XIIIth International Terroir Congress
17–18 November 2020
Virtual Congress | Adelaide, Australia

SOIL MICROBIAL AND ARTHROPOD BIODIVERSITY UNDER ORGANIC AND BIODYNAMIC VITICULTURE

Johanna Döring[1]*, Matthias Friedel[1], Jacob Agerbo Rasmussen[3,4,5], Maximilian Hendgen[2], Sofia Di Giacinto[2], Randolf Kauer[1]

[1]Department of General and Organic Viticulture, Hochschule Geisenheim University, Von-Lade-Str. 1, D-65366 Geisenheim, Germany
[2]Department of Soil Science and Plant Nutrition, Hochschule Geisenheim University, Von-Lade-Str. 1, D-65366 Geisenheim, Germany
[3]Section for Evolutionary Genomics, The GLOBE Institute, Faculty of Health and Medical Sciences, University of Copenhagen, Øster Farimagsgade 5A, 1352 Copenhagen, Denmark
[4]Biological Institute, Genome Research and Molecular Biomedicine, University of Copenhagen, Universitetsparken 13, 2200 Copenhagen, Denmark
[5]Center for Evolutionary Hologenomics, University of Copenhagen, Øster Farimagsgade 5A, 1352 Copenhagen, Denmark

*Corresponding author: johanna.doering@hs-gm.de

Abstract

Aims: The aim of the study was to investigate whether organic or biodynamic management have a long-term impact on 1) the microbial biomass and enzymatic activity in the soil, 2) the soil microbial community, 3) flying as well as soil living arthropods and associated fungi.

Methods and Results: The studies presented here were conducted in a field trial comparing integrated, organic and biodynamic viticulture at least 10 years after the implementation of the different management systems. The vineyard is located in Geisenheim, Germany, and the study is conducted on *Vitis vinifera* L. cv. Riesling.
One study assessed soil enzymatic activities (GLU, CAT, UR, DHA, PHO) and microbial biomass by quantifying PLFAs and NLFAs, respectively. For the second study soil fungal and bacterial biodiversity were investigated using an amplicon sequencing approach. For the third study eDNA was extracted from arthropods in bulk and soil samples. A DNA metabarcoding approach was used to investigate whether diversity of arthropods and fungi in these samples was affected by the management system.
Fungal and bacterial biomass as well as enzymatic activities in the soil were shown to be highly affected by the management system. The organic and the biodynamic systems had significantly more fungal and bacterial biomass. In contrast, the integrated system had a significantly higher mycorrhizal biomass compared to the organic and the biodynamic system. Enzymatic activities measured were significantly higher under organic and biodynamic management.
Fungal species richness assessed by DNA sequencing did not differ among management systems, but fungal community composition was significantly affected. Bacterial species richness was significantly higher under organic and biodynamic management, whereas bacterial community composition was less affected by the management system.
Richness of flying and soil-living arthropods and their related fungi assessed by eDNA sequencing was not significantly affected by the management system alone. In contrast, management systems significantly differed in the arthropod community composition in bulk samples as well as in fungal community composition associated with flying as well as soil-living arthropods.

Conclusions: Different management systems have a clear impact on soil microbial activity, biomass, and biodiversity, as well as on arthropod biodiversity and fungal biodiversity associated with arthropods. In the current studies soil enzymatic activities as well as soil microbial biomass and bacterial species richness in the soil were positively affected by organic and biodynamic management. Fungal community composition in the soil, in samples of soil-living as well as in samples of flying arthropods were highly affected by the management system. The hypothesis of whether arthropods in the vineyard act as vectors for bacteria and fungi will be discussed.

Significance and Impact of the Study: Arthropods as well as microbial biodiversity are important facets of terroir. By choosing a management system we highly influence microbial activity, biomass and biodiversity as well as arthropod biodiversity in the vineyard. Differences in fungal community composition associated with soil-living

and flying arthropods might also impact fungal community composition in the carposphere of ripening winegrape berries.

Keywords: Organic, biodynamic, soil microbial activity, soil microbial biomass, microbial biodiversity, arthropod biodiversity

