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Highlights

- Organic management enhanced plant alpha and gamma diversity in vineyards
- Higher proximity to semi-natural habitats increased plant alpha and gamma diversity
- High disturbance frequency decreased alpha but increased beta diversity in vineyards
- Community composition was most affected by differential management in vineyards

Extensive vegetation management and semi-natural habitats increase plant alpha and gamma diversity in European vineyards

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Abstract

Permanent crops like vineyards have the potential to contribute to halting the biodiversity loss due to their spatiotemporal stability and lower disturbance frequency in vineyard inter-rows. However, anthropogenic pressures can be quite high in such agroecosystems and little is known about the relative impacts of local management intensity and landscape context on plant communities in viticultural landscapes. In this study, we examined how plant communities were affected by management intensity and landscape context in two European wine-growing regions. We established four plots within one inter-row and three transects in two neighboring inter-rows and one undervine row in each of 70 paired vineyards (organic versus conventional farming) along a gradient of proportion of semi-natural habitats in the landscape. We analysed how alpha, beta and gamma diversity and plant species community composition at the vineyard scale responded to farming system, disturbance frequency, and semi-natural habitats. We found a positive impact of organic farming on alpha and gamma diversity and a significant influence of farming and transect type on species community composition. Besides farming system, disturbance frequency (tillage and mulching) reduced alpha diversity but increased beta diversity in the transects of both wine-growing regions. This difference could be attributed to the establishment of different plant communities of vineyards managed with higher or lower mulching and/or tillage intensity. At the landscape scale, higher proximity to and higher proportion of semi-natural habitats increased plant alpha and gamma diversity. Both landscape variables also explained significant variance of the plant community composition. Conservation of farmland biodiversity in vineyards should focus on supporting low-intensity diversified management operations and increasing shares of semi-natural habitats in the landscape.

Keywords

biodiversity; beta diversity; management intensity; perennial crop; semi-natural habitats; viticulture

Introduction

Global biodiversity loss is besides climate warming one of the main challenges facing human well-being in the current century (Cardinale et al., 2012). Overexploitation and agriculture are the major drivers of global species loss, with crop farming endangering more than 50% of those species (Maxwell et al., 2016). On the other hand, there exist estimations that more than 50% of all species depend on agricultural habitats in Europe (Kristensen, 2003). Beyond those numbers, it is crucial to distinguish different land use and management practices which may support or reduce farmland biodiversity by intensive high-input management practices (e.g. Kleijn et al., 2012). In order to reach the ambitious EU biodiversity targets until 2030, biodiversity conservation needs to take place also in crop fields by supporting management practices which sustain and balance both in- and off-field biodiversity and crop production (Adeux et al., 2019).

Organic farming is often seen as one of the key management practices which supports higher biodiversity in fields and therefore contributes to biodiversity conservation (Katayama et al., 2019; Tuck et al., 2014; Puig-Montserrat et al., 2017; Winter et al., 2018). However, the field-scale effect of organic farming differs depending on the landscape context, with greatest benefits of organic farming expected in simpler, crop-dominated landscapes (Batáry et al., 2011; Tuck et al., 2014). Yet, limited benefits of organic farming are expected without implementing further landscape-scale diversification measures (Tscharntke et al., 2021). Besides local management practices, higher proportions of semi-natural habitats (SNHs) resulting in higher landscape heterogeneity in agricultural habitats are generally considered beneficial for biodiversity (Billeter et al., 2008; Priyadarshana et al., 2024). SNHs provide food resources, over-wintering sites, refuges and by acting as source populations for animals and plants in highly-disturbed crop habitats (Tscharntke et al., 2005; Holland et al., 2016). Furthermore, the effects of landscape diversity might interact with local management intensity by (i) filtering out species due to intensive pesticide use, tillage or fertilizer use leading to overall homogenized communities and/or (ii) by enabling dispersal between isolated habitats in mosaic-type landscapes with higher proportions of SNHs (Dormann et al., 2007).

Most studies only report biodiversity as alpha diversity of local species assemblages in smaller sampling units, without considering the important aspect of beta diversity. This diversity partition is related to the spatiotemporal differences of local species assemblages (but see Boinot & Alignier, 2023; Clough et al., 2007) and thereby contributes to increasing overall regional biodiversity measured as gamma diversity (Socolar et al., 2016). Consequently, high beta diversity values are related to large differences in species community composition or more unique species instead of similar sets of the same species assemblages at multiple locations (Clough et al., 2007) which seems to be promoted by intensive agriculture (Dormann et al., 2007; Gabriel et al., 2006). Few available studies showed that there exist divergent effects of organic management on alpha and beta diversity of different organism groups (Clough et al., 2007; Dormann et al., 2007) and that drivers differ for alpha and beta diversity in field margins (Boinot & Alignier, 2023).

Vineyards are especially relevant crop systems to study management effects on alpha, beta and gamma diversity, as many wine-growers manage the inter-rows between the undervine rows differently with several tillage and/or mulching operations, whereas the undervine rows are in most cases kept free of vegetation by tillage and/or herbicide applications (Fried et al. 2019; Hall et al., 2020). In addition to shading effects provided by the vines, the increasing use of spontaneous vegetation or cover crop mixtures to reduce soil erosion, resulted in different plant communities compared to the traditionally intensively tilled vineyards. This implementation of vegetation cover in vineyards significantly increased local plant species richness in comparison to bare soil vineyards (Lososova et al. , 2003; Hall et al., 2020; Winter et al., 2018). In this study we investigated how alpha, beta and gamma diversity as well as plant species community composition at the vineyard scale responded to (1) organic and conventional management and, (2) disturbance frequency (tillage, mulching) at the field scale, (3) proportion and nearest distance to SNHs at the landscape scale and (4) the interaction between local practices and the landscape context in two European wine growing regions.

