



## Tillage intensity and herbicide application influence surface-active springtail (Collembola) communities in Romanian vineyards



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### ABSTRACT

Vineyards are important perennial, often intensively managed agroecosystems. In most vineyards, ground vegetation is controlled by tillage and/or the application of broadband herbicides with scarcely known effects on the soil fauna. We studied a total of 16 commercial vineyards in the Târnave wine region, a typical viticultural region in Transylvania, Central Romania. As a model organism for surface-dwelling arthropods we examined the response of springtail (Collembola) species richness and activity density to vineyard tillage practices, fertilization, and herbicide application. A total of 24 species in 10 families were found in the studied vineyards. Principal coordinates analysis (PCoA) identified three distinct springtail communities linked to tillage and fertilization practice. Springtail species richness was positively associated with high tillage intensity (frequency: once or twice a year). Springtail activity density in inter-rows was positively correlated with inter-row tillage and herbicide application under grapevines. For the first time we could show that springtail species assemblages in vineyards were characterized by high niche overlap regarding soil quality (organic matter, pH, CaCO<sub>3</sub>, P and K), indicating similar resource utilization. We conclude that the positive influence of vineyard management and disturbance on surface-dwelling springtail communities is possibly due to the exclusion of potential competitors and predators, the stimulation of microorganisms and/or an increased nutrient input.

### 1. Introduction

Agricultural management is a major driver of biodiversity in vineyards (Thomson and Hoffmann, 2007; Trivellone et al., 2012; Winter et al., 2018) and knowledge about the effects of tillage intensity on soil biological properties and soil biodiversity is of great interest (Paoletti et al., 1998; Sánchez-Moreno et al., 2015). In vineyards, inter-row vegetation competes for water and nutrients with grapevines and is therefore controlled by tillage, mulching and/or the application of broadband herbicides (Pardini et al., 2002). Vineyard inter-row soil management has been shown to affect both aboveground (Kratschmer et al., 2018, 2019) and belowground (Buchholz et al., 2017; Faber et al., 2017) biodiversity and associated ecosystem services (Winter et al.,

2018).

Tillage intensity and frequency are known to influence soil biota in arable agroecosystems (e.g. Capowiez et al., 2009; Ivask et al., 2007). In perennial agroecosystems such as vineyards, tillage has been shown to decrease plant (Hall et al., 2020; Kazakou et al., 2016) and animal diversity (Paoletti et al., 1998; Sánchez-Moreno et al., 2015). Tillage and non-chemical weed control (harrowing, mulching), nutrient application, and other interventions affect soil functioning to varying extents (Favretto et al., 1992; Ivask et al., 2007; Thomson and Hoffmann, 2007; Capowiez et al., 2009). Further, management of inter-row vegetation through sown cover crops or spontaneous species and fertilizers impact the abundance and diversity of arthropods in vineyards (Franin et al., 2016). In addition, the application of pesticides can affect overall

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biodiversity in agroecosystems (Puig-Montserrat et al., 2017; Brühl and Zaller, 2019). Importantly, the detrimental effects of agrochemicals on biodiversity may be both directly, by killing of target and non-target species, and indirectly due to alterations of resource availabilities and/or competitive and predator-prey relationships (e.g., MacFadyen et al., 2009; Zaller et al., 2018).

Many soil functions, such as litter decomposition (Hättenschwiler et al., 2005) or carbon and nutrient cycling (Filser, 2002) are mediated by interactions between the biological activity of soil organisms and aboveground processes (Sanginga et al., 1992; Wurst et al., 2018). Further, soil organisms are often used as indicators of the soil health status (Briones, 2014; van Capelle et al., 2012). Among the many soil organisms, springtails or Collembola are characteristic inhabitants of agroecosystems (Culik et al., 2002; Querner et al., 2013). Springtails accelerate decomposition by feeding on a variety of food materials (Fiera, 2014; Hopkin, 1997), thereby influencing microbial activity and nutrient cycling in the ecosystem (Linden et al., 1994). Gut contents of generalized feeders show a random selection of different components of their environment (Fiera, 2014b), while phytophagous species affect the distribution of mobile elements such as potassium, and detritivorous species influence mineralization rates of less mobile elements such as phosphorus or calcium (Anderson and Ineson, 1983; Steasted and Crossley, 1984).