Introduction

Vineyards usually host a wide range of complex communities, including micro- and macro-organisms such as bacteria, fungi and arthropods (Isaia *et al.*, 2006). In temperate Europe, they usually provide habitats for rare and endangered species, because they typically occupy warm and dry climates (Bruggisser *et al.*, 2010). The composition of these communities, their species richness and abundance, influences health, yield, and vigor of grapevines, but also wine flavor and aroma, and thus are an important part of terroir (Gilbert *et al.*, 2014). The micro- and macro-fauna of vineyards directly affect soil fertility, nutrient supply, presence of antagonists to pathogenic micro- and macro-organisms and influence vine health, growth and grape quality. The microbiome of a soil impacts organic matter decomposition, nutrient cycling and buffering, soil structure, and the degradation of pollutants (Emmerling *et al.*, 2002). Furthermore, it influences plant health and growth through positive benefits for processes such as or mycorrhization, symbiotic interaction and resistance induction, or negatively through pathogenic infection (Jackson *et al.*, 2012; Tonelli *et al.*, 2011; Coninck *et al.*, 2015). Thus, the microbiota can be considered as a key player in soil functionality, ensuring soil productivity and product quality in agricultural production systems (Gisi, 1990). Fungi and bacteria above-ground play a major role as pathogens or antagonists to pathogens and the microbiome in the carposphere of ripening winegrape berries highly influences final wine quality when spontaneous fermentation is applied (Morrison-Whittle *et al.*, 2017). Flying as well as soil-living arthropods are an important part of agroecosystems, since they might act as natural antagonists to insect pests. The conservation or the increase of their population and thus the use of their regulating potential are central aims of integrated and sustainable agriculture and crop production (Ruppert, 1993). Moreover, arthropods might act as vectors of microorganisms (Agerbo Rasmussen *et al.*, 2020).

Despite the fact that little is known about the importance of single organisms for ecosystem functionality, it is commonly agreed upon that high biodiversity can ensure vital and productive agroecosystems and buffers negative impacts, especially under changing climatic and environmental conditions (Altieri, 1999).

Modern winemakers are increasingly interested in replacing conventional or integrated (INT) production with organic (ORG) and biodynamic (BD) management strategies which are claimed to be more environmentally sound (Bengtsson *et al.*, 2005). The aim of the current studies was to investigate whether ORG and BD management have a long-term impact on 1) the microbial biomass and enzymatic activity in the soil, 2) the soil microbial community, 3) flying as well as soil living arthropods and associated fungi.

Materials and Methods

The field trial comparing integrated, organic, and biodynamic management is located in Geisenheim, Germany, and owned by Hochschule Geisenheim University. The experimental vineyard is 0.8 ha in size and was planted in 1991 (cv. `Riesling`, clone Gm 198-30, grafted on *Vitis berlandieri* x *Vitis riparia* cv. `SO4` and *Vitis riparia* x *Vitis cinerea* cv. `Börner`, respectively). The vine spacing is 1.2 m within rows and 2 m between rows using a Vertical Shoot Positioning (VSP) system. Rows were oriented in a North to South direction. Until the end of 2005 the vineyard was managed conventionally according to the *code of good practice*. In 2006, conversion to organic and biodynamic management started (Council Regulation (EC) No. 834/2007 and Commission Regulation (EC) No 889/2008). The soil of the vineyard plots was analyzed for uniformity before data collection started (Döring *et al.,* 2015). The experimental site was set up as a complete block design. Each management system was replicated in four blocks. The management systems differ with regards to plant protection strategies, under-vine management and fertilization, and cover cropping strategy (Table 1). Each replicate of one management system consisted of four rows, including two buffer-rows and two center-rows, where sampling took place.

Table 1: Characteristics of the respective management systems modified according to Döring *et al.* (2015).

	INT	ORG	BD
cover crop	sward (every 2nd row cultivated)	multi-species mixture (every 2nd row cultivated)	
under-vine-management	herbicides	mechanically	
fertilization	green waste compost + mineral fertilizers (according to N_{min} analysis)	farmyard manure + rolling or cultivation of cover crop	farmyard manure with biodynamic preparations (or cow pat pit preparation) + rolling or cultivation of cover crop
plant protection	systemic fungicides botryticides	copper (max. 3 kg/ha and year), wettable sulfur plant resistance improvers	
	mating disruption method against grape berry moth		
biodynamic preparations	-	-	horn manure, horn silica compost preparations

Soil samples for enzymatic activities and PLFA/NLFA analysis were collected once a month over a period of four months (May–August) in 2016. Samples were taken from the middle of untilled rows under cover crop in the central row of each experimental block, leaving the outer rows as a buffer. Six samples were extracted with an iron drill at depths of 0–20 cm and pooled to get a representative sample for each of the 12 vineyard plots. Enzyme essays followed the method of Alef (1991). Phospholipid fatty acids (PLFA) and neutral lipid fatty acids (NLFA) were analysed according to Frostegård *et al.* (1993). All statistical analyses were computed using the R software package (R Development Core Team, 2006). A mixed linear model with treatment as a fixed factor and block and date as random factors was applied. A likelihood ratio test was performed to test the significance of the factor treatment. If the treatment effect was significant ($p < 0.05$), a general linear hypothesis test with Bonferroni-Holm adjustment was carried out to compare the factor levels (Di Giacinto *et al.*, 2020).

