

Article

Contrasting Effects of Tillage and Landscape Structure on Spiders and Springtails in Vineyards

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Abstract: Interactions between predatory species and their potential prey are little studied in vineyards, especially considering the surrounding landscape structure. We examined the effects of soil tillage intensities in vineyard inter-rows on the activity density and diversity of spiders (Araneae) and springtails (Collembola), their potential preys, and assessed whether these effects are altered by non-crop elements in the surrounding landscape. We collected data in 16 vineyards in Austria; eight were periodically mechanically disturbed (PMD), eight had permanent green cover (PGC). The study vineyards were embedded in landscapes ranging from structurally simple to complex. Both, spiders and springtails were collected with pitfall traps. Data analyses using generalized linear mixed models (GLMM) showed different effects of soil tillage intensities on spiders and springtails and an interaction with semi-natural elements (SNEs) in the surrounding landscape. Activities of springtails were higher under PMD than under PGC while spider activity density remained unaffected. Spider family Shannon diversity was lower under PMD than under PGC, while springtail species Shannon diversity was unaffected by tillage. Under PMD, spider activity and family diversity decreased with increasing SNEs in the surroundings indicating spider emigration away from vineyards. Under PGC, spider activity density increased with increasing SNE proportions in the surroundings when springtail activity density was high. Our findings suggest that recommendations on sustainable vineyard management should include both site and landscape factors.

Keywords: agroecology; viticulture; soil cultivation; landscape ecology

1. Introduction

Viticulture is a very old sector of agriculture, dating back to about 6000 BC [1]. Modern conventional vineyards are usually intensively managed with frequent use of pesticides and tillage during the vegetation period [2]. Inter-row soil management practices are imposed to control weeds

and can include intensive tillage (bare soil), alternate tillage where every second inter-row is tilled, or no tillage with permanent green cover, or by the use of herbicides to control weeds [3]. Inter-row soil management in vineyards has been shown to affect aboveground [4] and belowground [5,6] biodiversity and associated ecosystem services [7]. However very little is known about influences on organisms comprising different trophic levels that might affect predator-prey interactions.

Spiders (Araneae) are all predators comprising the largest order of Arachnids with around 46,800 species worldwide [8]. Their habitat requirements are defined by several abiotic (temperature, humidity, wind, light intensity) and biotic (type of vegetation, food supply, intra- and interspecific competition, predators) factors [9,10]. Spiders live in different vegetation layers and are often divided in two functional groups: Sedentary web spiders and non-web builders. Spider abundances can vary considerably in different ecosystems with mean abundances in temperate climate in grassland with 92 ind. m⁻², forests with 53 ind. m⁻², and arable fields of 21 ind. m⁻² [11]. Spiders are important generalist predators in many ecosystems [9,12,13], however their abundance and diversity is commonly decreased in managed agroecosystems [10,14,15]. While spider communities, their feeding behaviors and possible implications for biological control have frequently been investigated in arable agroecosystems [16,17], far less is known from vineyards [13,18–21].

Springtails (Collembola) are among the most widespread terrestrial microarthropods with about 8800 species worldwide representing an important component of soil fauna in many terrestrial ecosystems [22]. Springtail species diversity is usually affected by land use [15,23]. Springtails can be grouped into soil dwelling (eu- and hemiedaphics) and surface dwelling species (epedaphics) [24]. As members of the decomposer community they are feeding on fungi, bacteria and dead organic matter thereby mobilizing nutrients [25]. Abundance of springtails can vary considerably between different ecosystems [11,26], ranging from abundances in grassland of 29,545 ind. m⁻², forests of 1826 ind. m⁻² to arable fields of 6056 ind. m⁻² [11]. Additionally, land management intensity including tillage, residue management or fertilization [27,28], pesticide use [29]. Springtails are also an important source of prey to spiders and comprise up to 72% of their diets [16,30–32]. Furthermore, springtails provide essential nutrients and amino acids in the diet of spiders [33,34].

Few studies have investigated the effect of management practices in vineyards on spiders [18,20,35,36] or springtails [5]. Tillage of vineyard inter-rows commonly has negative effects on the abundance of soil invertebrates, although rapid recovery of specific invertebrate groups (e.g., earthworms) has been shown [6]. Studies conducted in arable and viticultural landscapes that assessed combined effects of management and the surrounding landscape on spiders [37–40] or springtails [5] found that complex landscapes contain a higher biodiversity than simpler structured landscapes [41]. However, spiders appeared to respond differently to landscape structure: Ambush and habitat specific spiders are more abundant in diverse landscapes whereas web builders are more abundant in simple landscapes [38]. Species richness of spiders was significantly enhanced in wheat fields with more non-crop habitats in the surroundings [17,42,43], although opposite responses have also been reported [44]. Also, springtail populations showed a response to land-use intensity and the surrounding landscape structures [5,45,46]. However, to the best of our knowledge no study investigated both spiders and springtails in vineyards in response to the surrounding landscape.

The aims of the current study were (i) to assess the response of spider and springtail activity and diversity in vineyards to periodically mechanically-disturbed (PMD) versus permanently green covered (PGC) inter-rows, (ii) to analyze whether the proportion of semi-natural habitats in the surrounding landscape and the presence of springtails alter responses of spiders and (iii) to assess spider family assemblages and their relation with local management and potential springtail prey. We hypothesized that permanent green cover will benefit both spiders and springtails because of less disturbance. A higher proportion of non-crop habitats in the surroundings is expected to increase the diversity and activity of spiders and springtails in vineyards due to migration into vineyards.

2. Materials and Methods

2.1. Site Description and Study Design

The study sites were located in the two neighboring wine regions Carnuntum (48° 4' N, 16° 47' E) and Neusiedlersee-Hügelland (47° 54' N, 16° 41' E) about 40 km south east of Vienna, Austria. The annual total precipitation for the region Bruckneudorf (which is located in the center of the study regions) is around 619 mm at an altitude of 167 m and an annual average temperature of 10.2 °C [47]. The study regions are strongly shaped by a Pannonian, continental-like climate with hot, dry summers and cold winters. The most frequent soil types are Chernozems and Cambisols with medium to high usable field capacity, neutral pH-values and high nutrient contents [48].

Within the regions, 16 vineyards were selected for the current investigations (Figure 1). In these regions vineyards are small (0.4–1 ha) and typically surrounded by landscapes with various degrees of heterogeneity. Landscape heterogeneity was calculated as the proportion of semi-natural habitats (hedges, tree rows, grass stripes, natural grassland, pasture, fallow, heathland, wetland and woodlots) within a radius of 750 m centered in the plot. This area is within the activity ranges of both spiders [17,49] and springtails [46] in agricultural landscapes. In eight of the study vineyards, the inter-rows had a permanent green cover (PGC) whereas in eight vineyards every second inter-row was periodically mechanically disturbed (PMD). Both management regimes were distributed across both regions and practiced for at least five years. The inter-row cover crops were sown with seed mixtures, except for three vineyards with spontaneous vegetation. Inter-row vegetation was cut or mulched several times per season. Grapevines were cultivated in a vertical trellis system for at least 10 years with within-row grapevine distance of 0.75–1.3 m and inter-row distance varying between 2.15–3 m. On each site one inter-row sampling area of 2 × 40 m in the middle of the vineyard was selected; this area had a distance of at least 5 m to the vineyard edge. Furthermore, in PMD sites samples were taken in the current undisturbed inter-rows that had been cultivated in the year before and thus was vegetated.