Information on the response of springtails to management practices in vineyards is scarce and inconsistent (Favretto et al., 1992; Renaud et al., 2004; Buchholz et al., 2017; Pfingstmann et al., 2019). A greater availability of organic substrate and a reduced tillage has led to increased springtail numbers in one study (Favretto et al., 1992), while others show that tillage can also increase springtail densities (Buchholz et al., 2017) and activities (Pfingstmann et al., 2019) compared to no tillage. Herbicide application in vineyards has been shown to reduce springtail abundance (Renaud et al., 2004).

Soil organic matter content is the primary nutrient source for detritivorous arthropods and an additionally deteriorated soil physical environment through soil cultivation can create less suitable habitats (Kautz et al., 2006; Parisi et al., 2005). Consequently, the niche space occupied by single springtail species and also the total niche space spanned by the whole community should mirror habitat suitability (Wiens, 2011). Particularly, variability in small-scale soil properties should trace the respective variability in ecological types and increase the total niche space covered by local springtail communities (Salmon et al., 2014). However, few studies investigate niche overlap of Collembola (Sha et al., 2015) or other invertebrates (Jacques et al., 2018; Romba et al., 2018; Steffan-Dewenter and Tscharrntke, 2000) in agricultural systems.

The aim of this study was to examine the response of surface-active springtail communities to vineyard management consisting of tillage, fertilization and weed control. We used quantitative surveys of 16 vineyards in Romania and investigated: (i) whether and how vineyard management intensity influences springtail species richness, community composition and activity densities, and (ii) whether community composition and niche overlap is triggered by soil characteristics.

## 2. Materials and methods

### 2.1. Study area

The study was carried out in 2015 in the Târnavă wine region, a typical Romanian viticulture region, located near the city of Blaj (46.15971°N/23.92991°E) in Transylvania (Fig. 1) (Fiera et al., 2020). We selected a total of 16 commercial vineyards along an elevational range of 251–502 m (Table 1). Vineyards received natural rainfall without additional irrigation and were cultivated with a trellis system consisted of within-row grapevine distances of 1.0 m and inter-row distances of 2.15–3.00 m. The dominant soil type was deep brown soil (Marginean et al., 2013).

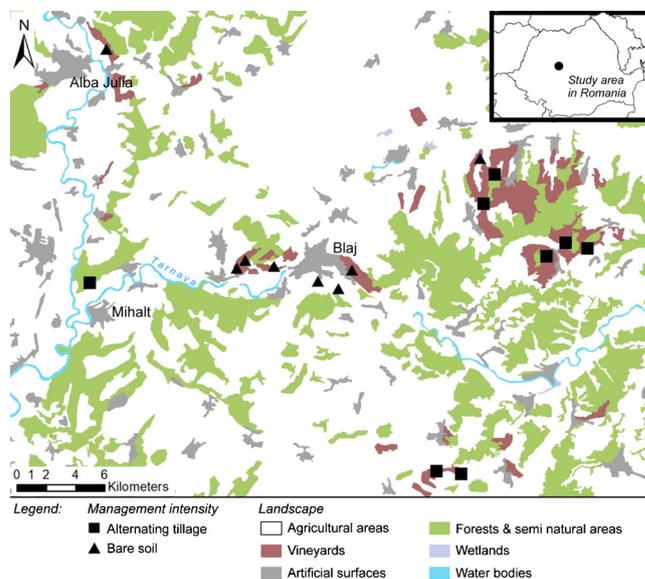


Fig. 1. Location of the studied vineyards in Central Romania including respective tillage regime: bare soil as a result of high tillage intensity as opposed to alternating tillage every second inter-row (after Fiera et al., 2020).

### 2.2. Vineyard management

The study vineyards were differently managed: (i) bare soil management through frequent tillage of the inter-rows (high intensity, further called HI); and (ii) alternating tillage of every second inter-row with vegetation cover in the other inter-row (LO). Interviews with wine growers provided information about management practices, such as duration of current management type, type of inter-row vegetation (spontaneous versus cover crops), and frequency and date of tillage or mowing.