Soil samples for community analysis of bacteria and fungi were collected in August 2015 using a Pürckhauer soil sampler. Drill cores were taken in-row under cover cropping, and under-vine, respectively. The cores were divided into topsoil (5–30 cm) and subsoil (30–60 cm), and the first 5 cm under the surface were discarded to avoid major heterogeneities and point pollutions. Within each block, mixed samples consisting of four different drillings were generated for each management regime, each position and each depth. Soil samples were collected in sterile plastic bags, manually homogenized and immediately stored in a cooler. DNA extraction of all samples was conducted the same day. DNA was extracted from 0.25 g of freshly homogenized soil using a PowerSoil DNA Isolation Kit (MoBio Laboratories Inc., Carlsbad, CA, USA), following the manufacturer's protocol. The obtained DNA was stored at −80 °C until further processing. For amplification of fungal ITS2 regions, a primer mix P5-5 N-ITS4 and P5-6 N-ITS4 (forward) together with P7-3 N-fITS7 and P7-4 N-fITS7 (reverse) was used according to Ihrmark *et al.* (2012). Amplification of bacterial 16S-rRNA genes utilized a primer mix P5-8 N-515 F and P5-7 N-515 F (forward) in combination with the primer mix P7-2 N-806r and P7-1 N-806r (reverse), as modified by Caporaso *et al.* (2012). For more details on polymerase chain reaction and processing of raw data please see Hendgen *et al.* (2018).

Statistical analyses were performed using R (R Development Core Team, 2006) as well as Geneious (version 9.1.2), und Past (version 2.17c). Univariate analyses of variance were estimated by means of R packages *lme4* and *lmerTest* for generating mixed linear models, with management system, soil depth and sampling position as independent variables as well as a subsequent exclusion of random block effects. Least Significant Difference was performed as a Post-hoc test using the R packages *lsmeans* and *multcomp*, levels of significance were FDR adjusted. Species richness values were normalized previously. Furthermore, *permutational multivariante analyses of variance* (PERMANOVA) were conducted via the *adonis* command, based on Bray-Curtis distances with 999 permutations. Multivariate homogeneity of group dispersions was calculated and plotted as *principal coordinates analysis* (PCoA) using the *betadisper* command for the factors management and position, respectively (Hendgen *et al.*, 2018).

Flying arthropods were collected during 5 days at bloom at harvest 2017, respectively, using vane traps (SpringStar Inc.) consisting of a 1.9 L plastic container, screw-top funnel and two plastic vanes, colored either blue or yellow. Each trap contained 300 ml of 50% propylene glycol (MP Biomedicals). Pairs of blue and yellow vane traps were hung on the guiding-wires next to vines at each replicate, at a height of approximately 150 cm from the soil surface. A soil sample was also collected for each pair of vane traps, with an aim of investigating the soil fungal and arthropod communities. Soil samples were collected in 50-ml tubes within the vine stock row,

directly under the vine guideline. DNA was extracted from the trap samples using a method which leaves external arthropod morphology intact (Nielsen *et al.,* 2019). DNA was extracted from soil samples using the PowerSoil® DNA Isolation Kit (Qiagen) following the manufacturer's protocol. PCR amplification was carried out using two primer sets, one set aimed at arthropods (Zeale *et al.*, 2011) and one aimed at fungi (D2) (Putignani *et al.*, 2008). For further details on polymerase chain reaction and metabarcoding please see Agerbo *et al.* (2020). Comparison of richness, extrapolation, and similarity was assessed using unweighted Hill numbers (Hill, 1973), as implemented by the R-package *hilldiv* (Alberdi and Gilbert, 2019). Hill numbers were also used to analyze composition, using q = 0 to minimize biased effects of relative abundance (Alberdi and Gilbert, 2019; Jost, 2006). Richness of OTUs was analyzed using ANOVA. Permutational multivariate analyses of variance (PERMANOVA) were conducted, using *vegan*, based on Jaccard distances with 999 permutations. The R-package *metacoder* (Foster *et al.,* 2017) was applied to compare differential abundance of OTUs on different taxonomic levels between management systems.

Results and Discussion

Mineralized nitrogen (N min) content in topsoil was generally low ranging between 1.4 kg ha^{-1} NO3-N in the INT treatment in June and 51 kg ha^{-1} NO3-N in the organic treatment in August. N min content was significantly affected by the management system with INT showing significantly lower values compared to ORG and BD, respectively (Table 2). Together with this N% was significantly higher in ORG and BD plots (Di Giacinto *et al.*, 2020). pH in the experimental site ranged between 7.35 and 7.47 with BD plots showing a significantly higher soil pH compared to INT (Di Giacinto *et al.*, 2020). Mean copper (Cu) contents ranged between 82.4 and 98.7 mg kg^{-1} of soil and were significantly higher in ORG and BD plots compared to the INT management system (Di Giacinto *et al.*, 2020). Management systems did not differ in either relative water content (RWC) (Table 2) nor in humus content and C/N ratio (Di Giacinto *et al.*, 2020).

