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## Decrease of plant alpha and beta-diversity with management intensity in vineyards and the influence of landscape context

Arne Saatkamp, Laurence Affre, Peter Poschlod, Philip Roche, Ulrcih Deil, Thierry Dutoit

### Résumé

Diversity of plants in agricultural landscapes is decreasing continually until today and this has cascading effects on ecosystem services and persistence of rare plants. Plant diversity, however, is not equally distributed among different habitat types. On a larger scale differences among habitats can contribute strongly to the global diversity of an agro-ecosystem. Landscape context and intensity of agriculture can also have effects on diversity. In this work, we present a thorough analysis of  $\alpha$ -diversity in Mediterranean vineyard ecosystems, showing the effect of geology based landscape units for the outcome of  $\alpha$ -diversity as well as management intensity for  $\beta$ -diversity of threatened plants. The change in  $\beta$ -diversity according to landscape context emphasizes the importance of landscape heterogeneity and vineyard habitats for local plant diversity. Low intensity agriculture was identified to maintain the highest levels of plant  $\alpha$ - and  $\beta$ -diversity and to promote persistence of rare plants.

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# Decrease of plant alpha and beta-diversity with management intensity in vineyards and the influence of landscape context

Arne SAATKAMP<sup>1, 2, \*</sup>, Laurence AFFRE<sup>1</sup>, Peter POSCHLOD<sup>2</sup>, Philip ROCHE<sup>3</sup>, Ulrich DEIL<sup>4</sup>, Thierry DUTOIT<sup>1</sup>

1. IMBE, universit  d'Aix-Marseille, CNRS, IRD, universit  d'Avignon, Marseille, France

2. Institut of Plant Sciences, University of Regensburg, D-93040 Regensburg, Germany

3. IRSTEA, UR EMAX, 3275 route C zanne, CS 40061, 13182 Aix-en-Provence cedex 5, France

4. Institut f r Geobotanik, Universit t Freiburg, Sch nzlestrasse 1, 79104 Freiburg, Germany

\* Corresponding author: arne.saatkamp@imbe.fr

## Abstract

*Diversity of plants in agricultural landscapes is decreasing continually until today and this has cascading effects on ecosystem services and persistence of rare plants. Plant diversity, however, is not equally distributed among different habitat types. On a larger scale differences among habitats can contribute strongly to the global diversity of an agro-ecosystem. Landscape context and intensity of agriculture can also have effects on diversity. In this work, we present a thorough analysis of  $\beta$ -diversity in Mediterranean vineyard ecosystems, showing the effect of geology based landscape units for the outcome of  $\beta$ -diversity as well as management intensity for  $\alpha$ -diversity of threatened plants. The change in  $\beta$ -diversity according to landscape context emphasizes the importance of landscape heterogeneity and vineyard habitats for local plant diversity. Low intensity agriculture was identified to maintain the highest levels of plant  $\alpha$ - and  $\beta$ -diversity and to promote persistence of rare plants.*

**Keywords:** additive diversity partitioning, arable weeds, field edge, landscape.

## Introduction

Plant diversity in agro-ecosystems generally declined in Europe with a strong decline since 1980 (Jauzein 2001; Robinson & Sutherland 2002; Baessler & Klotz 2006), which is still continuing (Geiger *et al.* 2010; Tsiafouli *et al.* 2014). There is now growing concern about this loss of biodiversity, as many specialised plant species from agro-ecosystems are listed on regional and national Red Data Books (Roux & Nicolas 2001). In Europe, species that are specialized to arable systems, such as cereal weeds are among the most threatened plants. Moreover, there are also serious concerns due to the functional role of these plants in the agro-ecosystems and the services they provide for agriculture (Marshall *et al.* 2003), since cereal weeds provide indirect services by supporting predator populations in fields (van Emden 2002) and on their edges (Thomas & Marshall 1999; Smith *et al.* 2008). Furthermore, the decline of plant diversity reduces effective pollinator communities, which in turn results in decrease of

pollinator-dependent plants with special interest for conservation (Gibson *et al.* 2006) and this effect of pollinator decline in farmland can even be more exacerbated in urban contexts (Lhotte *et al.* 2014).