High management intensity (HI) was characterized by tillage twice a year, in late autumn and early spring at a depth of 25–30 cm by ploughing. Foliar fertilization (1–2 times per year) with NPK during the vegetation period was used; only a few farmers used manure in autumn of the previous year near the vine row. The vegetation in the vineyards consisted of spontaneous vegetation. Weeds in the inter-rows were controlled mechanically by tillage, harrowing and mulching and underneath the vines by the application of herbicides with the active ingredients flazasulfuron, glufosinate, or glyphosate. If inter-rows were not tilled, the vegetation was mulched. The main management activities performed in each study vineyard are summarized in Table A (Supplementary Material). Details of pesticide treatments are given in Table B and Fig. S1 (Supplementary Material).

### 2.3. Collembola sampling

We used pitfall traps to collect surface dwelling Collembola in the study vineyards (Thomson et al., 2004; Buchholz et al., 2017). Pitfall catches reflect the movement activity of the captured species and therefore can be used as an estimation of their activity density (Melbourne, 1999). We installed four pitfall traps in each sampling site (17 mm diameter, 60 mm depth) in May 2015 (see Buchholz et al., 2017 for details of the sampling method). Traps were filled with ethylene glycol and a drop of odorless detergent. They were placed about 10 m from each other along a transect in the middle of the inter-row surrounded by an area of approximately  $2 \times 60$  m. In spring, most Collembola species are active ensuring that the majority of surface active species can be captured. After an exposure of 12 days, the traps were removed (20–22 May 2015). All collected invertebrate specimens were stored in 80% ethanol for further analysis (Fiera et al., 2020). All samples were expressed in terms of activity densities and determined to

**Table 1**

Basic characteristics of the study vineyards in Central Romania, springtail species richness, activity density and grouping of Principal Coordinates Analyses (PCoA) used in Fig. 2.

Vineyard ID	Municipality	Longitude	Latitude	Elevation (m)	Management intensity*	Species Richness	Activity densities	PCoA community grouping
01-HI	Ciumbud	46.32064	23.76167	291	Bare soil	13	184	B
02-LO	Mihalț	46.1795	23.7196	274	Permanent vegetation	7	100	A
03-HI	Craciunelul de Jos	46.18076	23.85841	295	Bare soil	5	329	C
04-HI	Craciunelul de Jos	46.17650	23.84996	251	Bare soil	7	155	C
05-HI	Craciunelul de Jos	46.17469	23.88289	303	Bare soil	11	210	C
06-HI	Blaj	46.15971	23.92991	327	Bare soil	3	9	A
07-HI	Blaj	46.15579	23.93625	288	Bare soil	3	4	A
08-HI	Blaj	46.16575	23.95033	302	Bare soil	5	113	C
09-LO	Cenade	46.03583	24.00887	455	Alternating tillage	7	188	C
10-LO	Cenade	46.03225	24.02165	463	Alternating tillage	10	166	B
11-LO	Tăumi	46.1577	24.1225	423	Alternating tillage	9	680	B
12-LO	Tăumi	46.1643	24.1408	417	Alternating tillage	3	422	B
13-LO	Tăumi	46.1518	24.1524	502	Alternating tillage	11	315	B
14-LO	Jidvei	46.1135	24.0431	440	Alternating tillage	9	441	C
15-LO	Jidvei	46.1216	24.0438	430	Alternating tillage	8	430	C
16-HI	Jidvei	46.1323	24.0433	330	Bare soil	10	946	C

\* Management intensity refers to intensive tillage resulting in bare soil (HI), and alternating tillage where only every second inter-row is tilled (LO); vineyard 2-LO was not tilled and with permanent vegetation cover.

species level according to Bretfeld (1999); Dunger and Schlitt (2011); Fjellberg (1998; 2007), Pomorski (1998); Potapov (2001) and Thibaud et al. (2004).