Enzymatic activities in soil differed significantly among treatments when assessed throughout the growing season in 2016. The integrated plots showed the lowest GLU, CAT, UR, and DHA activities, respectively. Plots did not differ in PHO activity (Table 2).

Four main PLFAs and NLFAs were analysed as chemotaxonomic markers using four months within the growing season 2016 to quantify microbial biomass in soils of INT, ORG and BD management systems (Table 2). Bacteria, fungi and AMF populations were strongly influenced by the management system while protozoa marker (PLFA 20:4ω6) did not differ among treatments. PLFA 16:1ω7 and PLFA 18:2ω6, bacteria and fungi population indicators, were significantly higher in both ORG and BD systems compared to INT. NLFA 16:1ω5, the AMF marker, was significantly higher in INT soil as compared to ORG and BD systems.

Table 2: Soil enzymatic activities and microbial community analysis (PFLA) in the different management systems (modified according to DiGiacinto *et al.*, 2020).

Parameter	INT (mean ± sd)		ORG (mean ± sd)		BD (mean ± sd)		treat
Soil Analysis							
N min [NO_3-N kg ha^{-1}]	4.42 ± 2.43	b	12.27 ± 11.78	a	11.79 ± 6.81	a	**
RWC [%]	47.74 ± 11.15	-	47.01 ± 13.20	-	48.52 ± 12.73	-	ns
Enzymatic activity							
GLU [µg ρNP g^{-1} h^{-1}]	564.52 ± 163.10	b	730.96 ± 176.79	a	753.96 ± 192.63	a	***
CAT [% of O_2 released]	8.76 ± 3.35	b	13.38 ± 6.78	a	12.61 ± 6.98	ab	*
UR [µg NH_4-N g^{-1} h^{-1}]	24.07 ± 5.44	b	27.31 ± 5.35	ab	29.44 ± 4.92	a	*
DHA [µg TPF g^{-1} h^{-1}]	0.656 ± 0.137	b	0.714 ± 0.152	ab	0.756 ± 0.132	a	*
PHO [µg ρNP g^{-1} h^{-1}]	217.81 ± 82.03	-	222.09 ± 73.95	-	227.8 ± 82.7	-	ns
Fatty acid - indicator							
PLFA 16:1n7 - Bacteria [nmol g^{-1} soil]	5.90 ± 1.01	b	7.09 ± 0.91	a	7.43 ± 0.72	a	***
PLFA 18:2n6 - Fungi [nmol g^{-1} soil]	2.44 ± 0.49	b	3.06 ± 0.66	a	3.07 ± 0.63	a	**
PLFA 20:4n6 - Protozoa [nmol g^{-1} soil]	0.63 ± 0.20	-	0.63 ± 0.30	-	0.58 ± 0.14	-	ns
NLFA 16:1n5 - AMF [nmol g^{-1} soil]	31.13 ± 12.18	a	15.82 ± 8.27	b	14.31 ± 5.44	b	***

ORG and BD systems were clearly characterized by a higher N min content and N%, higher Cu content in soils as well as higher PLFA 16:1ω7 and PLFA 18:2ω6 marker, respectively, indicating significantly higher bacterial and fungal biomass. Enzymatic activities of GLU, CAT, UR, and DHA were significantly lower in INT. These parameters together indicate a generally higher fungal and bacterial activity in ORG and BD soils compared to INT plots. The INT management system was shown to have significantly lower N min content, N %, and Cu content in the soil, but higher NLFA 16:1ω5 marker indicating a significantly higher AMF biomass. This might be due to lower N min content in the INT system. These differences among the management systems were stable during the whole growing season 2016 and thus seem to be characteristic for the respective management regimes. RWC cannot account for these differences in fungal, bacterial, AMF biomass, and enzymatic activities since it did not differ among treatments. It is more likely that the fertilization, the type of cover crop used in the respective management systems as well as the differences in cover crop and under-vine management between INT and ORG/BD plots might be of major influence concerning microbial traits of the management regimes. Higher Cu contents in ORG and BD soils most likely originate from plant protection agents used in the respective treatments. Still average Cu concentrations in the current trial were well below levels which might have significantly negative effects on the soil microbial community (Díaz-Raviña *et al.*, 2007). None of the microbial soil parameters showed a significant correlation with Cu concentrations in the soil (Di Giacinto *et al.*, 2020).

While enzymatic activities and PLFA and NLFA markers are clear indicators of microbial activity and biomass in the soil, they do not provide information about soil microbial diversity or community composition. In order to elucidate soil fungal and bacterial biodiversity in the current trial, a DNA sequencing approach was chosen in 2015. Fungal species richness in top- and subsoil did not differ significantly among the management systems when assessed in 2015 (Figure 1A), but community composition was significantly different in INT vs. ORG and BD treatments (Figure 1B).