Materials and methods

Study sites and design

We investigated the effects of local management and landscape context on plant community composition in two European wine growing regions in: (i) Leithaberg in Austria (AT) and (ii) Bordeaux in France (FR) both characterised by a fully humid warm temperate climate with warm summers (Cfb) (Kottek et al., 2006). All investigated commercial vineyards were planted with a range of different *Vitis vinifer*a L. ssp*. vinifera* grape varieties (mainly Merlot in France and a large variety of white and red grape varieties in Austria – for details see supplementary Table S1 in Möth et al., 2023) and were trained in trellis systems. We chose a paired sampling design to investigate the effects of the farming system by selecting two neighbouring vineyards including one conventional (referring in fact to integrated pest management practices – IPM, which must be implemented by all farmers across the EU) and one organic vineyard with a maximum distance of 200 m. To evaluate the effect of the landscape context, we selected pairs of vineyards along a gradient of proportion of SNHs (AT: ranging from 10.4% to 55.5% with mean and standard deviation (SD) of 29.4±13.9% and FR: ranging from 12.1% to 65.1% with a mean and SD of 31.9 ± 14.1) in a 500 m radius. SNHs included hedgerows, solitary trees, tree rows, woodlands, fallows, grasslands and grass strips from field margins which were digitized with ArcGIS 10.6.1 in Austria and QGIS 2.18.1 in France. The proportion of SNHs within the 500 m buffers and the distance of the sampled vineyards to the nearest SNHs were calculated with the R package “landscapemetrics” (Hesselbarth et al. 2019).

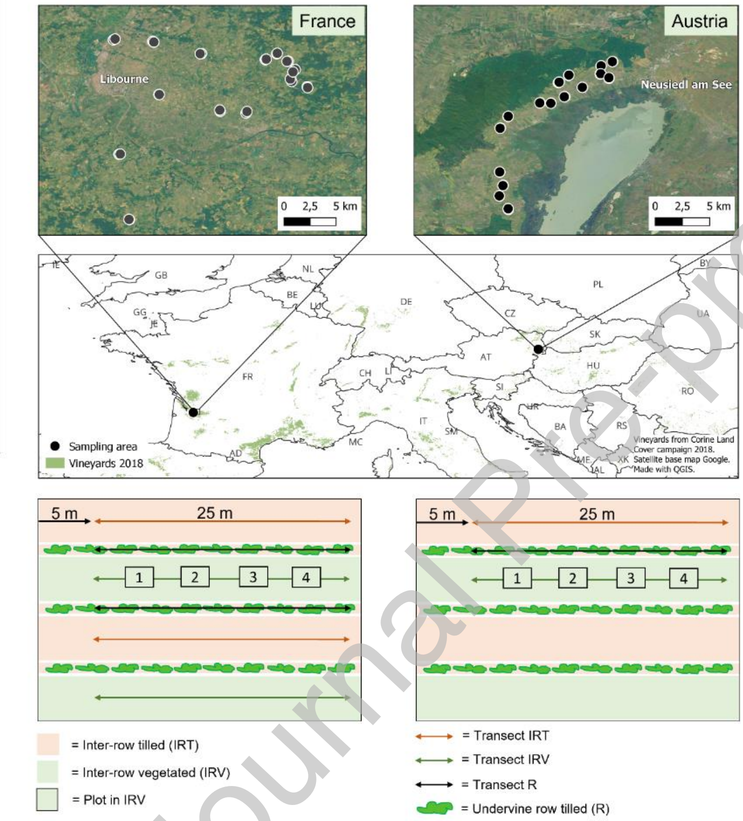


Fig. 1. Map showing the location of the two European study regions and the spatial arrangement of the paired vineyards each displayed as one dot (green shading shows the vineyard area according to the Corine Land Cover 2018). The lower part of Fig. 1 displays the sampling design in the French (left) and Austrian (right) case study region with the associated differences in the number of sampled (inter)-rows and overall transect lengths.

Overall, we investigated **70 vineyards** with 19 paired vineyards in France (n = 38) and 16 pairs in Austria (n = 32 vineyards). Comprehensive data regarding vineyard management practices of each sampled vineyard was collected via structured interviews with the winegrowers. Inter-rows were managed alternatively, with soil tillage operations in every second inter-row (AT: 16, FR: 31), with only non-tilled inter-rows managed mainly by mulching (AT: 16, FR: 6) or tillage in every inter-row (FR: 1). Austrian farmers used either species-rich (n=14 with 20-34 species), species-poor (n=12 with 4-9 species) cover crop mixtures or only spontaneous vegetation cover (n=6) in vineyard inter-rows, whereas vegetation in French vineyards was always spontaneous (n=38). Vegetation underneath the vines was in most cases managed by different mechanical tillage operations or removed by applying herbicides (see Table S1). Herbicide application frequency in the undervine rows differed between the two case-study regions: in Austria, herbicides were only applied in four out of 16 vineyards, whereas in the French region all but three conventional vineyards applied herbicides. All sampled vineyards were rainfed without any additional irrigation.