Soil samples were taken with a soil corer (5.5 cm diameter, 10 cm depth) on three randomized locations within inter-rows. From these samples we determined soil carbonates using the Scheibler method (SR ISO 10693:1995), soil organic matter (OM) using the Walkley-Black method (SR ISO 14235:2000), pH potentiometry (SR ISO 10390:2005), phosphorus (P), and potassium (K) using the Egnér-Riehm-Domingo method. Element concentrations were estimated with photo- (STAS 7184/18-80) and calorimetry (STAS 7184/19-82) (Marin et al., 2017) (see Table C – Supplementary Material).

#### 2.4. Data analysis

We used principal coordinates analysis (PCoA, Bray-Curtis similarity applied to the species  $\times$  sites matrix of species activity densities) to group vineyards according to Collembola species composition.. As species richness and abundances are frequently exponentially distributed we related the respective ln-transforms (metric response variables) as well as compositional group membership (categorical response variable) to vineyard soil variables as predictors using generalized linear models (GLM; Poisson error structure, identity link function) along with corrected Akaike information criterion (AICc) model selection. Differences in species composition were inferred from dissimilarity matrix-based one-way ANOVA (PERMANOVA Anderson, 2001). All analyses were performed with Statistica 12.0 and Primer 7.0.

The eigenvector ellipsoid method of Ulrich et al. (2017a) was used to compare niche spaces and niche overlap of pairs of species by applying Sørensen similarity. This enabled to analyze whether niche overlap with regard to soil characteristics is determined by the geographic position and species composition.

For each species we calculated four-dimensional soil eigenvector ellipsoids (axes from soil OM, pH, CaCO<sub>3</sub>, P, K) and their centroid position in environmental space according to Ulrich et al. (2017a). This method uses the variance-covariance dissimilarity matrix  $\Sigma$  of environmental characteristics at the  $k$  sites where the focal species occurs to calculate the respective eigenvector ellipsoid  $E(C)$  from:

$$E(C) = (x - c)^T U^T \Lambda^{-1} U (x - c) \leq L \quad (1)$$

where the vector  $c$  denotes ellipsoid center, and  $U$  and  $\Lambda$  the eigenvector and eigen values, respectively, of the variable dissimilarity matrix  $\Sigma$  (Ulrich et al., 2017b). We used the 99% quantile of a  $\chi^2$  distribution with  $k$  degrees of freedom to define  $L$ . To obtain sufficiently

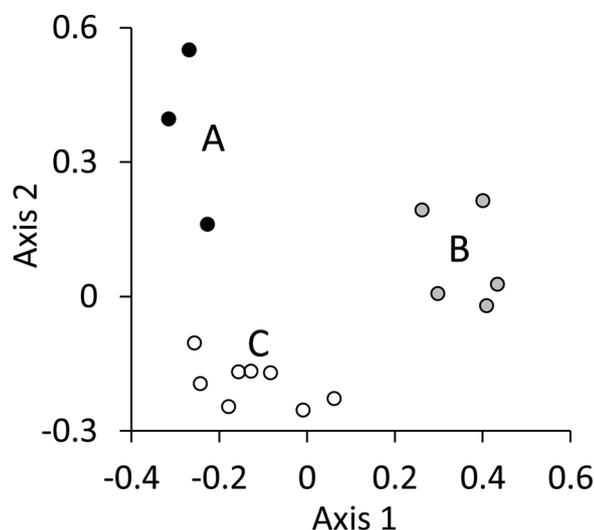
unbiased estimates of environmental variances we used only species with at least three occurrences in subsequent comparisons. We calculated these ellipsoids for average soil conditions, as well as for geographic position (latitude and longitude). Such niche and geographic ellipsoids characterize environmental and spatial niche width and distance of the compared species. These calculations were done with the Fortran software application NicheNew (Ulrich et al., 2017a, b) that is freely available from [www.keib.umk.pl/niche](http://www.keib.umk.pl/niche).