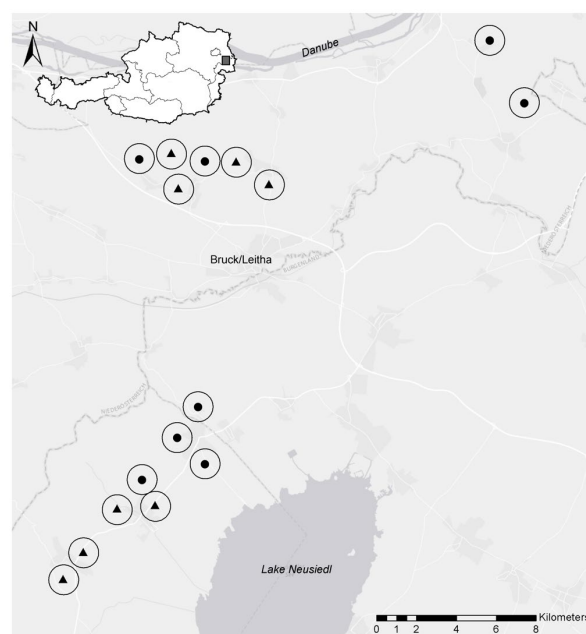


Figure 1. Location of study sites (circles with radius 750 m) in Eastern Austria in the viticultural areas Carnuntum (upper eight circles) and Neusiedlersee-Hügelland (bottom eight circles). Black circles denote vineyards with permanent green cover (PGC), black triangles those with periodically mechanical disturbance (PMD).

2.2. Sampling and Measurements

2.2.1. Spider and Springtail Sampling

To collect surface active springtails and spiders, six pitfall traps (diameter 17 mm, depth 60 mm) were installed on 21 April 2015 at each vineyard site. Each trap was filled with ethylene glycol and a drop of odorless detergent. They were inserted along a transect in the middle of inter-rows with a distance of 6 m between each other. The focus was to assess spring communities of spiders and springtails to check the pest control potential for the first generation of grape berry moths (*Eupoecilia ambiguella* Hübner), an important pest insect in the study region. Springtails can act as alternative prey for generalist predators such as spiders and thus sustaining the population of natural enemies within the fields [50,51]. After 13 days the traps were removed. Determination of spiders was only performed at family level because of many juvenile individuals in the traps [50,51]. Spiders were classified according to their feeding behavior into non-web or web building spiders. Hunters were summed up under the collective name of non-web building spiders including Lycosidae, Gnaphosidae, Pisauridae and Dysderidae. Web builders were comprised of families Linyphiidae, Theridiidae and Hahniidae [52]. Springtails were sorted and determined to species level [53–61]. The number of trapped springtails and spiders during the sampling is referred to as activity density.

All land owners gave their permission to sample spiders and springtails on their private properties. No protected species/families were collected. The study complied with all relevant regulations.

2.2.2. Landscape Parameters

Field mapping was carried out in July 2015. As a reference we used the official Austrian land utilization map from 2012 (Integriertes Verwaltungs- und Kontrollsystem, INVEKOS). Landscape elements within a 750 m-radius from the center of the vineyards were classified into habitat types according to CORINE Land Cover and EUNIS Habitat Classification [62,63]. Of these habitat types the proportion of semi-natural elements (SNE) such as hedges, tree rows, grass strips, natural grassland, pasture, fallow, heathland, wetland and woodlots were calculated because of their importance for spiders and springtails. Mapping and analysis was carried out using the programs ArcGis 10.2.195, QGIS 2.8.1, FRAGSTATS 4.296 and CHLOE201297 [64].

2.3. Statistical Analysis

To account for significant differences between the two management regimes for springtails and spider activity density and diversity we used Wilcoxon signed-rank tests, a non-parametric statistical hypothesis test used to compare dependent samples from populations with similar distributions.

To account for the effects that soil tillage, landscape heterogeneity as well as alternative prey in the form of the surface-dwelling springtail activity density could have on the spider activity density and family Shannon diversity index, we used Generalized linear mixed models (GLMM) with Poisson error distributions. We built two sets of 18 different models that we tested for the two response variables modelled in this study, spider activity density and family diversity, covering all the possible combinations of the explanatory variables mentioned above with their interactions. Samples of the individual traps were not pooled but treated separately to be able to account for vineyard as a random factor. This way we could include the variability within vineyards and focus the explanatory power on the response variables described above. To account for large eigenvalues, we rescaled the springtail variables by dividing the average of the total springtail activity density by the standard deviation and subtracted it by the total springtail activity density.

Model selection with Akaike information criteria corrected for small sample size (AICc) was used as an alternative to traditional hypothesis testing [65]. AIC is an estimator of the relative quality of statistical models for a given set of data. Given a collection of models for the data, AIC estimates the quality of each model, relative to each of the other models. Models with a difference in $AICc > 2$ indicate that the worse model has virtually no support and can be omitted from further consideration.

Furthermore, models with AIC_c less than two units above model with the lowest AIC were also considered and were averaged. Selected models were plotted and used for additional interpretation. When relevant, the size of the effect of springtail activity density was illustrated in lines with the values low (5%), moderate (50%) and high (95% of total springtail activity density). Vineyard was used as a random factor in the models. We calculated the R² for the best models to account for the variability explained by mixed models with Gaussian or Poisson error distributions [66]. Though this approach cannot be applied to models with a negative binomial error distribution, it allows for two components of R² to be calculated: (i) A marginal R² (R²_m) that only includes the variance explained by fixed effects; and (ii) a conditional R² (R²_c) that represents the variance explained by both fixed and random effects. In case of two or more best fitting models, R²_m and R²_c were calculated for the more complex model. For models without random effects we calculated the adjusted R².

In addition, Nonmetric multidimensional scaling (NMDS) was used to investigate the overall pattern of families' composition on the spider assemblages, and group families that could respond similarly to landscape heterogeneity, management system and resource availability. Data were square-root transformed and then submitted to Wisconsin double standardization [67]. We used the Bray-Curtis dissimilarity distance to compute the resemblance matrix among sites. To explore associations between particular spider families or assemblages and springtails, we generated smooth surfaces for the springtail activity densities on the NMDS ordination diagram. Smooth surfaces are the result of fitting thin plate splines using general additive models and interpolating the fitted values on the NMDS plot [68].