For these reasons, it is important to know which factors determine plant diversity in agro-ecosystems, and on which spatial scale. Arable plant diversity has been shown to be strongly decreased by high-intensity agriculture, change to highly competitive crops, synthetic fertilizers and consolidation of fields (Schneider *et al.* 1994; Robinson & Sutherland 2002). The important land use changes especially in North West Mediterranean areas from extensive farming practices to either abandon or intensification lead to important changes in taxonomic composition of species pools at a landscape and regional scale (Véla *et al.* 2000; Lavergne *et al.* 2005). Moreover, plant diversity in agricultural systems is also determined by the landscape context, *i.e.* the number and size of different habitats, soil type and altitude of the surrounding landscape (Cousins & Eriksson 2008; Fried *et al.* 2008). Whereas the general effects of these factors are clear, the relative importance and concerned scales are not well known, especially in Mediterranean climate areas.

Species diversity can be measured as  $\alpha$ -diversity, *i.e.* species richness for a fixed surface, or as  $\beta$ -diversity, *i.e.* differences in species between different stands, both diversity indices can be estimated for different spatial scales –from patches to regions (Wagner *et al.* 2000; Crist *et al.* 2003). The global diversity in terms of numbers of species in a larger area, thus summing up  $\alpha$  and  $\beta$  diversities, is termed  $\gamma$ -diversity. Once diversity types and scales are well defined this additive framework allows analysing the contribution of  $\alpha$  and  $\beta$ -diversity to  $\gamma$ -diversity at different spatial scales and gives insights into the importance of landscape and land use factors for plant diversity (Allan 1975; Lande 1996; Wagner *et al.* 2000; Crist *et al.* 2003).

Since  $\beta$ -diversity measures the difference in species composition between habitats, or at a larger scale, parts of a landscape, it has a functional value for explaining  $\alpha$  or  $\gamma$ -diversity: at smaller scales, when  $\beta$ -diversity is high, dispersal from species rich adjacent habitats can increase  $\alpha$ -diversity. At larger scales, for similar  $\alpha$ -diversity values, different communities (higher  $\beta$ -diversity) contribute to a higher  $\gamma$ -diversity. Despite its importance,  $\beta$ -diversity

is analysed only recently in systems with differing intensities of agriculture, and this mainly for cereal fields (Fried, 2008 (Roschewitz *et al.* 2005; Gabriel *et al.* 2006; Fried *et al.* 2008). Little is known on the  $\beta$ -diversity between the different habitats, which are part of larger units or the entire landscape (Thomas & Marshall 1999; Dutoit *et al.* 2007). However, this is especially interesting in crop systems where different habitats are part of the cultivated unit, as it is especially the case with vineyards. Vineyard  $\alpha$ -diversity has thoroughly been analysed by Maillet (1992). Until now, we know still little about which spatial scales contribute to plant diversity in vineyard landscapes. Moreover, we lack knowledge on the role of habitats outside the main cultivated plots such as embankments or surfaces for turning of machines as well as the combination of fields with contrasting management for different levels of plant diversity (Dutoit *et al.* 2007).

More basically, it can be asked if there are new and characteristic species in the transition zones among adjacent habitats. This has been addressed conceptually by van der Maarel (1990) and, for Mediterranean areas, has been applied by Dutoit *et al.* to cereal fields (2007). In terms of additive diversity partitioning, this approach classifies transition zones between two habitats according to the amount of absolute  $\beta$ -diversity. However, these works generally do not consider different spatial scales and they fail to consider that  $\beta$ -diversity in these transition zones may also be modified by factors from outside the transition zone, most importantly the structure of the surrounding landscape. It is therefore conceptually interesting to study if surrounding landscape has an impact on  $\beta$ -diversity between two habitats on a finer scale.