Vegetation sampling

Vegetation surveys were conducted in all investigated vineyards once in spring (April) and once in summer (June) to capture as many species as possible. Across both countries, we established four 1 x 1 m plots in one vegetated inter-row per vineyard where we recorded total vegetation cover and the cover of all vascular plant species according to the scale of Londo (1976). Vegetation data were recorded in 2019 in Bordeaux (FR) and in 2020 in Austria (AT). Those data were aggregated across both sampling dates using the maximum cover value per species. In addition, we also recorded plant species richness in three transects per vineyard. In Austria, those 25 m long transects were established in two neighbouring inter-rows and in one undervine row. In France, all transects were 2 x 25 m long (see Fig. 1). Transect width differed between inter-rows, undervine rows and slightly also between vineyards (see landscape files on Zenodo). Some transects had to be excluded from the analysis because they could not be sampled in both spring and summer, therefore overall sample sizes differ slightly between tilled and vegetated inter-rows (see Table 1). Plant taxonomy follows EPPO global database preferred scientific names and codes with the first three letters abbreviating the genus and the second part the specific epithet to identify the species.

Table 1: Overview of number of sampled transects in both seasons according to management type (organic and conventional) and vegetation cover (tilled versus vegetated) in Austria and France.

Transect type	Country: France		Country: Austria	
	Organic (O)	Conventional (C)	Organic (O)	Conventional (C)
Inter-row tilled (IRT)	16	13	16	16
Inter-row vegetated (IRV)	16	17	16	16
Undervine row tilled (R)	18	18	16	16
SUM	**50**	**48**	**48**	**48**

Data analysis

Statistical analyses and data visualization were done with R version 4.1.2 (R Core Team, 2021) using the packages “vegan” (v2.6.3, Oksanen et al., 2019), “lme4” (v1.1.35.5, Bates et al., 2015), “fitdistrplus” (v1.2.1, Delignette-Muller & Dutang, 2015) and dependent packages. Species accumulation curves were calculated using the sample-based rarefaction method to assess if plant species/sampling sites were sufficiently sampled (Chiarucci et al., 2008).

Statistical modelling was performed for the plot dataset of one vegetated inter-row per vineyard for both the Austrian and French data, whereas transect datasets for Austria and France were analysed separately due to differences in transect length. First, alpha, beta (calculated according to Whittaker’s multiplicative law: alpha x beta = gamma) and gamma diversity were calculated at the vineyard scale for the plot and transect datasets and used as response variables (Clough et al., 2007). The farming type (organic versus conventional), the nearest distance to and the proportion of SNHs at the landscape-scale were used as uncorrelated explanatory variables for all datasets. Furthermore, country and mulching frequency of the vegetated inter-row were added for the plot dataset and disturbance frequency (aggregating mulching and tillage intensity of the vegetated and tilled inter-rows) for the transect dataset. The interactions of farming type*nearest distance to SNHs and farming type*proportion of SNHs was tested due to expected interactions between local-scale management and the landscape context (Batáry et al., 2011).

In order to account for potential influence of different transect width on species richness data per transect, we fitted linear models with the previously mentioned variables in addition to the transect width. As this factor was not significant, we assumed that this was not a major cofounding factor in our study. We also tested the potential confounding factor cover crop mixture type for the Austrian plot data (no use of cover crops in France). We found no difference between species-rich and -poor cover crop mixtures. On the contrary, highest species richness was found without the use of any (species-rich) cover crop mixtures. Consequently, we decided to exclude this factor for the plot analysis across both countries.

Following the data exploration (Zuur et al., 2009), the Gaussian distribution was used for all response variables with the exception of the beta diversity of the plot dataset which had to be transformed with log10 (log10(y+1)) to perform Linear models (LM) and Linear mixed models (LMM). Model assumptions like normal distribution of residuals and homoscedasticitiy were evaluated to validate possible violations (Zuur et al., 2009). The variable site was used as random factor in the LMMs and was excluded when boundary issues caused by a low variance (at zero) of the random effect were detected. Accordingly, global models were performed for each response variable with all possible combinations of the explanatory variables. Explanatory variables with a variance inflation factor (VIF) of > 2 were excluded in the models (Zuur et al., 2009). The second-order Akaike's Information Criterion corrected for small sample size (AIC_c) with a minimum difference of Δi of 2 (Burnham & Anderson, 2002) was used to select the most parsimonious set of models.