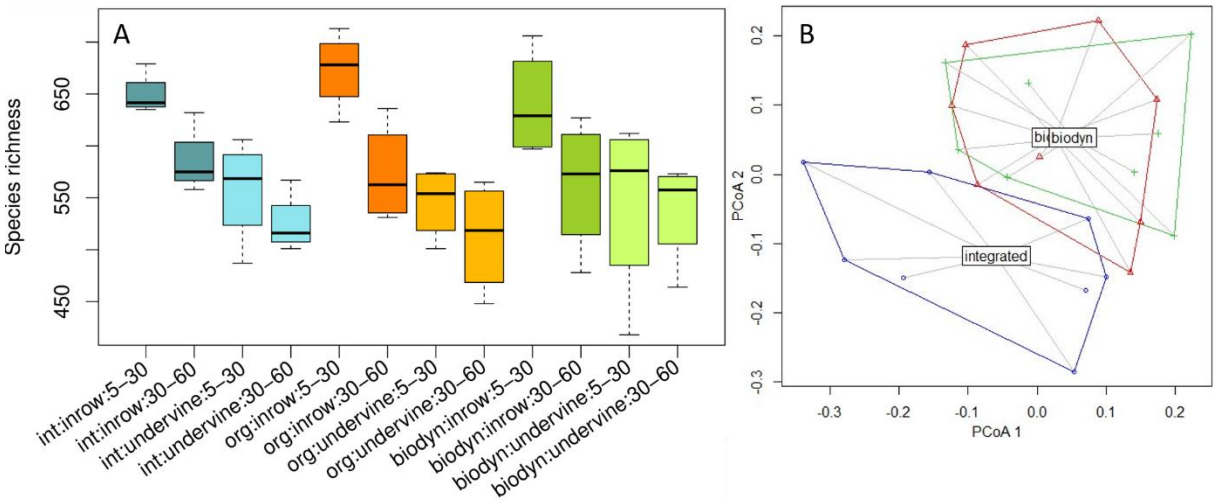

Figure 1: Fungal species richness in top- and subsoil (A) and fungal community composition in topsoil (B) of INT, ORG and BD treatments (modified according to Hendgen *et al.*, 2018).

In relation to other studies on vineyard soil microbiota our fungal species richness of about 400–700 species was shown to be higher (Orgiazzi *et al.*, 2012; Corneo *et al*., 2013). As this fungal community shift was most evident in topsoil in the middle of the row (in-row), it might be likely that cover crops influence fungal community composition by root exudates, litter composition, soil aggregation and moisture. Since cover crop mixtures differ between INT and ORG/BD systems they might determine fungal community composition in vineyard soils to a high extend. The BD treatment in this case did not show significant differences compared to ORG plots (Hendgen *et al*., 2018). Since INT as well as ORG and BD plant protection strategies comprise different groups of fungicides and are characterized by frequent applications throughout the growing season, a side effect of the latter on fungal community composition might be possible.

Bacterial community composition, in contrast, did not differ significantly among treatments (Figure 2B), whereas bacterial species richness was higher in ORG and BD treatments compared to INT plots (Figure 2A). Still bacterial species richness was significantly higher only for the ORG treatment compared to INT plots.

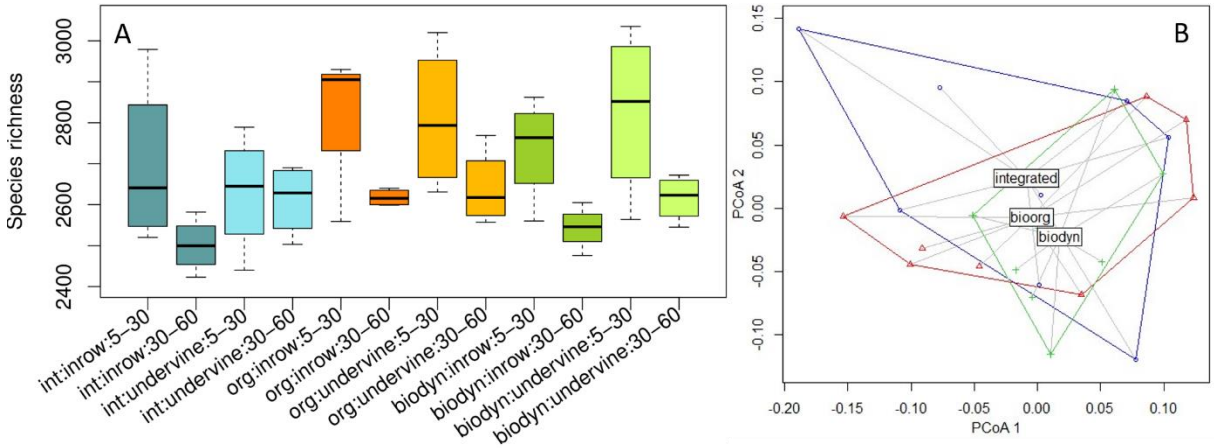

Figure 2: Bacterial species richness in top- and subsoil (A) and bacterial community composition in topsoil (B) of INT, ORG and BD treatments (modified according to Hendgen *et al.*, 2018)