Therefore, we studied (a) what factor out of landscape context, intensity of agriculture and habitat type is important to explain plant diversity in Mediterranean vineyards. Moreover, (b) on which spatial scales do these factors act? What is the relation of floristic differentiation ( $\beta$ -diversity) to these factors? (c) Do target species for conservation follow these patterns? And finally: (d) How recent historical factors such as former cereal cultivation influence  $\alpha$ -diversity of target species?

## Materials and methods

### Study area

The study has been done in an area of agricultural landscapes in South Eastern France, south of the Luberon mountain ridge (Figure 1). Our study area of about 300 km<sup>2</sup> is on molasses and sands and smooth limestone of the Tertiary (Moutier & Balme 1997). Climate is Mediterranean with mild winters and summer drought. Forest remnants are dominated by *Quercus pubescens* Willd., *Quercus ilex* L. and *Rubia peregrina* L.; matorrals by *Quercus coccifera* L., *Rosmarinus officinalis* L. and several *Cistus* species. Some occur also in vineyards as a secondary habitat e.g. *R. peregrina* on the vine-rows and *Cistus* species

on the embankments. Floristic composition differed among habitat types and according to soil factors as described in more detail in Saatkamp *et al.* (2007), with seed banking annuals (Saatkamp *et al.* 2011) being more frequent inside vineyards and perennials on the embankments as well as specialized species for sites with high soil clay and sand content.

### Interviews and documentation of former land-use

In summer 2004, we interviewed systematically all farmers on management of the 45 studied vineyards, noting the number of treatments per year, application of herbicides and fertilization. Systematic interviews of farmers