The analyses were performed using the “vegan” [68], “MuMIn” [69] and “lme4” [70] packages in the R environment (RStudio v1.0.143) [71].

3. Results

We found a total of 503 spider specimens comprising 9 families (Supplementary Table A1): >95% of all individuals were from four families, Lycosidae (wolf spiders, 70%, 352 individuals) followed by Theridiidae (cobweb spiders, 12%, 59 ind.), Linyphiidae (sheetweb spiders, 7%, 37 ind.), Gnaphosidae (ground spiders, 6%, 29 ind.) and Thomisidae (crab spiders, 4%, 19 ind.). Less frequently encountered were Hahniidae (dwarf sheet spiders, 0.8%, 4 ind.) as well as Pisauridae, Salticidae and Dysderidae (0.2%, 1 ind. for each family). The mean activity density across treatments was 5.40 ± 0.87 (mean \pm SE) ind. per trap and sampling period. The activity density of web builders (0.63 ± 0.13 under PGC vs. 0.63 ± 0.15 under PMD) were unaffected by the two tillage systems ($p = 0.542$). Non-web building spider diversity was significantly lower under PMD than under PGC ($p = 0.037$), while web builder's diversity was unaffected by tillage treatments ($p = 0.861$).

We found a total of 6,244 surface-dwelling springtails comprising 34 species (Supplementary Table A2). Across treatments the most abundant surface-dwelling springtail species was *Isotoma viridis* (33%, 2061 ind.), followed by *Heteromurus major* (22%, 1356 ind.), *Lepidocyrtus cyaneus* (11%, 668 ind.), *Orchesella cincta* (8%, 501 ind.), *Entomobrya marginata* (5%, 298 ind.) and *E. olivacea* and (5%, 284 ind.). The mean density was 70.04 ± 6.06 ind. per trap and sampling period. Springtail activity density was significantly higher under PMD than under PGC ($p = 0.038$, Figure 2A) whereas their Shannon species diversity was unaffected ($p = 0.933$; Figure 2B). Species richness was similar between the two tillage systems ($p = 0.956$).

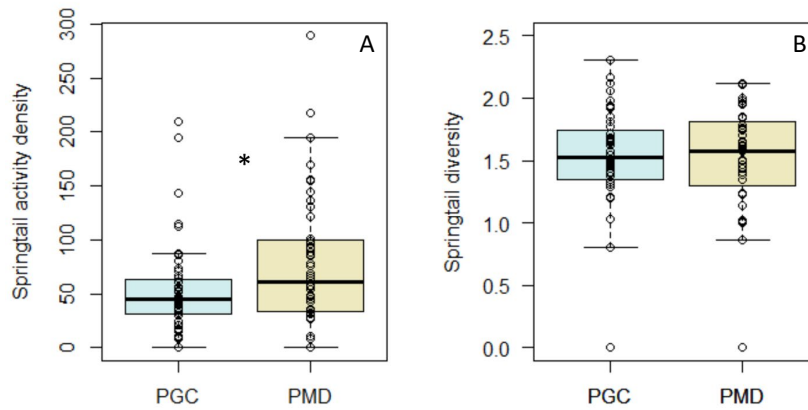


Figure 2. Springtail activity density (A) and Shannon species diversity (B) in vineyard inter-rows with permanent green cover (PGC; green) or periodically mechanical disturbance (PMD; red). Asterisk denotes significant difference between treatments.

Results from the GLMM indicated five best models to explain influence factors on spider activity density which all included effects of the surrounding SNEs, management and springtail activity density ($R^2_m = 0.41$, Table 1, Figure 3 A,B). Under PGC, the overall spider activity density remained relatively unchanged and was not affected by SNE when the springtail density was low or moderate. However, when the activity density of springtails was high, spider activity also increased with increasing SNE. For PMD the spider activity density decreased with an increasing proportion of SNE in the surroundings.

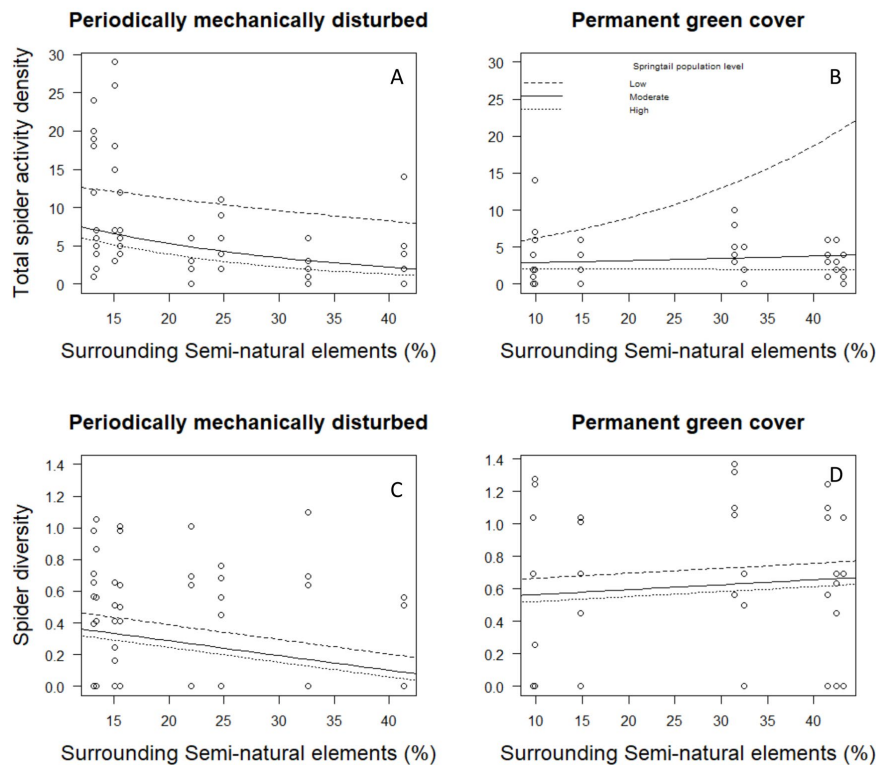


Figure 3. Spider activity density (A,B) and spider Shannon family diversity (C,D) in vineyards in response to surrounding semi-natural elements and two different tillage systems (PMD = periodically mechanically disturbed; PGC = permanent green cover) with effect size of springtail activity density level (low = 5%, moderate = 50%, high = 95% of total springtail activity density).

Table 1. Listing of best fitting models (using AICc) for spider activity density and family diversity in vineyards. The best models (lowest AICc) with which the average will be formed, are indicated in bold. R²m (R² marginal), R²c (R² conditional) refer to the most complex model of the best models. Mgmt = Management intensity, Coll = Collembola activity density, SNE = Semi-natural element.