Bacterial richness in the current study exceeded fungal richness indicating a higher bacterial diversity and occurrence compared to fungal diversity. Absolute bacterial richness was comparable to other studies conducted in vineyards (Vega-Avila *et al.,* 2015). Bacterial species richness was slightly higher under ORG and BD management, but community composition remained more stable throughout the management systems compared to the fungal community. Hence, the bacterial community can be assumed to be insensitive against changes in soil management exhibited by the different management regimes. Bacterial phyla composition and proportions mostly followed taxonomic community patterns similar to those revealed by other groups (Burns *et al.*, 2015; Fujita *et al*., 2010; Zarraonaindia *et al*., 2015) thus indicating high consistency of bacterial communities over several locations and climates, mostly affected by land use patterns (Hendgen *et al*., 2018).

A third study was conducted in the current trial in 2017 in order to assess biodiversity of soil-living as well as flying arthropods in the respective management systems. Species richness of arthropods was significantly influenced by sampling period (full-bloom vs. harvest 2017) and by the sampling type (flying vs. soil-living arthropods), but it was not influenced by the management system. Considering interactions between management and sampling type species richness of flying arthropods was significantly higher in INT treatment (Figure 3A), especially during bloom, whereas species richness of soil-living arthropods was significantly higher under ORG and BD treatments, respectively (Figure 3B). Arthropod community composition did not differ among treatments neither in bulk nor in soil samples (Agerbo Rasmussen *et al.*, 2020).

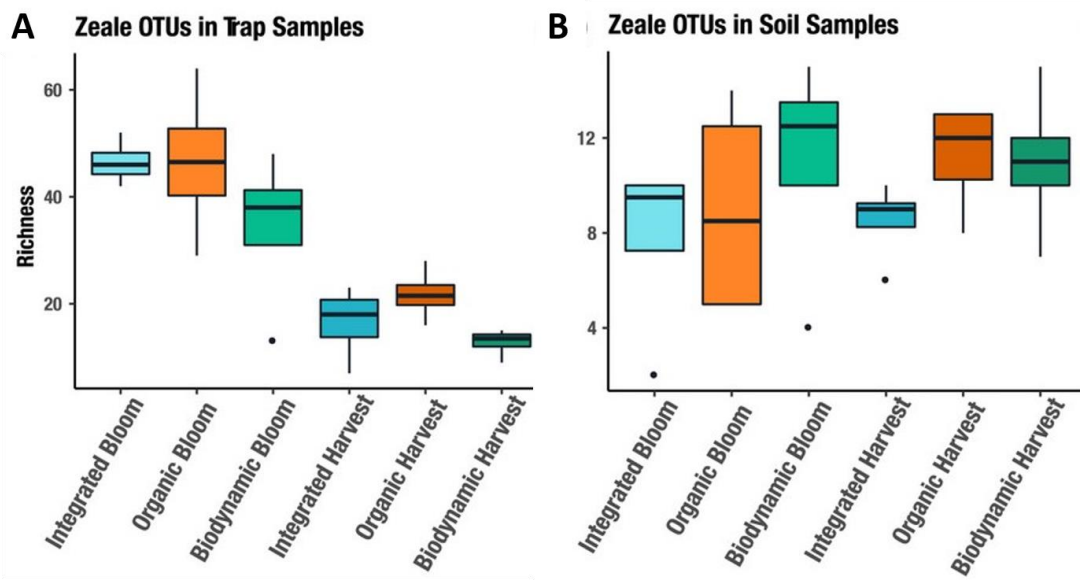

Figure 3: Species richness of (A) flying arthropods and (B) soil-living arthropods assessed during the growing season 2017 (modified according to Agerbo Rasmussen *et al*., 2020).

Concerning fungi associated to arthropods in bulk and soil samples no management effect was observed concerning species richness. In contrast, community composition of fungi associated to soil-living arthropods (D2 OUT community) differed significantly among management systems, indicating that the different management systems affect the composition of D2 primer profiled OTUs in soil (Agerbo Rasmussen *et al*., 2020). This finding is in line with results by Hendgen *et al.* (2018) who observed a significant management effect on fungal community composition in topsoil and suggests that differences in the soil fungal community of the different management systems are stable. The soil microbial communities might be influenced by management factors such as cover crop, type of mowing/rolling, herbicide application or mechanical under-vine management.