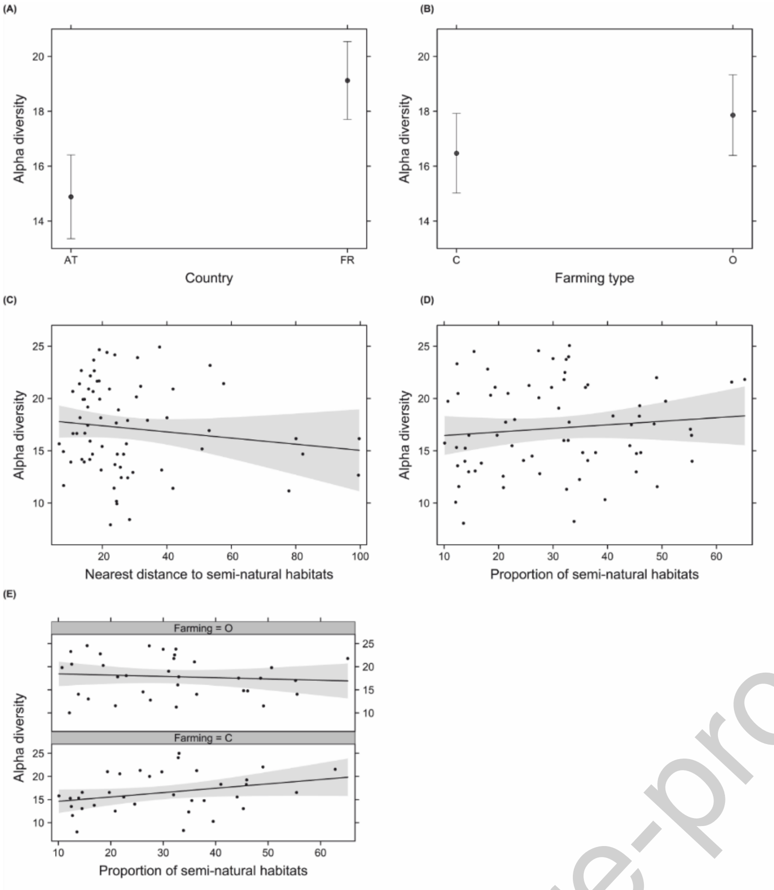
In addition, we also performed a Permutational Multivariate Analysis of Variance (PERMANOVA) to analyse the effects of farming type, management intensity and proportion and proximity to SNHs on species community composition with the adonis2 function of the vegan package (Oksanen et al., 2018). PERMANOVA compares groups testing the null hypothesis that the centroids and dispersion of the groups do not differ between groups (Anderson, 2017). As species communities differ between the case-study regions, we analysed both case-study regions and the transect and plot dataset separately, vineyard ID was defined as strata to account for the nested data structure (Oksanen et al., 2018). PERMANOVA model selection was based on the p-values of the explanatory variables and a minimum difference of $\Delta AIC_c < 2$ between the most parsimonious models (Burnham & Anderson, 2002) using the AICcPermanova package (v0.0.2, Corcoran 2023). To identify species associated to certain management practices, we also performed an indicator species analysis for both countries and datasets separately with the R package "indicspecies" (v1.7.15, De Cáceres & Legendre, 2009). According to these authors, the indicator value index is the product of two factors, A and B. Here, A represents the conditional probability that the sampled site belongs to the target site group, given that the species has been found (specificity). Meanwhile, B denotes the probability of finding the species in sites that belong to the specific site group (sensitivity). Furthermore, to display the association of influential management and landscape parameters on plant communities, we also computed non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity index, a maximum of 200 iterations and k=3 for the Austrian and French plot and transect datasets with the vegan package (Oksanen et al., 2018). Significant (alpha level 0.05) management, landscape and alpha species diversity vectors were fitted on the NMDS.

Results

In total, 201 plant taxa (most at species level) were recorded in the 32 studied Austrian vineyards and 206 in the 38 French vineyards (species list and associated presence/absence data see data deposited on Zenodo: **10.5281/zenodo.13921649**). Species accumulation curves for the Austrian and French plot and transect data indicated sufficient sampling as the curve reached an asymptote (Fig. S1A, B, S1A, B). The analysis of the main drivers of alpha, beta and gamma diversity resulted in similar results in both European case-study regions with positive effects of organic farming and SNHs on alpha and gamma diversity across the plot and transect datasets (Fig. 2, 4, S3, S5, Tables S2-S4).

Drivers of plant alpha diversity

Besides the positive impact of organic management, higher proximity to SNHs and higher proportions of SNHs at the landscape-scale were also associated with higher alpha diversity in the inter-row plots (Fig. 2, Table S2). Overall, alpha diversity was significantly higher in the French than in the Austrian case-study region (Fig. 2A). The interaction between farming type and the proportion of SNH was also included in the most parsimonious models showing a strong positive impact of higher cover of SNHs for conventional but not for organic vineyards (Fig. 2E). The highest adjusted R^2 of 0.23 was observed in the most complex model including all previously mentioned explanatory variables. Plant alpha diversity was highest in the vegetated transects in Austria (mean: 37.3±9.3), followed by the tilled inter-rows (32.5±9.8) and the undervine rows (23.9±6.9). In the French case study region, the differences in alpha diversity of the vegetated and tilled transects were much more pronounced with an average alpha diversity of 33.2±6.12 for the vegetated, 24.8±8.4 for the tilled inter-rows and 22.7±7.2 for the undervine rows. The transect datasets showed similar positive effects of organic farming in both case-study regions and a negative impact of increasing distance to SNHs in France (Fig. S3, Tables S3, S4). In addition, higher disturbance frequency in the inter-rows resulted in both wine-growing regions in lower alpha diversity in the transects. The highest marginal R^2m (variance explained by the fixed factors) of the most parsimonious alpha diversity transect models in Austria was 0.18 including farming type and disturbance frequency, and in France $R^2m = 0.21$ of the best model included farming type, nearest distance to SNHs and disturbance frequency (Tables S3, S4). However, the null model was also included in the list of most parsimonious models of the French alpha diversity transects (Table S4).