### 3. Results

In total, we collected 4692 surface-active springtails belonging to 10 families and 24 species. In LO vineyards we collected 2742 individuals from 21 species, in HI vineyards 1950 individuals from 19 species (Table 1). Species richness among the vineyards ranged between 3 and 13 species, the mean activity density ( $\pm$  SE) of surface-dwelling springtails was  $343 \pm 190$  individuals per LO site (most abundant: *Lepidocyrtus paradoxus* Uzel, 1891) and  $244 \pm 303$  individuals per HI site (most abundant: *Hypogastrura vernalis* (Carl, 1901)) (Supplementary material S2). Total species richness and activity densities of HI and LO vineyards did not differ significantly from each other at the 5% error level ( $P_t > 0.1$ ).

Principal coordinates analysis (Fig. 2) identified three statistically highly supported (Table 2) groups of vineyards with distinct springtail communities. One-way PERMANOVA indicated that these three groups were significantly linked to local activity density ( $P_{F2,13} < 0.01$ ) separating sites of low (A:  $3465 \pm 1732$  individuals; mean  $\pm$  SE), intermediate (B:  $24,929 \pm 6086$ ) and higher activity density (C:  $27,454 \pm 6894$ ). Due to the positive species ( $S$ )–activity density ( $D$ ) relationship ( $S = 1.5D^{0.24}$ ,  $P_{F2,14} = 0.03$ ) sites differed only marginally according to species richness ( $P_{F2,13} = 0.09$ ) (A:  $4.3 \pm 1.3$ , B:  $9.2 \pm 1.7$ , C:  $7.7 \pm 0.7$ ).

Community composition as inferred from the dissimilarity in species activity densities among sites was significantly linked to tillage and fertilization frequency (Table 2). High tillage intensity and high mineral fertilization increased average springtail richness (Table 3, Fig. 3a) and activity densities (Table 3, Fig. 3b). Further, increased herbicide, positively influenced species activity densities and species richness (Table 3, Fig. 3b). Tillage, fertilization, mechanical weed control (harrowing, mowing and mulching) and herbicides significantly influenced species richness, activity densities, and community composition (Table 2, Fig. 3). Further, springtail activity densities and community composition were influenced by soil CaCO<sub>3</sub> and species richness by soil K contents (Table 4).



**Fig. 2.** Principal coordinates analysis (Bray-Curtis dissimilarity) based on springtail species activity densities identified three distinct groups of vineyards (site identities as in Table 1). The first two axes explain 24% and 19% of variance, respectively.

**Table 2**

One way PERMANOVA (Bray Curtis dissimilarity) of species activity densities pointed to tillage mode and type of fertilization as influencing community composition. Management intensity refers to HI and LO intensity.

Factor	df	P
Tillage	2	< 0.001
Fertilization	2	< 0.01
Mulching	3	0.03
Herbicides	2	0.12
Fungicides	1	0.06
Management intensity	1	0.02
Community composition	2	< 0.001

**Table 3**

GLM of effects of management factors on species richness and ln-transformed activity densities as metric and PCoA groups as categorical response variables. Given are  $\chi^2$  estimates and associated parametric significances. The respective most informative model (AICc selected) is given in bold. df refers to the degrees of freedom, P to the parametric significance level.

Management factor	df effect	Species richness		ln activity density	
		$\chi^2$	P	$\chi^2$	P
High tillage	2	<b>8.02</b>	<b>0.02</b>	<b>15.95</b>	< 0.001
Fertilization	2	0.56	0.76	2.26	0.32
Mechanical weed control	3	4.02	0.26	4.91	0.18
Herbicides	2	1.79	0.41	<b>12.53</b>	< 0.01
Fungicides	1	0.29	0.59	1.78	0.18
Management intensity	1	0.41	0.52	0.19	0.66

Geographic overlap in species occurrences was not correlated with soil niche overlap (Fig. 4a). However, we observed a distinct pattern with regard to geographic and niche distances (Fig. 3b). Co-occurring species (small average geographic distance) were divided into those that had similar niche distances or markedly separated niches spaces (Fig. 4b). Pairwise overlap in soil niche was significantly positively correlated with the similarity in occurrence (Fig. 4c). Soil niche distances among species pairs decreased significantly with increasing occurrence similarity (Fig. 4d).