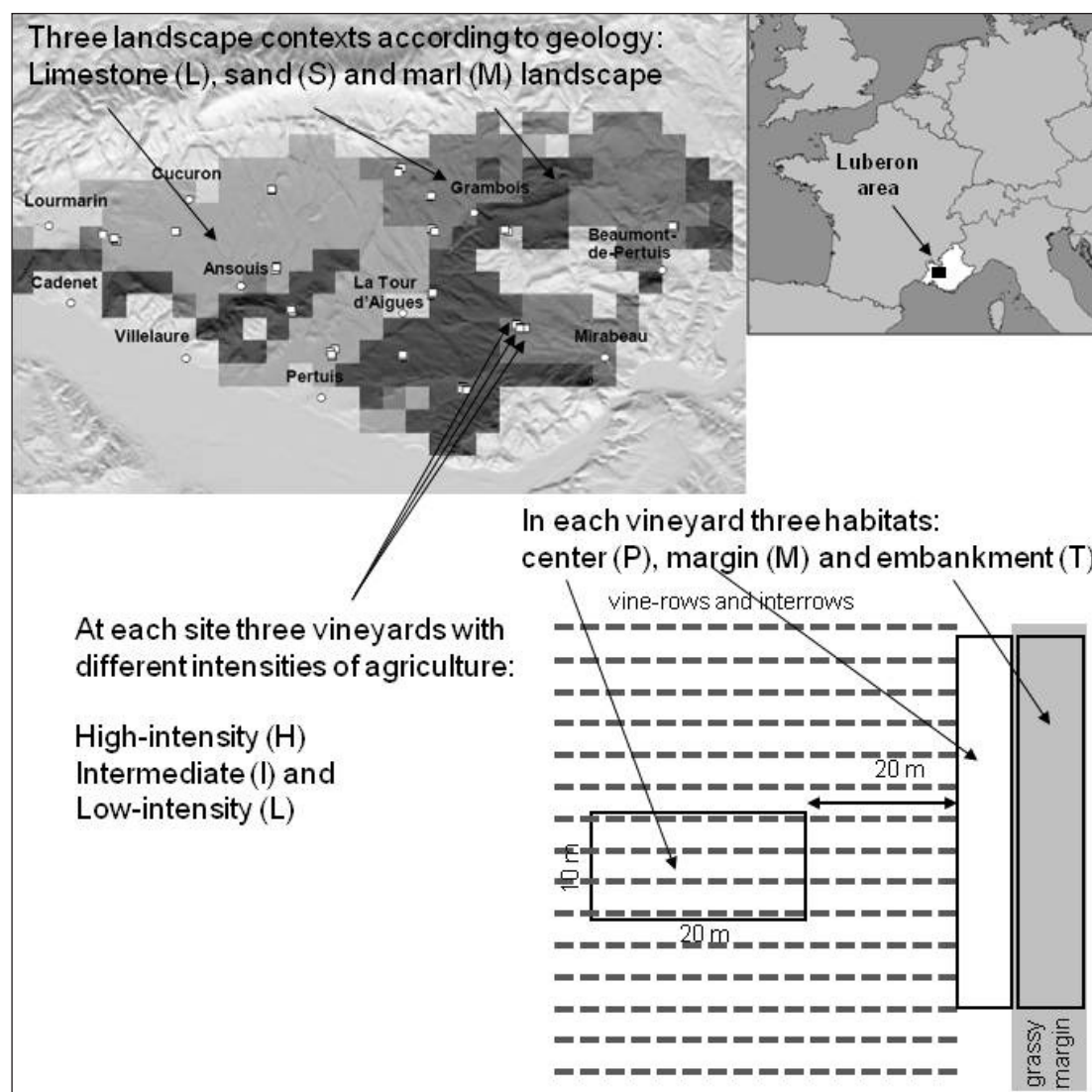


Figure 1 – Sampling design and its nested structure according to landscape type, intensity of agriculture and habitats in vineyards, map of the fifteen study sites with three vineyards each (□), the 1 km grid of the three landscape contexts and villages (○); dark grey: “sand landscape” class, middle grey “marl landscape” class and light grey “limestone landscape” class.

**Table 1 – Management types, mean number of treatments (ploughing, fertilization, herbicide application) and % of fertilized fields.**

Management intensity	Visual criteria	Mean number of treatments per year	% fields fertilized
High intensity (H)	herbicide application: wilting or dead plants with bright colour; vegetation cover <50%	14.8	86
Intermediate (I)	ploughing or herbicide application, but living green plants present, ploughed between vineyard rows, herbicide treatment on rows	13.5	85
Low intensity (L)	no traces of herbicide application at the date of first visit, no traces of ploughing, vegetation cover >50%	10.3	69

showed that the three types of management intensity used below differed in the number of treatments per year and in the use of fertilization (Table 1), but did not differ in herbicide treatments. Even though no absolute limits between these classes can be given, we think that this classification reflects best the gradient of management intensities in the area.

We noted former land use type for vineyards from topographic maps (1986, 1:25000, IGN, Paris), which differentiated vineyards and arable fields with cereals being formerly the most widespread crop (Müller 1991). Concerned farmers also stated that all “young” vineyards were previously cultivated with cereals.

### Sampling design

In our sampling design we used five replicates of three nested factors (1) landscape context, (2) management intensity and (3) habitat type, with each three levels. The resulting sampling design of  $5 \times 3 \times 3$  plots is resumed in Figure 1.

In order to study the effects of landscape context on plant diversity, we subdivided our study region in a 1 km<sup>2</sup> grid (Figure 1) and classified each cell according to data on prevailing type of geological units from Moutier and Balme (1997). This was necessary to have a broad landscape context classification since initial geological units were too finely differentiated to give broader scale landscapes. Also this classification coincided with relief complexity and types and diversity of land use (P. Roche unpublished work). The first class (“limestone landscape” 36% of study site) consists of flat sites with south facing slopes on calcareous molasses (Figure 1). The second “sand landscape” type (29% of study site) has north-facing slopes on Miocene sands, with vineyards and cereal fields. The third “marl landscape” type (35% of study site) has a complex relief, with forests, vineyards and

cereal fields, mostly on Oligocene marls. The number of geological units per 1 km<sup>2</sup> was higher in marl landscapes (3.2) than in the sand (2.9 per km<sup>2</sup>) and limestone (2.6 per km<sup>2</sup>) landscapes, but this reflects probably influences of geological methodology.