(E)

Fig. 2. Effect plots showing the response of both Austrian and French inter-row plot-based alpha diversity (average of four plots) in response to the (A) country (AT = Austria, FR = France), (B) farming type (C = conventional and O = organic), (C) nearest distance to SNHs (m), (D) proportion of SNHs (%) and (e) interaction between farming type and proportion of SNHs. Dots display the partial residuals indicating the lack of fit.

Drivers of plant beta diversity

In contrast, beta diversity of the inter-row plots calculated at vineyard level showed higher values in Austrian vineyards, in longer distance to SNHs and lower mulching frequency (see Fig. 3). In both case-study regions, higher disturbance frequency resulted in higher beta diversity in the transects

(Fig. S4). The French transect dataset showed higher beta diversity in conventional vineyards and in vineyards situated in landscapes with higher proportions of SNHs (Fig. S4). The most parsimonious model with the highest marginal R^2 of 0.28 of the French transects included the variables farming type, proportion of SNHs and disturbance frequency (Table S4). However, with the exception of the French transects, the most parsimonious models also included the null model and the adjusted R^2 was nearly zero for the plot dataset (Table S2-S4).

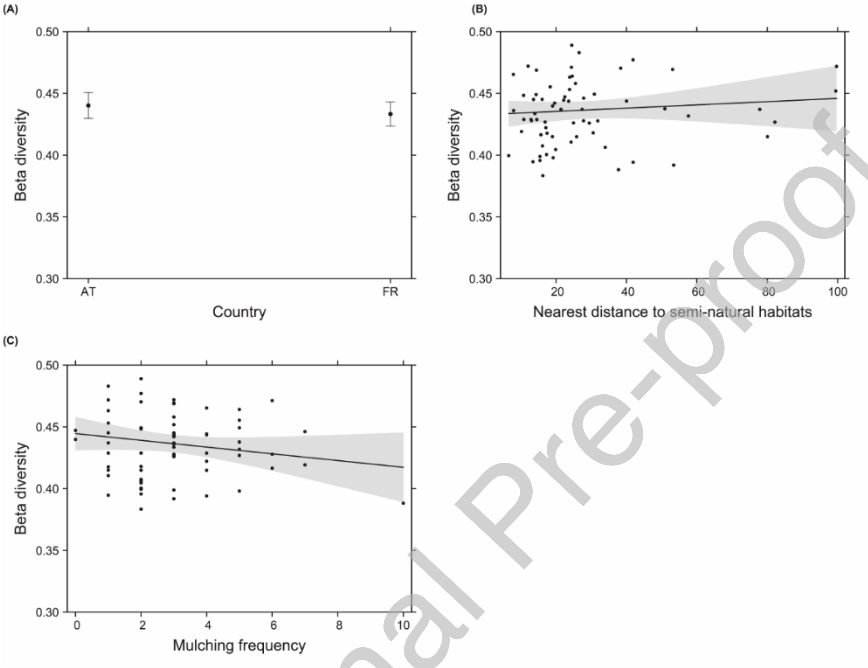


Fig. 3. Effect plots showing the response of both Austrian and French inter-row plot-based beta diversity in response to the (A) country (AT = Austria, FR = France), (B) nearest distance to SNHs (m) and (C) mulching frequency. Beta diversity was transformed with log10 (log10(y+1)). Dots display the partial residuals indicating the lack of fit.

Drivers of plant gamma diversity

In accordance with the most parsimonious alpha diversity models, gamma diversity was also higher under organic management, in the French inter-row plots, with lower distance to and higher proportions of SNHs. In addition, the interaction displayed that only conventional vineyards benefitted from a higher cover of SNHs (Fig. 4). The highest adjusted R^2 of 0.23 among the most parsimonious models of the plots included the full list of explanatory variables (Table S2). The most parsimonious models of both transect datasets included the null model with very low adjusted R^2 values, therefore, the results need to be interpreted with great care (Tables S3-S4). However, with the exception of the Austrian transects showing a negative response of gamma diversity to higher SNH cover, the results align with the inter-row plot analysis across both case-study regions (Table S2).