## 4. Discussion

### 4.1. Vineyard management effects

The results of this study demonstrate that intense vineyard management influences the composition of springtail communities: the number of individuals was significantly higher in LO compared to HI vineyards. Hence, our results corroborated previous findings that springtails are influenced by tillage, fertilization, and herbicide application. Tillage is known to detrimentally affect soil arthropod communities (Moore et al., 1984; Sánchez-Moreno et al., 2015). However, in the present study high tillage intensity fostered Collembola assemblages. Indeed, springtails appeared to be more sensitive to tillage intensity than to other management intensities or N fertilization (Coulibaly et al., 2017). Prior work had already shown that Collembola can show large population sizes despite high management intensity (Filsler and Fromm, 1995; Fiera et al., 2020) and be less affected by farming practice than other soil organisms, such as earthworms or epigeic predators (Faber et al., 2017; Holland et al., 1994). High management intensity is suggested to mainly affect epigeic and hemiedaphic Collembola species (Heimann-Detlefsen, 1991). Thus, our results corroborate prior findings that springtails might be weak indicators of soil management and disturbance intensity (Sterzyńska et al., 2018). However, other studies conducted in vineyards show that mechanical disturbance through frequent tillage is not always detrimental to Collembola, at least when compared with alternate tillage with rather compacted soils (Buchholz et al., 2017; Pfungstmann et al., 2019).

Pesticides can directly or indirectly influence populations of edaphic arthropods (Lins et al., 2008; Zaller et al., 2016). We were therefore surprised to see that more frequent herbicide applications underneath the grapevines increased springtail richness and abundance in the neighboring inter-rows of the study vineyards. This might be due to a combination of (i) an avoidance of sprayed rows and migration to unsprayed inter-rows (Zaller et al., 2016), (ii) increased springtail activity after herbicide treatment due to a nutrient input via herbicides (Lins et al., 2007; Liu et al., 2016) or a stimulation of microorganisms (Mandl et al., 2018), and (iii) a fast recolonization of disturbed (tilled) areas (Buchholz et al., 2017; Maderthaner et al., 2020). However, more detailed studies including more sampling dates per season are necessary to elucidate the underlying processes. It is also important to note that we only investigated epigeic springtail species and different Collembola life forms might well respond differently. Indeed, approaches calculating an ecomorphological index reveal that euedaphic species might actually be more sensitive to a variety of mechanical disturbances than epigeic springtail species (Joimel et al., 2017).

However, surface-active springtail communities are probably more exposed to pesticide treatments than soil-dwelling species. Also, species with low dispersal ability should take longer to recover. Some authors have claimed that there is no direct effect of herbicides on soil animals and that the increase or decrease in population sizes were indirect effects, mostly caused by vegetation changes (Curry, 1970; Edwards and Thompson, 1973). However, others identified a significant negative effect of bromoxynil and diclofop-methyl herbicides on the activity of two species of Collembola (Greenlade et al., 2010). These contrasting results might be explained by different reactions of soil springtails to post- and pre-emergence herbicides (Reinecke et al., 2002; Renaud et al., 2004; Sturm et al., 2002). Further, the composition of herbicide formulations might cause differential reactions of springtails (Maderthaner et al., 2020). Applications of herbicides can reduce or avoid the need to disturb the soil, but may kill Collembola directly (Subagja and Snider, 1981), or indirectly for instance by changing specific fungal food sources (Edwards and Thompson, 1973; Frampton and Wratten, 2000; Lönsjö et al., 1980; Mandl et al., 2018). In a greenhouse experiment, glyphosate-based herbicides have been shown to stimulate the surface activity of springtails compared to