	Landscape Effect	Prey Effect	Nomenclature	Total Spider Density	Total Spider Diversity	
in	Null	Null	No	553.75	109.98	
	Null	Coll effect	Col	532.48	112.07	
	SNE	Null	SNE	553.44	112.16	
	SNE	Coll effect	SNE + Coll	532.41	113.84	
	Interaction (SNE & Coll effect)		SNE + Coll + (SNE × Coll)	530.50	115.99	
	Management models	Null	Null	Mgmt	550.63	110.22
		SNE	Null	Mgmt + SNE	551.29	112.37
		Null	Coll effect	Mgmt + Coll	531.09	111.58
		SNE	Coll effect	Mgmt + SNE + Coll	531.89	113.77
		Interaction (Mgmt & SNE)		Mgmt + SNE + (Mgmt × SNE)	551.53	111.61
		Interaction (Mgmt & Collembola effect)		Mgmt + Coll + (Mgmt × Coll)	532.80	113.04
		SNE	Coll effect + Interaction (Mgmt & Coll effect)	Mgmt + SNE + Coll + (Mgmt × Coll)	533.84	115.13
		SNE + Interaction (Mgmt & SNE)	Coll effect	Mgmt + SNE + Coll + (Mgmt × SNE)	530.69	112.77
		Interaction (SNE & Coll effect)		Mgmt + SNE + Coll + (SNE × Coll)	531.26	115.70
		Interaction (Mgmt & Collembola effect) + Interaction (Coll effect & SNE)		Mgmt + SNE + Coll + (Mgmt × Coll) + (Coll × SNE)	529.61	114.49
		Interaction (Mgmt & SNE) + Interaction (Mgmt & Coll effect)		Mgmt + SNE + Coll + (Mgmt × SNE) + (M × Coll)	532.67	113.90
		Interaction (Mgmt & SNE) + Interaction (Coll effect & SNE)		Mgmt + SNE + Coll + (Mgmt × SNE) + (Coll × SNE)	532.68	117.30
		Interaction (Mgmt & SNE) + Interaction (Mgmt & Coll effect) + Interaction (Coll effect & SNE)		Mgmt + SNE + Coll + (Mgmt × SNE) + (Mgmt × Coll) + (Coll × SNE)	531.09	115.89
				R²m	0.30	
				R²c	0.76	

For spider family diversity we found four best fitting models containing effects of surrounding SNEs and management, one model also contained the variable springtail activity density (Table 1, Figure 3 C,D). Under PMD, the spider diversity decreased with increasing SNEs in the surroundings. Under PGC, the surroundings showed little effect on spider diversity in vineyards.

The relationship between spiders and springtails was analyzed by Non-metric multidimensional scaling (NMDS; Figure 4). It was shown that a higher activity density of springtails led to a higher activity density of Lycosidae spiders (LYC). In contrast, the families Pisauridae, Hahniidae and Salticidae displayed a relationship with lower springtail activity densities. The rest of the spider families were related with medium springtail activity densities.

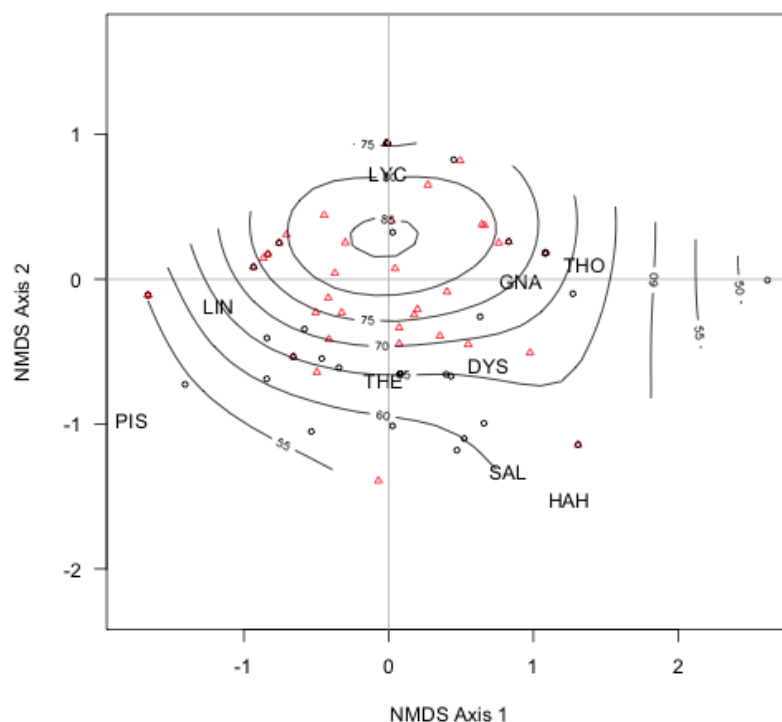


Figure 4. Non-metric multidimensional scaling results on spider and springtail activity density in vineyards in response to two different management systems (O = periodically mechanically disturbed, Δ = permanent green cover). Isolines represent springtail activity density. LYC = Lycosidae, THO = Thomisidae, GNA = Gnaphosidae, LIN = Linyphiidae, THE = Theridiidae, DYS = Dysderidae, HAH = Hahniidae, PIS = Pisauridae, SAL = Salticidae.

4. Discussion

We found contrasting responses of spider activity density and family diversity to interrow tillage: Spider activity density was unaffected by tillage, but family diversity lower under PMD. Springtail activity density was higher under PMD while springtail diversity remained unaffected by tillage. This can be explained by more surface roughness and better shelter for both taxa. Likewise, PGC vineyards tended to have a more compacted topsoil providing less favorable habitats for springtails [5]. Contrarily, others have shown that periodic soil tillage can lead to prey diversification in soil which could also enhance spider diversity [72,73].

In line with our expectations spider family diversity was higher when less soil disturbance occurred under PGC. We attribute this result to the smoother and more compacted soil surface enabling a higher spider family diversity to establish. Indeed, the spider families that benefited under PGC were non-web builders of the families Lycosidae, Gnaphosidae, Pisauridae and Dysderidae known to be sedentary waiting for passing prey [74]. Whether diversity of prey other than springtails was also higher under PGC, we did not investigate in the current study. In contrast to our findings, others have shown that a higher disturbance level in vineyards (mulching vs. mowing) actually favored spiders [20]. In contrast, in salt grasslands no effect on spider diversity was seen between grazed, i.e., disturbed, compared to ungrazed grassland [75]. Hence, it is likely that more factors than only disturbance influence the diversity of spider communities.

The prevalence of Lycosid spiders in our study is in contrast to others that found Linyphiids dominating in vineyards [76,77]. This might also be due to the sampling method we used. While pitfall traps are commonly used to study spiders in ecosystems they underestimate foliage-dwelling spiders [37,78,79]. Another reason for the small number of Linyphiid spider findings may also be the sampling time. We wanted to assess spiders as potential predators for early instars of the Grape berry moths, therefore, our sampling took place in spring. At this time juvenile Linyphiid spiders start to recolonize surrounding landscapes by frequently ballooning after using vineyard inter-rows as

overwintering sites or refuge habitats [17,80]. In our traps, most Lycosid spiders were adults or too large to use ballooning because this ability is restricted to small-sized instars which leads to the assumption, that the closer surrounding is supposed to be of greater importance for them [17].