For each of the three landscape contexts, we selected five sites. At each site we chose three spatially grouped vineyards of contrasting management intensity. Since we had no precise data on management intensity we first used visual criteria as presented in Table 1 to select vineyards of three different management intensities: (H) high intensity, (I) intermediate and (L) low intensity vineyards.

For the resulting 45 individual vineyards (Figure 1), we studied three different habitat types. *P*: at 20 m from the margins, inside each vineyard, we placed a plot with a size of 10 × 20m that included 4 vine-rows and 3 inter-rows. *M*: the margin habitat at the end of the vine-rows where machines turn from one to another row, with a plot size of 200 m<sup>2</sup> but varying shape according to possibilities in the field mostly these plots were also 10 × 20 m. *T*: a plot of 4 × 50 m on an adjacent embankment, not ploughed nor chemically weeded. The more elongated form of the margin might have increased its alpha diversity but fixing size to a longer strip within vineyards would have meant to make these strips perpendicular to the margins, in this way distances between margins and inside vineyard plots would have varied, and distance within the P plot would be greater than between P and M plots.

We visited plots between April and June 2004, plants were identified using Jauzein (1995). Since initially we had no data on management history of fields, we could not include it as a stratification variable in this design, and thus added it as a fourth variable later in the analyses.

## Target species for conservation

We scanned our species lists for species of high conservation interest according to recent Red Data Books and floras for the study area (Jauzein 1995; Roux & Nicolas 2001) and their status as cereal weed (Guende & Olivier 1997) presented in Table 5. We used this list of cereal weeds for the following analyses on target species for conservation.

## Diversity measures

We studied diversity on different scales as summarised in Table 2:  $\alpha$ -diversity on the plot scale,  $\beta_1$ -diversity on the vineyard scale,  $\beta_2$ -diversity on the site scale and  $\gamma$ -diversity on the site scale. Since we had three habitat types in each vineyard,  $\beta_1$ -diversity values have been calculated between each of these different types. We used an index to highlight which comparison we used:  $\beta_{TM}$  for comparison of embankments to margins,  $\beta_{MP}$  for margins to cultivated plots. For example,  $\beta_{TM}$ -diversity between embankments (T) and margins (M) of vineyards denotes the difference between the species overlap between both habitats and the sum of species of both habitats. Similarly, we further calculated a  $\beta_2$ -diversity at the site scale between individual vineyards of different intensity that were grouped at one place as the difference between  $\gamma$ -diversity of two vineyards united and their species overlap. We thus calculated a  $\beta_{LI}$ -diversity between low-intensity (L) and intermediately (I) managed vineyards, as well as a  $\beta_{IH}$ -diversity between intermediately (I) and high-intensity (H) managed vineyards. Finally, we analysed  $\alpha$ -diversity and  $\gamma$ -diversity at the plot, vineyard and landscape scale (Table 2, Figure 2).

## Data analysis

We tested response variables for normality using Shapiro-Wilk's test and equality of variances using the F-test. To take account for the nested sampling structure of our data, we applied linear mixed models with vineyards

nested within sites as random effects using the nlme software (Pinheiro *et al.* 2009). Similarly,  $\beta_1$ -diversity has been analysed using linear mixed models using sites as random effect. Since, for  $\beta_2$ - and  $\gamma$ -diversity all 15 sites were randomly distributed and not nested, we analysed these variables with classical analysis of variance. For the analysis of cereal weed species richness and former crop cultivation, we used non-parametrical Kruskal-Wallis test to account for the non-normality in these data. All calculations and statistical analyses have been done using R (Team 2014).

## Results

Our study recorded 359 different species in the 135 studied plots, the prevailing life form were annuals (therophytes) followed by hemicryptophytes, geophytes and climbers. Frequent families were Asteraceae, Fabaceae and Brassicaceae. The linear mixed model analysis of  $\alpha$ -diversity showed that habitat types most strongly influenced species richness, followed by intensity of agriculture and landscape context (Table 3, Figure 2). Furthermore, there was a significant interaction between habitat type and intensity of agriculture (Table 3), showing that high intensity agriculture decreased  $\alpha$ -diversity to a lower level inside cultivated plots (mean of 17.7 species) than on margins or embankments (31.1 and 55.3 species per 200 m<sup>2</sup>).