Fungal community composition associated with soil-living and flying arthropods might also impact fungal community composition in the carposphere of ripening winegrape berries. In order to assess taxa of potential relevance for fermentation and thus wine production, the taxonomic composition of the top 50 most abundant OTUs in both trap and soil samples was explored. Results revealed clear patterns concerning management effects as well as concerning seasonal effects. The differential abundance analysis revealed an elevated abundance of wine relevant fungal genera in both organic and biodynamic trap samples, including beneficial as well as pathogenic taxa. These differences were most evident at harvest and might have implications for spontaneous fermentation. In contrast, fewer significant differences in differential abundance between fungal genus in the soil samples were found. The variation of the community composition of fungi associated to soil-living arthropods are not explained by the top 50 most abundant fungal OTUs in soil (Agerbo Rasmussen *et al.* 2020).

Conclusions

Parameters assessed in the current studies showed clear differences among management systems meaning that by managing the vineyard viticulturists and farmers clearly influence soil microbial as well as arthropod biodiversity. ORG and BD management systems showed higher enzymatic activities in the soil and higher fungal and bacterial biomass, whereas INT plots showed higher AMF biomass. ORG plots were shown to have a significantly higher bacterial species richness in top- and subsoil, whereas bacterial community composition did not differ among treatments. Treatments showed a distinct fungal community composition in topsoil. Concerning species richness of arthropods the INT treatment showed a positive effect on species richness of flying arthropods, whereas ORG and BD systems showed a positive effect on soil-living arthropods. Community composition of fungi associated with soil-living arthropods differed significantly among treatments suggesting a link to community composition of fungi in topsoil. Concerning abundance of fungi related to wine production management systems differed significantly. This might have possible implications for fermentation and wine quality.

The current studies provide a first glimpse into biodiversity within different management systems in viticulture. In order to assess sustainability of the different management systems, parameters such as carbon footprint, water footprint, and long-term input-output relations concerning energy and nutrient fluxes should be considered on a yield- and area-based scale.

References

Agerbo-Rasmussen, J., Nielsen, M., Mak, SST., Döring, J., Klincke, F., Gopalakrishnan, S., Dunn, RR., Kauer, R., Gilbert, MTP., 2020. eDNA-based biomonitoring at an experimental German vineyard to characterize how management regimes shape ecosystem diversity. Environmental DNA, 00: 1-13.

Alberdi, A., Gilbert, M TP., 2019. Hilldiv: An R package for the integral analysis of diversity based on Hill numbers. bioRxiv: 1-12.

Alef, K., 1991. Methodenhandbuch Bodenmikrobiologie: Aktivitäten, Biomasse, Differenzierung. Landsberg/Lech: Ecomed Verlag.

Altieri, MA., 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems & Environment, 74: 19–31.

Bengtsson, J., Ahnström, J., Weibull, AC., 2005. The effects of organic agriculture on biodiversity and abundance: A meta-analysis. Journal of Applied Ecology, 42: 261-269.

Bruggisser, O.T., Schmidt-Entling, M.H., Bacher, S., 2010. Effects of vineyard management on biodiversity at three trophic levels. Biological Conservation, 143: 1521-1528.
Burns, KN., Kluepfel, DA., Strauss, SL., Bokulich, NA., Cantu, D., Steenwerth, KL., 2015. Vineyard soil bacterial diversity and composition revealed by 16S rRNA genes: Differentiation by geographic features. Soil Biology & Biochemistry, 91: 232–247.

Caporaso, JG., Lauber, CL., Walters, WA., Berg-Lyons, D., Huntley, J., Fierer, N., Owens, SM., Betley, J., Fraser, L., Bauer, M., Gormley, N., Gilbert, JA., Smith, J., Knight, R., 2012. Ultra-high-throughput microbial community analysis on the Illumina HiSeq and MiSeq platforms. ISME Journal, 6(8): 1621–1624.

Coninck BD., Timmermans P., Vos C., Cammue, BPA., Kazan K., 2015. What lies beneath. Belowground defense strategies in plants. Trends in Plant Science, 20: 91–101.

Corneo, PE., Pellegrini, A., Cappellin, L., Roncador, M., Chierici, M., Gessler, C., Pertot, I., 2013. Microbial community structure in vineyard soils across altitudinal gradients and in different seasons. FEMS Microbiology Ecology, 84(3): 588–602.

Díaz-Raviña, M., de Anta, RC., Bååth E., 2007. Tolerance (PICT) of the Bacterial communities to copper in vineyards soils from Spain. Journal of Environmental Quality, 36(6): 1760–1764.

Di Giacinto, S., Friedel, M., Poll, C., Döring, J., Kunz, R., Kauer, R., 2020. Vineyard management system affects soil microbiological properties. OENO One, 54(1): 131-143.

Döring, J., Frisch, M., Tittmann, S., Stoll, M., Kauer, R., 2015. Growth, yield and fruit quality of grapevines under organic and biodynamic management. PLoS ONE, 10(10), e0138445.

Emmerling, C., Schloter, M., Hartmann, A., Kandeler, E., 2002. Functional diversity of soil organisms - a review of recent research activities in Germany. Journal of Soil Science and Plant Nutrition, 165: 408–420.