Overall, our data suggest that spiders in vineyards were less closely linked to SNE than spiders in arable fields where a major impact of SNEs on spider activity density, diversity and species richness was found [37,43]. Perhaps, spider activity densities in perennial systems like vineyards are less dependent on SNE because vineyards provide food and shelter and vegetated inter-rows act as quasi non-crop refuges [81]. However, our findings also indicate that spiders are affected by an interaction between vineyard inter-row management, springtails and the surrounding SNEs. Under PMD, both spider diversity and activity decreased with increased SNE, while under PGC, spider activity increased with increased SNE especially when a high activity density of springtails was found within the vineyards. Although, we cannot prove whether an increasing spider activity density responded to an increasing springtail activity density, others have shown that springtails are indeed an important source of prey for spiders [30,82,83]. NMDS also indicated that mainly spiders of the families Lycosidae, Gnaphosidae and Tomisidae benefited from higher springtail activity densities. Linyphiid spiders have also been shown to locate their webs in areas with high springtail densities which let us conclude that an increase in the number of spiders can be associated with an increase of surface-dwelling springtail density [84]. However, it is important to note that also different habitat properties differentially affect activity density of spiders and Collembola [85], and more detailed studies are needed to better understand predator-prey relationships between spiders and springtails.

The decrease of spider activity density and diversity with increasing SNE under PMD suggest that disturbances make spiders leave the vineyard to find shelter in SNEs in the surrounding landscape. Additionally, vineyards are disturbed by various other management activities such as pruning, foliage work or pesticide applications and therefore refuge habitats in the landscape are of great importance for spiders and other arthropods [4].

5. Conclusions

Taken collectively, our findings suggested that both spiders and springtails in vineyards might be altered by SNEs in the surrounding landscape. Obviously, our results also showed that vineyards are important habitats for spiders and springtails. Both activities of spiders and springtails seem to benefit from alternating tillage activities, however in order to increase spider diversity vineyards with permanent vegetation seem advisable. To what extent a higher spider activity density and diversity contributes to biological control of viticultural pest species would need to be investigated in more detailed experiments.

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Appendix A

Table A1. Spider families collected with pitfall traps in vineyards with periodical mechanical disturbance (PMD) or permanent green cover (PGC). Means \pm SD.

Spider family	Inter-row management	
	PMD	PGC
<i>Lycosidae</i>	34.5 \pm 6.2	9.5 \pm 2.2
<i>Theridiidae</i>	4.1 \pm 1.0	3.3 \pm 0.9
<i>Pisauridae</i>	0.0 \pm 0.0	0.1 \pm 0.2
<i>Gnaphosidae</i>	1.9 \pm 0.6	1.8 \pm 0.5
<i>Linyphiidae</i>	2.5 \pm 0.7	2.1 \pm 0.7
<i>Hahniidae</i>	0.1 \pm 0.1	0.4 \pm 0.3
<i>Thomisidae</i>	1.1 \pm 0.9	1.3 \pm 0.6
<i>Saltiicidae</i>	0.0 \pm 0.0	0.1 \pm 0.2
<i>Dysderidae</i>	0.1 \pm 0.1	0.0 \pm 0.0

Table A2. Springtail species collected with pitfall traps in vineyards with periodical mechanical disturbance (PMD) or permanent green cover (PGC). Means \pm SD.

Springtail species	Inter-row management	
	PMD	PGC
<i>Ceratophysella succinea</i> (Gisin 1949)	0.6 \pm 3.7	1.1 \pm 2.1
<i>Cyphoderus albinus</i> (Nicolet 1842)	0.2 \pm 0.8	0.2 \pm 0.9
<i>Cyphoderus bidenticulatus</i> (Parona 1888)	0.1 \pm 0.2	0
<i>Desoria fennica</i> cf. (Reuter 1895)	0	0.1 \pm 0.2
<i>Desoria olivacea</i> (Tullberg 1871)	4.7 \pm 8.5	1.7 \pm 2.2
<i>Entomobrya handschini</i> (Stach 1922)	1.8 \pm 1.9	4.8 \pm 4.5
<i>Entomobrya marginata</i> (Tullberg 1871)	2.7 \pm 6.1	0.5 \pm 1.1
<i>Entomobrya multifasciata</i> (Tullberg 1871)	0	0.1 \pm 0.2
<i>Heteromurus major</i> (Moniez 1889)	17.4 \pm 17.3	13.2 \pm 15.9
<i>Heteromurus nitidus</i> (Templeton 1835)	1.0 \pm 1.2	0.9 \pm 2.0
<i>Heterosminthurus claviger</i> (Gisin 1958)	0.1 \pm 0.3	0
<i>Isotoma viridis</i> (Bourlet 1839)	29.0 \pm 25.0	17.7 \pm 25.3
<i>Lepidocyrtus cyaneus</i> (Tullberg 1871)	13.2 \pm 14.6	2.2 \pm 2.9
<i>Lepidocyrtus lanuginosus</i> (Gmelin 1788)	0.7 \pm 2.0	0.1 \pm 0.6
<i>Lepidocyrtus lignorum</i> (Fabricius 1775)	0	0.2 \pm 0.7
<i>Lepidocyrtus paradoxus</i> (Uzel 1891)	1.1 \pm 2.0	1.5 \pm 2.7
<i>Metaphorura affinis</i> (Börner 1902)	0	0.1 \pm 0.2
<i>Orchesella cincta</i> (Linnaeus 1758)	5.8 \pm 7.8	5.4 \pm 6.5
<i>Orchesella pannonica</i> (Stach 1960)	0.1 \pm 0.2	0.1 \pm 0.2
<i>Parisotoma notabilis</i> (Schäffer 1896)	1.2 \pm 2.7	2.3 \pm 6.5
<i>Pogonognathellus flavescens</i> (Tullberg 1871)	0.1 \pm 0.3	0.1 \pm 0.5
<i>Pseudachorutella asigillata</i> (Börner 1901)	0	0.2 \pm 0.6
<i>Pseudachorutes parvulus</i> (Börner 1901)	0.1 \pm 0.2	0.6 \pm 1.9
<i>Pseudosinella alba</i> (Packard 1873)	0.8 \pm 2.4	0.4 \pm 1.2
<i>Pseudosinella petterseni</i> (Börner 1901)	0.1 \pm 0.2	0
<i>Pseudosinella sexoculata</i> (Schött 1902)	0.3 \pm 0.7	0.1 \pm 0.3
<i>Seira</i> spp.	0	0.1 \pm 0.2
<i>Sminthurinus aureus</i> (Lubbock 1862)	4.0 \pm 4.1	1.5 \pm 1.8
<i>Sminthurus multipunctatus</i> (Schäffer 1896)	0.1 \pm 0.4	0.1 \pm 0.2
<i>Sminthurus viridis</i> (Linnaeus 1758)	0.1 \pm 0.2	0
<i>Sphaeridia pumilis</i> (Krausbauer 1898)	0.7 \pm 0.9	0.7 \pm 1.2
<i>Tomocerus vulgaris</i> (Tullberg 1871)	0	0.1 \pm 0.2