There were no significant differences in the number of treatments per year according to the three landscape contexts (Kruskal-Wallis<sup>2</sup> = 3.3, *d.f.* = 2, *p* = 0.1921), however, the marl landscapes had lower number of treatments (11.5) per year than the sand (13.5) and limestone (14) landscape.

The interaction between habitat type and intensity of agriculture showed, that the differences in  $\alpha$ -diversity between the three habitats became more distinct with increasing intensity

**Table 2 – Diversity levels, scales and independent factors analysed in this work.**

Type	Variables	Measurement scale	Factors analysed
$\alpha$ -diversity	$\alpha$	plots	habitat type, intensity of agriculture, landscape context
$\beta_1$ -diversity	$\beta_{TM}$ and $\beta_{MP}$	vineyards	intensity of agriculture, landscape context
$\beta_2$ -diversity	$\beta_{LI}$ and $\beta_{IH}$	sites	landscape context
$\gamma$ -diversity	$\gamma_{LI}$ and $\gamma_{IH}$	sites	landscape context

of agriculture. Inside fields the high intensity agriculture plots had the lowest diversity whereas for the embankment plots diversity was only slightly lower in high intensity vineyards. The analysis of  $\beta_1$ -diversity at the vineyard scale (Table 4, Figure 2) revealed that landscape context had a marginally significant effect on  $\beta_1$ -diversity for both habitat contrasts,

*i.e.* margin to inside field plots ( $\beta_{MP}$ ) and margin to embankment plots ( $\beta_{TM}$ ). In the limestone landscape  $\beta_1$ -diversity values were lower. Intensity of agriculture had no effect on  $\beta_1$ -diversity: the  $\beta_1$ -diversity among the three management intensities were at the same level. The analysis of  $\beta_2$ -diversity values at the landscape scale showed no significant effect of

**Table 3 – Results of the linear mixed model analysis on the  $\alpha$ -diversity in 200 m<sup>2</sup> plots, factors were habitat type, landscape context and intensity of agriculture, random effects were vineyards nested within sites.**

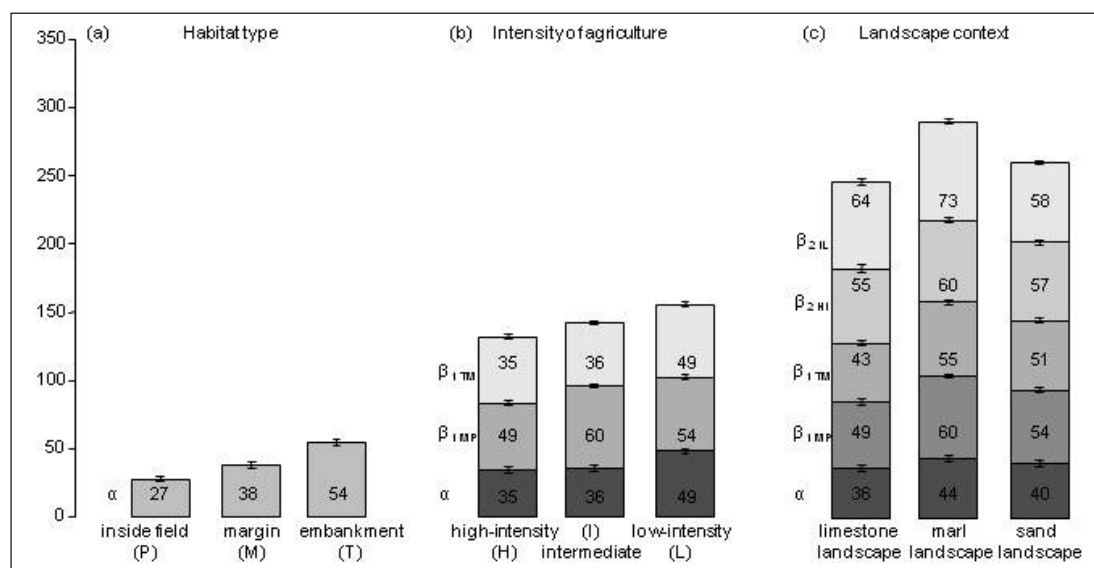
Factor	n, d.f.	F	p
Landscape context	2,36	3.9670	0.0277*
Intensity of agriculture	2,36	15.9287	< 0.0001***
Habitat type	2,72	81.6834	< 0.0001***
Landscape context x intensity of agriculture	4,36	0.0504	0.9950
Landscape context x habitat type	4,72	1.1808	0.3266
Intensity of agriculture x habitat type	4,72	3.8476	0.0069**
Landscape context x intensity of agriculture x habitat type	8,72	0.9354	0.4931