Foster, ZSL., Sharpton, TJ., Grünwald, NJ., 2017. Metacoder: An R package for visualization and manipulation of community taxonomic diversity data. PLoS Computational Biology, 13(2): e1005404.

Frostegård, Å., Tunlid, A. Bååth, E., 1993. Phospholipid fatty acid composition, biomass, and activity of microbial communities from two soil types experimentally exposed to different heavy metals. Applied Environmental Microbiology, 59(11): 3605–3617.

Fujita, K., Furuya, S., Kohno, M., Suzuki, S. Takayana, T., 2010. Analysis of microbial community in Japanese vineyard soils by culture-independent molecular approach. International Journal of Wine Research, 2: 75–104.

Gilbert, JA., van der Lelie, D., Zarraonaindia, I., 2014. Microbial terroir for wine grapes. Proceedings of the National Academy of Sciences of the United States of America, 111(1): 5– 6.

Gisi, U. *Bodenökologie*. Thieme Verlag, Stuttgart, New York, 1990.

Hendgen, M., Hoppe, B., Döring, J., Friedel, M., Kauer, R., Frisch, M., Dahl, A., Kellner, H., 2018. Effects of different management regimes on microbial biodiversity in vineyard soils. Scientific Reports, 8, 9393.

Hill, M. O., 1973. Diversity and evenness: A unifying notation and its consequences. Ecology, 54(2): 427– 432.

Ihrmark,K., Bödeker, ITM., Cruz-Martinez, K., Friberg, H., Kubartova, A., Schenck, J., Strid, Y., Stenlid, J., Brandström-Durling, M., Clemmensen, KE., Lindahl, BD., 2012. New primers to amplify the fungal ITS2 region - evaluation by 454-sequencing of artificial and natural communities. FEMS Microbiology Ecology, 82(3): 666–677.

Isaia, M., Bona, F., Badino, G., 2006. Influence of landscape diversity and agricultural practices on spider assemblage in Italian vineyards of Langa Astigiana (Northwest Italy). Environmental Entomology, 35: 297-307.

Jackson, LE., Bowles, TM., Hodson, AK., Lazcano, C., 2012. Soil microbial-root and microbial-rhizosphere processes to increase nitrogen availability and retention in agroecosystems. Current Opinion in Environmental Sustainability, 4: 517–522.

Jost, L., 2006. Entropy and diversity. Oikos, 113(2): 363– 375.

Morrison-Whittle, P., Lee, SA., Goddard, MR., 2017. Fungal communities are differentially affected by conventional and biodynamic agricultural management approaches in vineyard ecosystems. Agriculture, Ecosystems & Environment, 246: 306-313.

Nielsen, M., Gilbert, MTP., Pape, T., Bohmann, K., 2019. A simplified DNA extraction protocol for unsorted bulk arthropod samples that maintains exoskeletal integrity. Environnemental DNA, 1(2): 144– 154.

Orgiazzi, A., Lumini, E., Nilsson, R.H., Girlanda, M., Vizzini, A., Bonfante, P., Bianciotto, V., 2012. Unravelling soil fungal communities from different Mediterranean land-use backgrounds. PLoS ONE, 7(4): e34847.

Putignani, L., Paglia, MG., Bordi, E., Nebuloso, E., Pucillo, LP., Visca, P., 2008. Identification of clinically relevant yeast species by DNA sequence analysis of the D2 variable region of the 25–28S rRNA gene. Mycoses, 51(3) :209–227.

R Development Core Team., 2006. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://http//www.R-project.org.

Ruppert V., 1993. Einfluss blütenreicher Feldrandstrukturen auf die Dichte blütenbesuchender Nutzinsekten insbesondere der Syrphinae. Haupt Verlag, Bern, Stuttgart, Wien.

Tonelli, ML., Furlan, A., Taurian, T., Castro, S. Fabra, A., 2011. Peanut priming induced by biocontrol agents. Physiological and Molecular Plant Pathology, 75: 100–105.

Vega-Avila, AD., Gumiere, T., Andrade, PAM., Lima-Perim, JE., Durrer, A., Baigori, M., Vazquez, F., Andreote, FD., 2015. Bacterial communities in the rhizosphere of *Vitis vinifera* L. cultivated under distinct agricultural practices in Argentina. Anton Van Leeuwenhoek International Journal of General and Molecular Micr, 107(2): 575–588.

Zarraonaindia, I., Owens, SM., Weisenhorn, P., West, K., Hampton-Marcell, J., Lax, S., Bokulich, NA., Mills, D. A., Martin, G., Taghavi, S., van der Lelie, D., Gilbert, JA., 2015. The soil microbiome influences grapevine-associated microbiota. mBio, 6(2): e02527-14.

Zeale, MRK., Butlin, RK., Barker, GLA., Lees, DC., Jones, G., 2011. Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. Molecular Ecology Resources, 11(2): 236– 244.