<i>Willowsia nigromaculata</i> (Lubbock 1873)	0.1 ± 0.2	0
<i>Xenylla maritima</i> (Tullberg 1869)	0	0.1 ± 0.2

References

- McGovern, P.; Jalabadze, M.; Batiuk, S.; Callahan, M.P.; Smith, K.E.; Hall, G.R.; Kvavadze, E.; Maghradze, D.; Rusishvili, N.; Bouby, L.; et al. Early Neolithic wine of Georgia in the South Caucasus. *Proc. Natl. Acad. Sci. USA* 2017, 114, E10309–E10318, doi:10.1073/pnas.1714728114.
- Jackson, R. *Wine Science: Principles and Applications*, 4th ed.; Academic Press: London, UK, 2014; 978p.
- Zaller, J.G.; Cantelmo, C.; Santos, G.D.; Muther, S.; Gruber, E.; Pallua, P.; Mandl, K.; Friedrich, B.; Hofstetter, I.; Schmuckenschlager, B.; et al. Herbicides in vineyards reduce grapevine root mycorrhization and alter soil microorganisms and the nutrient composition in grapevine roots, leaves, xylem sap and grape juice. *Environ. Sci. Pollut. Res.* 2018, 25, 23215–23226, doi:10.1007/s11356-018-2422-3.
- Kratschmer, S.; Pachinger, B.; Schwantzer, M.; Paredes, D.; Guernion, M.; Burel, F.; Nicolai, A.; Strauss, P.; Bauer, T.; Kriechbaum, M.; et al. Tillage intensity or landscape features: What matters most for wild bee diversity in vineyards? *Agric. Ecosyst. Environ.* 2018, 266, 142–152, doi:10.1016/j.agee.2018.07.018.
- Buchholz, J.; Querner, P.; Paredes, D.; Bauer, T.; Strauss, P.; Guernion, M.; Scimia, J.; Cluzeau, D.; Burel, F.; Kratschmer, S.; et al. Soil biota in vineyards are more influenced by plants and soil quality than by tillage intensity or the surrounding landscape. *Sci. Rep.* 2017, 7, 17445, doi:10.1038/s41598-017-17601-w.
- Faber, F.; Wachter, E.; Zaller, J.G. Earthworms are little affected by reduced soil tillage methods in vineyards. *Plant Soil Environ.* 2017, 63, 257–263.
- Winter, S.; Bauer, T.; Strauss, P.; Kratschmer, S.; Paredes, D.; Popescu, D.; Landa, B.; Guzmán, G.; Gómez, J.A.; Guernion, M.; et al. Effects of vegetation management intensity on biodiversity and ecosystem services in vineyards: A meta-analysis. *J. Appl. Ecol.* 2018, 55, 2484–2495, doi:DOI: 10.1111/1365-2664.13124.
- World Spider Catalog. *World Spider Catalog*. Version 19.5. Natural History Museum Bern. Available online: <https://wsc.nmbe.ch> (accessed on 3 July 2017).
- Wise, D.H. *Spiders in Ecological Webs*; University Press: Cambridge, UK, 1993.
- Foelix, R.F. *Biology of Spiders*, 3rd ed.; Oxford University Press: New York, NY, USA, 2011.
- Menta, C.; Leoni, A.; Gardi, C.; Conti, F.D. Are grasslands important habitats for soil microarthropod conservation? *Biodivers. Conserv.* 2011, 20, 1073–1087, doi:10.1007/s10531-011-0017-0.
- Nyffeler, M.; Benz, G. Spiders in natural pest control: A review. *J. Appl. Entomol.* 1987, 103, 321–339.
- Michalko, R.; Pekár, S.; Entling, M.H. An updated perspective on spiders as generalist predators in biological control. *Oecologia* 2018, doi:10.1007/s00442-018-4313-1.
- Nyffeler, M.; Birkhofer, K. An estimated 400–800 million tons of prey are annually killed by the global spider community. *Sci. Nat. Naturwiss.* 2017, 104, 30, doi:10.1007/s00114-017-1440-1.
- Wood, J.R.; Holdaway, R.J.; Orwin, K.H.; Morse, C.; Bonner, K.I.; Davis, C.; Bolstridge, N.; Dickie, I.A. No single driver of biodiversity: Divergent responses of multiple taxa across land use types. *Ecosphere* 2017, 8, 17, doi:10.1002/ecs2.1997.
- Kuusk, A.K.; Ekbom, B. Lycosid spiders and alternative food: Feeding behavior and implications for biological control. *Biol. Control* 2010, 55, 20–26, doi:10.1016/j.biocontrol.2010.06.009.
- Drapela, T.; Moser, D.; Zaller, J.G.; Frank, T. Spider assemblages in winter oilseed rape affected by landscape and site factors. *Ecography* 2008, 31, 254–262.
- Costello, M.J.; Daane, K.M. Spider and leafhopper (*Erythroneura* spp.) response to vineyard ground cover. *Environ. Entomol.* 2003, 32, 1085–1098.
- Nyffeler, M.; Benz, G. Prey and predator importance of microphantid spiders in winter wheat fields and hay meadows. *J. Appl. Entomol.* 1988, 105, 190–197.
- Bruggisser, O.T.; Schmidt-Entling, M.H.; Bacher, S. Effects of vineyard management on biodiversity at three trophic levels. *Biol. Conserv.* 2010, 143, 1521–1528.
- Hanna, R.; Zalom, F.G.; Roltsch, W.J. Relative impact of spider predation and cover crop on population dynamics of *Erythroneura variabilis* in a raisin grape vineyard. *Entomol. Exp. Appl.* 2003, 107, 177–191, doi:10.1046/j.1570-7458.2003.00051.x.
- Bellinger, P.F.; Christiansen, K.A.; Janssens, F. Checklist of the Collembola of the World. Available online: <http://www.collembola.org> (accessed on 3 July 2017).