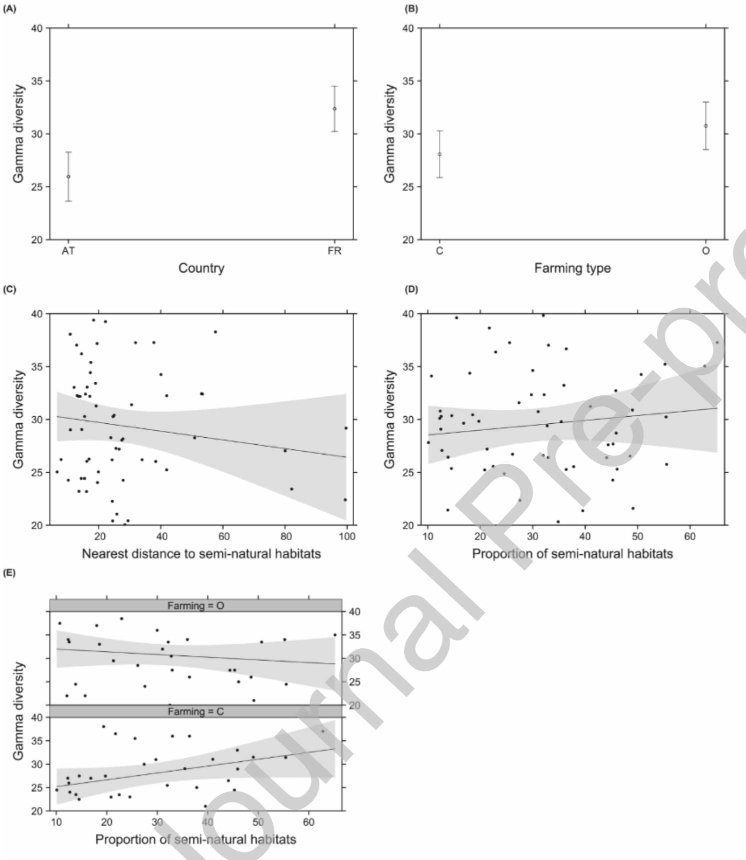
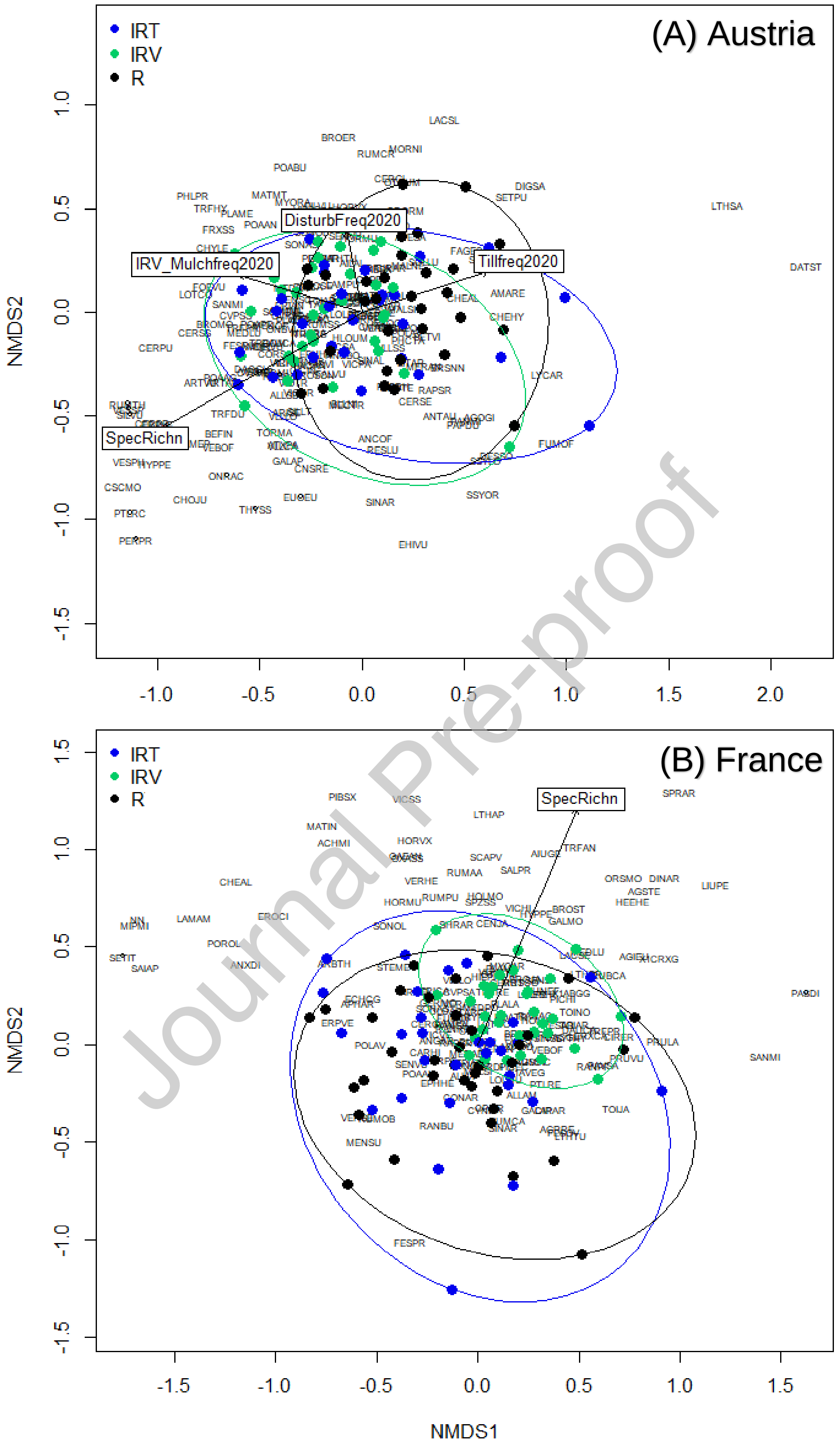


Fig. 4. Effect plots showing the response of Austrian and French inter-row plot-based gamma diversity in response to the (A) country, (B) farming type (C = conventional and O = organic), (C) nearest distance to SNHs (m), (D) proportion of SNHs (%) and (E) interaction between farming type and proportion of SNHs. Points display the partial residuals indicating the lack of fit.