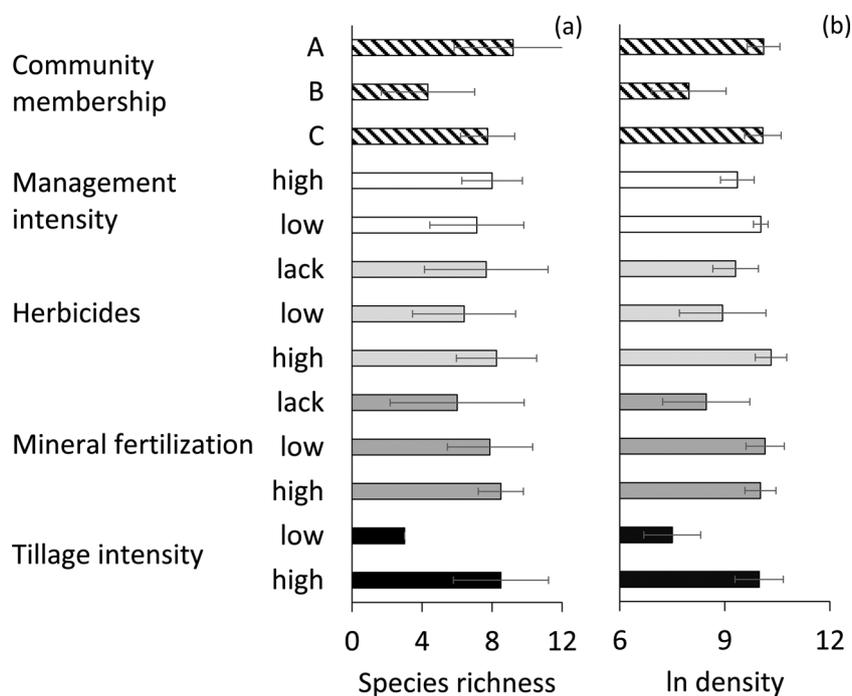


Fig. 3. Springtail species richness (a) and ln-transformed activity densities (b) with respect to community membership, management intensity, herbicide usage, mineral fertilization and tillage intensity. Means  $\pm$  SE.

**Table 4**

GLM of soil factors on species richness and ln-transformed activity densities as metric and principal coordinates analyses (PCoA) groups as defined in Fig. 2 as categorical response variables. Given are  $\chi^2$  estimates and associated parametric significances. The respective most informative model (AICc selected) is given in bold.

Soil factor	Species richness		ln activity density		PCoA groups	
	$\chi^2$	P	$\chi^2$	P	$\chi^2$	P
Organic matter	0.17	0.68	0.50	0.48	1.07	0.30
pH	0.07	0.79	0.40	0.53	0.01	0.93
CaCO <sub>3</sub>	1.27	0.26	<b>4.35</b>	<b>0.04</b>	<b>4.45</b>	<b>0.03</b>
P	0.31	0.58	0.31	0.58	0.57	0.45
K	<b>2.76</b>	<b>0.10</b>	0.14	0.71	0.61	0.44

mechanically weeding; however, this was also influenced by the soil organic matter content (Maderthaler et al., 2020).

Site conditions may influence the reactions of soil organisms to land use change. Soil biota living in the upper 0–10 cm of the soil reflect current management practice better than those at greater soil depth which better reflect management history and soil properties (Querner et al., 2013). The most important factors determining arthropod abundance and diversity in agroecosystems (particularly carabids, staphylinids and spiders) are the availability of food, shelter, and a suitable microclimate (Booij and Noorlander, 1992). These factors are closely related to the quantity and duration of vegetation cover. Therefore, vegetation is another key factor for surface-dwelling arthropods (Booij and Noorlander, 1992; House and Stinner, 1983) besides soil properties such as soil organic matter or aggregate stability (Guzmán et al., 2019).

Vegetation cover seems also to be the clue to understand why intensively tilled vineyards reach comparatively high springtail richness and abundances (Fig. 3 and Buchholz et al., 2017, but Coulibaly et al., 2017 for a contrary finding). The loss of vegetation cover disrupts the compartmentalization of the natural soil food web structure dominated by omnivory and many trophic levels (Moore, 1994; Haddad et al., 2011; Digel et al., 2014), and particularly decreases arthropod predator

abundances (Haddad et al., 2009; Pfingstmann et al., 2019). A top-down control in these food webs in association with reduced herbivore abundance would then be linked to increased omnivore, fungivore, and detritivore densities as reported here and in comparative studies (e.g. Thakur and Eisenhauer, 2015). Therefore, our finding of increased springtail densities in tilled vineyards apparently comes to the cost of the prior destruction of the natural soil community structure and disrupted predator control mechanisms.