23. Salamon, J.-A.; Wissuwa, J.; Moder, K.; Frank, T. Effects of *Medicago sativa*, *Taraxacum officinale* and *Bromus sterilis* on the density and diversity of Collembola in grassy arable fallows of different ages. *Pedobiologia* 2011, 54, 63–70, doi:10.1016/j.pedobi.2010.08.007.
24. Hopkin, S.P. *Biology of the Springtails (Insecta: Collembola)*; Oxford University Press: Oxford, NY, USA, 1997.
25. Rusek, J. Biodiversity of Collembola and their functional role in the ecosystem. *Biodivers. Conserv.* 1998, 7, 1207–1219, doi:10.1023/A:1008887817883.
26. Roy, S.; Bano, R.; Saxena, P.; Bhatt, R.K. Land uses and its impact on community structure of soil collembola. *Range Manag. Agrofor.* 2014, 35, 27–31.
27. Coulibaly, S.F.M.; Coudrain, V.; Hedde, M.; Brunet, N.; Mary, B.; Recous, S.; Chauvat, M. Effect of different crop management practices on soil Collembola assemblages: A 4-year follow-up. *Appl. Soil Ecol.* 2017, 119, 354–366, doi:10.1016/j.apsoil.2017.06.013.
28. Song, L.H.; Liu, J.; Yan, X.M.; Chang, L.; Wu, D.H. Euedaphic and hemiedaphic Collembola suffer larger damages than epedaphic species to nitrogen input. *Environ. Pollut.* 2016, 208, 413–415, doi:10.1016/j.envpol.2015.10.008.
29. Zaller, J.G.; König, N.; Tiefenbacher, A.; Muraoka, Y.; Querner, P.; Ratzenböck, A.; Bonkowski, M.; Koller, R. Pesticide seed dressings can affect the activity of various soil organisms and reduce decomposition of plant material. *BMC Ecol.* 2016, 16, 37, doi:10.1186/s12898-12016-10092-x.
30. Agustí, N.; Shayler, S.P.; Harwood, J.D.; Vaughan, I.P.; Sunderland, K.D.; Symondson, W.O.C. Collembola as alternative prey sustaining spiders in arable ecosystems: Prey detection within predators using molecular markers. *Mol. Ecol.* 2003, 12, 3467–3475.
31. Fiera, C. Application of stable isotopes and lipid analysis to understand trophic interactions in springtails. *North-West J. Zool.* 2014, 10, 227–235.
32. Sunderland, K.D.; Fraser, A.M.; Dixon, A.F.G. Distribution of linyphiid spiders in relation to capture of prey in cereal fields. *Pedobiologia* 1986, 29, 367–375.
33. Greenstone, M.H. Spider feeding behaviour optimizes dietary essential amino acid composition. *Nature* 1979, 282, 501–503.
34. Bilde, T.; Axelsen, J.A.; Toft, S. The value of Collembola from agricultural soils as food for a generalist predator. *J. Appl. Ecol.* 2000, 37, 672–683.
35. Costello, M.J.; Daane, K.M. Influence of ground cover on spider populations in a table grape vineyard. *Ecol. Entomol.* 1998, 23, 33–40.
36. Sharley, D.J.; Hoffman, A.A.; Thomson, L.J. The effect of soil tillage on beneficial invertebrates within the vineyard. *Agric. For. Entomol.* 2008, 10, 233–243.
37. Schmidt, M.H.; Roschewitz, I.; Thies, C.; Tschardtke, T. Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *J. Appl. Ecol.* 2005, 42, 281–287.
38. Isaia, M.; Bona, F.; Badino, G. Influence of landscape diversity and agricultural practices on spider assemblage in Italian vineyards of Langa Astigiana (Northwest Italy). *Environ. Entomol.* 2006, 35, 297–307.
39. Hogg, B.N.; Daane, K.M. Diversity and invasion within a predator community: Impacts on herbivore suppression. *J. Appl. Ecol.* 2011, 48, 453–461, doi:10.1111/j.1365-2664.2010.01940.x.
40. Wilson, H.; Wong, J.S.; Thorp, R.W.; Miles, A.F.; Daane, K.M.; Altieri, M.A. Summer Flowering Cover Crops Support Wild Bees in Vineyards. *Environ. Entomol.* 2017, 47, 63–69.
41. Tschardtke, T.; Klein, A.M.; Kruess, A.; Steffan-Dewenter, I.; Thies, C. Landscape perspectives on agricultural intensification and biodiversity—Ecosystem service management. *Ecol. Lett.* 2005, 8, 857–874, doi:10.1111/j.1461-0248.2005.00782.x.
42. Öberg, S.; Ekblom, B.; Bommarco, R. Influence of habitat type and surrounding landscape on spider diversity in Swedish agroecosystems. *Agric. Ecosyst. Environ.* 2007, 122, 211–219.
43. Schmidt, M.H.; Thies, C.; Nentwig, W.; Tschardtke, T. Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *J. Biogeogr.* 2008, 35, 157–166.
44. Gardiner, M.M.; Landis, D.A.; Gratton, C.; Schmidt, N.; O’Neal, M.; Mueller, E.; Chacon, J.; Heimpel, G.E. Landscape composition influences the activity density of Carabidae and Arachnida in soybean fields. *Biol. Control* 2010, 55, 11–19, doi:10.1016/j.biocontrol.2010.06.008.

