferred habitat of *Philodromus* (Nentwig et al., 2023), which makes vineyards suitable habitats for this genus. In contrast, negative effects on the abundances of *Dictyna* and *Salticus* are reported associated with woodland habitats in the landscape (Herrmann et al., 2010). As an open-habitat species (Nentwig et al., 2023), *Salticus* prefers simple structures even within vineyards (Pennington et al., 2019). Since landscape composition had variable effects on different spider genera, it is concluded that local management effects such as pesticide input are clearly more important for spider abundance and diversity than the surrounding landscape.

Spider guilds in the vineyards studied were similar to those reported on trees and consist of orb web weavers (mainly Araneidae), space web weavers (mainly Theridiidae) and hunters such as Philodromidae, Thomisidae and Salticidae (Herrmann et al., 2010; Pekár, 2012). Although these taxa can balloon, their aeronautic dispersal is less frequent than that of many species occurring in annual crops or herbaceous non-crop habitats (Bonte et al., 2003; Blandenier, 2009; Entling et al., 2011; Schirmel et al., 2016). The reduced dispersal ability of spider communities in less disturbed habitats can be explained by the habitat templet theory, which suggests that only species with suitable traits occur in particular habitats (Southwood, 1977). Further, Michalko & Birkhofer (2021) report agrobiont spiders in orchards, showing a preference for structurally similar semi-natural habitats, like scrubland (and forest). This indicates that semi-natural habitats in the surrounding landscape are less important for the recolonization of vineyards than for annual crops (e.g. Clough et al., 2005; Schmidt et al., 2008). Spiders that occur on the ground in vineyards have a stronger association with the surrounding landscape (Kolb et al., 2020) than the spiders on the grape vines in the current study. However, since the current study was primarily designed for testing the effects of pesticides, more detailed studies on the role of semi-natural habitats for spiders on grape vines are needed, and should also consider the role of directly adjacent woody habitats, such as hedgerows.

Effects of fungicide applications on spiders in vineyards prevailed over effects of landscape complexity. In addition to the direct effects of fungicides on spiders, both fungicides and woody semi-natural habitats may have indirectly affected spiders through their effects on prey populations. The diversity of flying insects in vineyards is strongly affected by woody habitats in the surrounding landscape, and their biomass is higher in conventional than organic vineyards (Kaczmarek et al., 2023). When prey availability is high, spiders can, for example, increase their consumption rate or immigrate from adjacent habitats (Marc et al., 1999). In this study the effects of fungicides and woody semi-natural habitats depended on the specific taxon considered. Dominant effects of fungicide applications in terms of total spider abundances were apparent at all taxonomic levels (family, genus, species) as well as for different hunting strategies, but not for all of the investigated variables to the same extent. However, effects of landscape complexity appeared only at the genus level. This indicates that spider identification to genus can be informative, especially in samples with high numbers of immatures that cannot be identified to species.

It is concluded that reducing the cumulative hazard effects of fungicides by reducing the number of fungicide applications is important for increasing the numbers of spiders on grape vines. Currently, a reduction can readily be achieved by cultivating fungus-resistant cultivars of grape vines in both organic and conventional viticulture over a large area. Landscape diversification with semi-natural habitats had no clear benefits for spiders on grape vines in vineyards, which contrasts with other organisms such as birds and above ground-nesting bees, that strongly rely on the presence of woody semi-natural habitats in the landscapes surrounding vineyards (Rösch et al., 2023; Wersebeckmann et al., 2023). Hence, it is likely an advantage in terms of natural pest suppression that spiders are also abundant in vineyard-dominated landscapes, but this should not be used as an argument against the restoration of semi-natural habitats in viticulture areas.

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