Plant community composition

The PERMANOVA showed that especially transect type significantly differentiated plant communities, contributing to 7.5% of observed variance (R^2) in the French transects (Table S5). Further significant explanatory variables included in the most parsimonious models were the proportion of SNHs (R^2: 4.1%), the nearest distance to SNHs (R^2: 2.2%) and the farming type (R^2: 2.8%). The Austrian transect PERMANOVA revealed similar parameters where the most parsimonious models including the explanatory variables transect (R^2: 6.6%) and farming type (3.0%), nearest distance to SNHs (R2: 2.7%), proportion of SNHs (R^2: 1.9%) and the interaction between farming type and nearest distance to SNHs (R^2: 2.8%). The low proportion of explained variance is also reflected in the NMDS plots (stress values: 0.18 and 0.19 of Austrian and French transects) which show a large overlap of the plant communities according to transect (Fig. 5) and farming type (Fig. S6). Interestingly, in Austria, the undervine row transects were slightly less dispersed than the inter-row transects, whereas in France the vegetated inter-rows showed a much more clumped distribution within the tilled inter-rows and undervine rows (Fig. 5). The organic vineyard transects in Austria were less dispersed than the conventional ones; the French transects did not differ according to farming type (Fig. S6). Management intensity vectors were significant in the Austrian NMDS pointing in different directions, with higher mulching frequency being associated with vegetated inter-rows, and higher tillage frequency with tilled inter-rows and undervine rows. Species richness was in both case study regions a significant vector (Fig. 5, S7), directing in the opposite direction of the management intensity vectors. The stress values for the Austrian plot datasets were poor (0.27) and therefore no NMDS were computed although the French stress values were okay (0.16). The indicator species analysis revealed a list of species with their respective indicator values for conventional and organic management as well as vegetated inter-rows or tilled and vegetated inter-rows (Tables S6-S9).


(A) Austria
● IRT
● IRV
● R
NMDS2
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0.0
-0.5
-1.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
DisturbFreq2020
IRV_Mulchfreq2020
Tillfreq2020
SpecRichn
LACSL
BROER
RUMCR
MORNI
POABU
DIGSA
SETPU
LTHSA
DATST
PHLPR
TRFHY
FLAME
MATMT
MYORA
FRXSS
POAAN
CHYLE
FAGES
AMARE
CHEHY
CHEAL
LOTCO
SANMI
CVPSS
CERSS
CERPU
LYCAR
ARTVU
RAPSR
CERSE
ANTAU
FUMOF
TRFDU
BEFIN
TORMA
VEBOF
ANCOF
FESLU
VESPH
HYPPE
ONRAC
GALAP
CNSRE
CSCMO
CHOJU
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SSYOR
PTSRC
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(B) France
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NMDS2
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NMDS1
SpecRichn
PIBSX
VICSS
LTHAP
SPRAR
MATIN
ACHMI
HORVX
SCAPV
AIUGE
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CHEAL
VERHE
RUMAA
SALPR
ORSMO
DINAR
AGSTE
HEEHE
LIUPE
HORMU
RUMPU
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ANXDI
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Fig. 5. Non-metric multidimensional scaling (NMDS) plots with fitted significant vectors displaying the species community composition of the (A) Austrian (stress: 0.18) and (B) French (stress: 0.19) transects (IRT = tilled inter-row, IRV = vegetated inter-row, R = undervine row). The vectors display the environmental vectors fitted onto the NMDS with p-values lower than 0.1 (SpecRichn = species richness of the transects).

Discussion

This study showed that organic management, low disturbance frequency and proportion and proximity to SNHs increased plant alpha and gamma diversity, whereas beta diversity and community composition were mainly affected by disturbance frequency and differential management practices within vineyards in both case study regions.

Management effects on alpha, beta and gamma diversity and community composition

The positive effects of organic farming on alpha and gamma diversity are in accordance with several studies showing higher alpha diversity in organic than in conventional vineyards (Nascimbene et al., 2012; Puig-Montserrat et al., 2017; Winter et al., 2018; Rotchés-Ribalta et al., 2023). Lower species richness could be attributed to herbicide use in conventional vineyards (Nascimbene et al., 2012), however, in the investigated vineyards herbicides were not applied in the vineyard inter-rows and in the undervine row frequent herbicide use was only reported in the French case study region.

In general, undervine rows are managed more intensively than inter-rows to limit competition for water and nutrients between weeds and vines (Pardini et al., 2002). This higher disturbance frequency was also reflected in the overall lowest alpha species richness of the rows, followed by the tilled inter-rows. The higher tillage frequency of the tilled inter-rows of France resulted in much lower diversity values compared to the Austrian case study region. Negative effects of intensive tillage or herbicide use on plant diversity were already previously shown (Lososova et al., 2003; Fried et al., 2019; Kazakou et al., 2016). The combination of both mowing and tillage in the inter-rows and tillage instead of herbicide use (or a combination of herbicide use and tillage) resulted in the highest plant species richness according to Fried et al. (2019). These results match our findings where we could always find the highest alpha species richness in the vegetated inter-rows in both countries and the lowest values in the undervine rows. Interestingly, the difference between the conventional and organic management was most pronounced in the undervine rows where intensive herbicide use in the French case study region resulted in the lowest mean alpha species richness. Overall, tillage, mulching and herbicide use frequency were much higher in the French than in the Austrian case study region.