45. Ponge, J.F.; Dubs, F.; Gillet, S.; Sousa, J.P.; Lavelle, P. Decreased biodiversity in soil springtail communities: The importance of dispersal and landuse history in heterogeneous landscapes. *Soil Biol. Biochem.* 2006, 38, 1158–1161, doi:10.1016/j.soilbio.2005.09.004.
46. Querner, P.; Bruckner, A.; Drapela, T.; Moser, D.; Zaller, J.G.; Frank, T. Landscape and site effects on Collembola diversity and abundance in winter oilseed rape fields in eastern Austria. *Agric. Ecosyst. Environ.* 2013, 164, 145–154.
47. Zentralanstalt für Meteorologie und Geodynamik. Klimamittel Bruckneudorf. Available online: <https://www.zamg.ac.at/> (accessed on 22 June 2017).
48. Blume, H.-P.; Brümmer, G.W.; Horn, R.; Kandeler, E.; Kögler-Knabner, I.; Kretzschmar, R.; Stahr, K.; Wilke, B.-M. *Lehrbuch der Bodenkunde*, 16th ed.; Spektrum Akademischer Verlag: Heidelberg, Germany, 2010.
49. Drapela, T.; Frank, T.; Heer, X.; Moser, D.; Zaller, J.G. Landscape structure affects activity density, body size and fecundity of *Pardosa* wolf spiders (Araneae, Lycosidae) in winter oilseed rape. *Eur. J. Entomol.* 2011, 108, 609–614.
50. Bährmann, R.; Müller, H.J. *Bestimmung wirbelloser Tiere—Bildtafeln für Zoologische Bestimmungsübungen und Exkursionen*; Spektrum Akademischer Verlag: Heidelberg, Germany, 2008.
51. Bellmann, H. *Der Kosmos Spinnenführer*; Franckh-Kosmos Verlag: Heidelberg, Germany, 2016.
52. Podgajski, L.R.; Joner, F.; Lavorel, S.; Moretti, M.; Ibanez, S.; Mendoca, M.D.S.; Pillar, V.D. Spider trait assembly patterns and resilience under fire-induced vegetation change in South Brazilian grasslands. *PLoS ONE* 2013, 8, e60207, doi:10.1371/journal.pone.0060207.
53. Gisin, H. *Collembolenfauna Europas*; Museum d’Histoire Naturelle: Genève, Switzerland, 1960.
54. Stach, J. *The Apterygotan Fauna of Poland in Relation to the World-Fauna of this Group of Insects. Tribe: Orchesellini*; Polska Akademia Nauk: Kraków, Poland, 1960.
55. Stach, J. *The Apterygotan Fauna of Poland in Relation to the World-Fauna of this Group of Insects. Tribe: Entomobryini*; Polska Akademia Nauk: Kraków, Poland, 1963.
56. Bretfeld, G. *Synopses on Palaearctic Collembola, Vol. 2 Symphypleona*; Staatliches Museum für Naturkunde: Görlitz, Germany, 1999.
57. Potapov, M. *Synopses on Palaearctic Collembola, Volume 3: Isotomidae*; State Museum of the Natural History Museum of Gorlitz: Görlitz, Germany, 2001.
58. Thibaud, J.M.; Schulz, H.-J.; da Gama Assalino, M.M. *Synopses on Palaearctic Collembola, Vol. 4. Hypogastruridae*; Staatliches Museum für Naturkunde: Görlitz, Germany, 2004.
59. Fjellberg, A. *The Collembola of Fennoscandia and Denmark, Part II: Entomobryomorpha and Symphypleona*; Brill: Leiden, The Netherlands, 2007.
60. Hopkin, S.P. *A Key to the Collembola (Springtails) of Britain and Ireland*; Field Studies Council: Shrewsbury, UK, 2007.
61. Dunger, W.; Schlitt, B. *Synopses on Palaearctic Collembola, Volume 6, Part 1: Onychiuroidea: Tullbergiidae*; State Museum of the Natural History Museum of Gorlitz: Görlitz, Germany, 2011.
62. European Commission. *CORINE Land Cover—Contents*; European Environment Agency: Copenhagen, Denmark, 1994; pp. 1–94.
63. Davies, C.E.; Moss, D.; Hill, M.O. *EUNIS Habitat Classification Revised*; European Topic Centre on Nature Protection and Biodiversity: Paris, France, 2004.
64. ESRI. *ArcGIS Desktop: Release 10.2*; Environmental Systems Research Institute: Redlands, CA, USA, 2013.
65. Paredes, D.; Cayuela, L.; Campos, M. Synergistic effects of ground cover and adjacent vegetation on natural enemies of olive insect pests. *Agric. Ecosyst. Environ.* 2013, 173, 72–80, doi:10.1016/j.agee.2013.04.016.
66. Nakagawa, S.; Schielzeth, H. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods Ecol. Evol.* 2013, 2, 133–142, doi:10.1111/j.2041-210x.2012.00261.x.
67. Legendre, P.; Gallagher, E.D. Ecologically meaningful transformations for ordination of species data. *Oecologia* 2001, 129, 271–280.
68. Oksanen, J.; Blanchet, F.J.; Kindt, R.; Legendre, P.; Minchin, P.R.; O’Hara, R.B.; Simpson, G.L.; Solymos, P.; Stevens, M.H.H.; Wagner, H. *Vegan: Community Ecology Package*. R Package Version 2.0-3. 2012. Available online: <http://CRAN.R-project.org/package=vegan> (accessed on 7 July 2017).

69. Bartoń, K. MuMIn: Multi-Model Inference. R Package Version 1.9.13. 2013. Available online: <http://CRAN.R-project.org/package=MuMIn> (accessed on 7 July 2017).
70. Bates, D.; Maechler, M.; Bolker, B.; Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 2015, 67, 1–48.
71. R Core Team. R—A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria, 2014; Available online: <http://www.R-project.org/>; Vienna, Austria (accessed on 7 July 2017).
72. Landis, D.A.; Wratten, S.D.; Gurr, G.M. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Ann. Rev. Entomol.* 2000, 45, 175–201.
73. Roger-Estrade, J.; Anger, C.; Bertrand, M.; Richard, G. Tillage and soil ecology: Partners for sustainable agriculture. *Soil Till. Res.* 2010, 111, 33–40.
74. Nentwig, W. Non-webbuilding spiders: Prey specialists or generalists? *Oecologia* 1986, 69, 571–576.
75. Zulka, K.P.; Milasowszky, N.; Lethmayer, C. Spider biodiversity potential of an ungrazed and grazed inland salt meadow in the National Park 'Neusiedler See- Seewinkel' (Austria): Implications for management (Arachnida: Araneae). *Biodivers. Conserv.* 1997, 6, 75–88.
76. Seung-Tae, K.; Uhm, K.-B.; Lee, J.-H.; Yun, J.-C.; Park, C.-G.; Jung, M.-P. Spiders in a grape vineyard in Korea. *J. Asia-Pac. Entomol.* 2002, 5, 181–184.
77. Bolduc, E.; Buddle, C.M.; Bostanian, N.J.; Vincent, C. Ground-dwelling spider fauna (Araneae) of two vineyards in Southern Quebec. *Environ. Entomol.* 2005, 34, 635–645.
78. Green, J.A. Sampling method and time determines composition of spider collections. *J. Arachnol.* 1999, 27, 176–182.
79. Thomas, L.J.; Hoffmann, A.A. Vegetation increases the abundance of natural enemies in vineyards. *Biol. Control* 2009, 49, 259–269.
80. Bell, J.R.; Bohan, D.A.; Shaw, E.M.; Weyman, G.S. Ballooning dispersal using silk: World fauna, phylogenies, genetics and models. *Bull. Entomol. Res.* 2005, 95, 69–114.
81. D'Alberto, C.F.; Hoffmann, A.A.; Thomson, L.J. Limited benefits of non-crop vegetation on spiders in Australian vineyards: Regional or crop differences. *Biol. Control* 2012, 57, 541–552.
82. Toft, S.; Wise, D.H. Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia* 1999, 119, 191–197.
83. Greenstone, M. The numerical response to prey availability of *Pardosa ramulosa* (McCook) (Araneae: Lycosidae) and its relationship to the role of spiders in the balance of nature. *Symp. Zool. Soc. Lond.* 1978, 42, 183–193.
84. Harwood, J.D.; Sunderland, K.D.; Symondson, W.O.C. Living where the food is: Web location by linyphiid spiders in relation to prey availability in winter wheat. *J. Appl. Ecol.* 2001, 38, 88–99.
85. Sereda, E.; Blick, T.; Dorow, W.H.O.; Wolters, V.; Birkhofer, K. Spatial distribution of spiders and epedaphic Collembola in an environmentally heterogeneous forest floor habitat. *Pedobiologia* 2012, 55, 241–245, doi:10.1016/j.pedobi.2012.03.007.