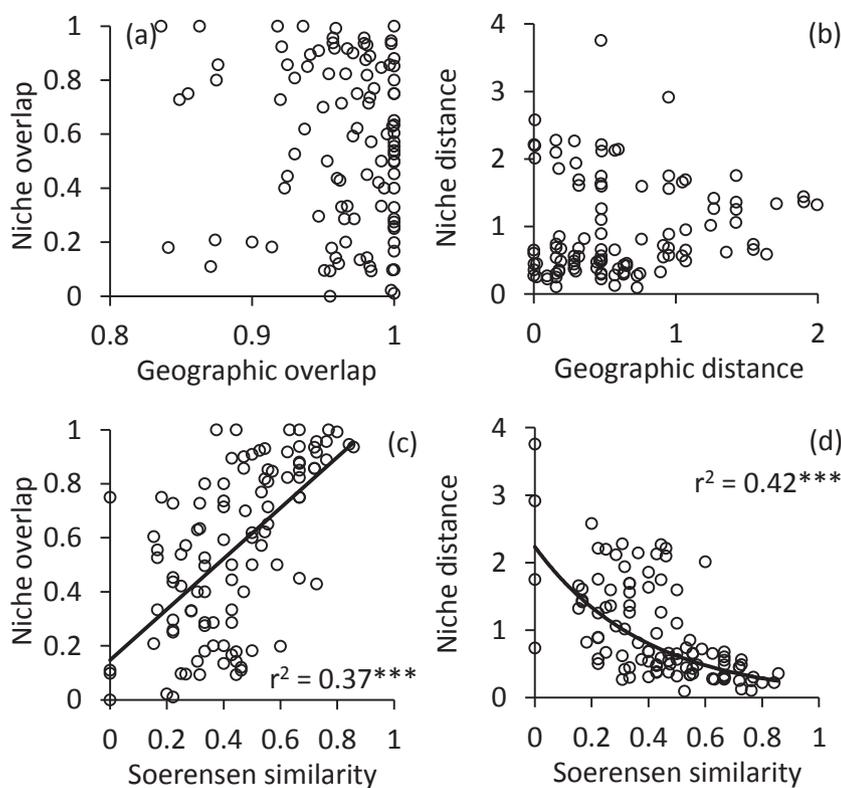
#### 4.2. Niche overlap

The current study is the first to describe niche overlap of Collembola in vineyards. We found that springtail assemblages were characterized by a high niche overlap with regard to soil organic matter content, pH, CaCO<sub>3</sub>, P and K concentrations indicating similar resource utilization. Trophic resource availability and quality are known to represent major ecological constraints for soil animals (Fiera, 2014, 2014b; Lavelle and Spain, 2001). Respective niche requirements (local environmental filters) determine the presence of species (Chase and Leibold, 2003).

In this respect, low ellipsoid overlaps (niche and geography) points to niche or geographic segregation (Ulrich et al., 2017a,b). We found an equiprobable random distribution of niche overlap among the springtail species (Fig. 4). This fact does not point to filter or competitive effects structuring springtail communities towards niche segregation (competition driven low overlap) or filter effects (high overlap). Rather, the equiprobable distribution of overlap and niche distances (Fig. 4b) is in line with a neutral species community assembly based on ecological drift, random colonization and local extinction.

#### Author contribution

D.P., J.B., P.Q., P.S., T.B., S.W. and J.G.Z. conceived and planned the experiment; J.B., D.P., C.I.B., and J.G.Z. conducted the field work; C.F. identified Collembola species; S.K. did GIS work; C.I.B., P.S., and T.B. conducted soil analyses, W.U. and C.F. analysed data and wrote the first draft; all authors were involved in significant parts of the study, wrote and/or reviewed the manuscript.



**Fig. 4.** Relationships between geographic and soil niche overlap (a) and centroid distances (b). c, d: niche overlap respective centroid distances in relation to the Sørensen similarity of pairwise species co-occurrences. Data for all springtail species pairs where each species was found in at least three vineyards. The linear (c) exponential (d) regressions are parametrically significant at \*\*\* $P < 0.001$ .

#### Declaration of Competing Interest

The authors declare no competing financial interests.

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#### Appendix A. Supplementary data

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