Interestingly, beta diversity increased with higher disturbance frequency in the transects in both case-study regions, which could be related to higher filtering effect of intensive mulching or tillage which benefits hemicryptophytes or therophytes, respectively (Lososova et al., 2003; Kazakou et al., 2016). In Austria, low intensity tillage every second or third year in the tilled inter-rows could lead to similar species communities in both the tilled and vegetated inter-rows which would decrease beta diversity. In contrast to the findings in wheat fields (Clough et al., 2007; Gabriel et al., 2006) and South African vineyards (Kehinde & Samways, 2014) but in accordance with Roschewitz et al. (2005), conventional management resulted in higher beta diversity exclusively in the French vineyards. The reason could be related to the higher management intensity and herbicide use frequency in the French case study region. At the plot scale, mulching frequency decreased beta diversity which could be attributed to the higher selection pressure for hemicryptophytes such as *Bellis perennis, Poa trivialis* or *Medicago lupulina* (Wilmanns, 1993).

Changes in community composition in response to management effects

NMDS and PERMANOVA revealed large overlap in plant communities of organic and conventional management, with significant differences in species community composition due to the different management practices in the respective transect types (IRV, IRT, R). Interestingly, the NMDS revealed that the vegetated inter-rows were more clustered within the more dispersed tilled inter-rows and undervine rows in the French region, whereas in Austria the tilled undervine rows built a slightly denser aggregated sub-cluster within the inter-row plant communities.

Indicator species analysis revealed a list of species associated with organic or conventional management such as *Epilobium tetragonum* which could be related to its higher herbicide resistance (Matulevičiute, 2016; Wilmanns, 1993). Organic farming indicator species like *Phacelia trancetifolia, Malva sylvestris, or Sinapis alba* are most likely associated with flower-rich seed mixtures used in those Austrian vineyards. Organic management was also shown to increase functional richness of insect-pollinated flowering plants in Austrian and South African vineyards (Kratschmer et al., 2021). In France, mulching frequency was slightly lower in the organic inter-rows which could be related to indicator species such as *Crepis sancta* or *Daucus carota* (Fried et al., 2019). Vegetated inter-rows in France were associated with indicator species typical for grasslands such as *Bellis perennis*, *Festuca arundinaceum*, *Hypericum perforatum*, *Medicago lupulina* or *Trifolium pratense*. In Austria most indicator species (e.g. *Trifolium repens*, *Achillea millefolium*, *Erigeron* spp.) differentiated vegetated and infrequently tilled inter-rows (Lososova et al., 2003) from the highly-disturbed undervine rows in accordance to the results of the NMDS. Besides the positive effects of extensive vegetation management on biodiversity and ecosystem services (Winter et al., 2018), competitive seed mixtures with grasses lead to a homogenization of plant communities and loss of species richness (Hall et al., 2020) by outcompeting therophytes or spring geophytes which depend on soil tillage for germination or bulb propagation (Lososová et al., 2003; Wilmanns, 1993).

Beneficial effects of SNHs at the landscape scale

Higher proportions and proximity to SNHs at the landscape scale increased both alpha and gammadiversity, with positive effects especially for conventional vineyards at the plot scale. This positive effects of higher landscape complexity or habitat diversity is in accordance with several other studies (Gabriel et al., 2005; Roschewitz et al., 2005). We were able to detect an interaction between farming type and SNHs at the landscape scale, with higher alpha and gamma diversity with increasing proportions of SNHs only in conventional vineyards. This positive effect of landscape complexity especially for conventional farming was already reported by other studies (e.g. Batáry et al., 2011; Roschewitz et al., 2005; Tscharntke et al., 2005). The reason for that difference could be related to the strong species filtering effects of intensive tillage, mulching and herbicide use in the French case study region, where neighbouring SNHs could enable seed dispersal into vineyards (Dormann et al., 2007).

Conclusions

Our results showed that organic farming, lower disturbance frequency and higher proportions of SNHs increased alpha and gamma diversity in vineyards across both case-study regions. Furthermore, different low-intensity management operations (e.g. tillage, mulching) at the vineyard scale in the inter-rows and undervine rows create diverse niches for different plants resulting in plant community differences which increase overall gamma diversity. Beta diversity decreased with higher mulching frequency at the plot scale but increased with higher disturbance intensity at the vineyard scale in both regions. Disturbance frequency was in general much higher in French vineyards compared to Austrian vineyards. In addition, mulching frequency was much higher in conventional than in organic vineyards in France which resulted in significantly higher beta diversity only in French conventional transects. Consequently, agri-environmental programmes should support diverse low-intensity management operations within both organic and conventional vineyards and primarily aim at increasing the share of SNHs in agricultural landscapes dominated by conventional management. Future research should investigate how functional structure of plant communities in vineyards respond to farming practices and landscape context to better understand community responses and explore the functional consequence on agroecosystem functioning.

CRediT authorship contributions

Silvia Winter: Conceptualization, Methodology, Data curation, Investigation, Formal analysis, Writing, Funding acquisition, Supervision – original draft. **Ricarda Weitzl**: Investigation, Formal analysis, Writing – Review & Editing. **Stefan Möth**: Data curation, Statistical analysis, Writing – original draft. **Bozana Petrovic and Sylvie Richart-Cervera:** Investigation. **Violette Aurelle and Pauline Tolle:** Data curation, Investigation, Methodology**. Thomas Costes:** Data curation**. Adrien Rusch**: Funding acquisition, Conceptualization, Methodology, Writing – Review & Editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships in relation to the research presented in this article.

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Supplementary materials

Supplementary material of this article can be found, in the online version, at: XXXXX. All data will be made available on ZENODO upon the acceptance of the paper here: **10.5281/zenodo.13921649**

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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