\* p < 0.05, \*\* p < 0.01, \*\*\*p < 0.001

**Table 4 – Results of the linear mixed model analyses on the absolute  $\beta_1$ -diversity according to intensity of agriculture and landscape context; note that  $\beta_1$ -diversity values are split into contrasts between margin and embankment plots ( $\beta_{TM}$ ), and between margin and inside of vineyards ( $\beta_{MP}$ ), which have been analysed by separate models, with sites as random effects.**

Dependent variable and factor	n, d.f.	F	p
$\beta_{MP}$ on intensity of agriculture	2,28	2.8705	0.0735
$\beta_{MP}$ on landscape context	2,12	3.4991	0.0635'
$\beta_{TM}$ on intensity of agriculture	2,28	2.0835	0.1434
$\beta_{TM}$ on landscape context	2,12	2.8723	0.0957'

' marginally significant



**Figure 2 – Bar plot showing the species numbers ( $\pm$  standard error) as contributed by  $\alpha$ -diversity (species richness on 200 m<sup>2</sup>),  $\beta_1$ -diversity and  $\beta_2$ -diversity to the global diversity of 359 species; bars are grouped according to studied factors with habitats nested within vineyards;  $\beta_1$ -diversity is split into contrast of margins to field centers (MP) and embankments to margins (TM) ;  $\beta_2$ -diversity is split into contrast of high-intensity to intermediate (HI) and low-intensity to intermediate (LI) management type.**

**Table 5** – List and status of typical cereal weeds found among 359 species of this study; species of high conservation value are marked in bold; underlined: all other species of high conservation value that are not cereal weeds. Status according to: (1) Roux & Nicolas (2) Filosa & Verlaque (1997); (3) Jauzein (1995): AC – quite common; AR – quite rare; R – rare; TR – very rare; \* special conservation efforts would be beneficial; (4) Montégut (1997), (5) frequency: number of sites where species occurred.

Species	(1)	(2)	(3)	(4)	(5)
<i>Adonis annua</i> L.	5	threatened	R*	decreasing	4
<i>Adonis flammea</i> Jacq.	5	threatened common	R*	rare	2
<u><i>Allium rotundum</i> L.</u>	-	-	R*	-	1
<i>Anthemis altissima</i> L.	-	-	-	-	1
<i>Anthemis arvensis</i> L.	-	-	-	-	22
<i>Bunias erucago</i> L.	-	-	-	-	12
<i>Caucalis platycarpus</i> L.	-	less threatened	AR	decreasing	3
<i>Ceratocephala falcata</i> (L.) Pers.	5	threatened common	R	very rare	2
<i>Cnicus benedictus</i> L.	5	threatened	AR	rare	3
<i>Euphorbia falcata</i> L.	-	-	-	-	5
<u><i>Fumaria parviflora</i> Lam.</u>	-	-	AC	decreasing	3
<i>Galium tricornutum</i> Dandy	-	less threatened	AR	decreasing	4
<i>Gladiolus italicus</i> Mill.	-	-	-	-	14
<i>Hypocoum pendulum</i> L.	2	rare & threatened	TR*	-	1
<i>Iberis pinnata</i> L.	-	threatened	AR	-	1
<i>Legousia hybrid</i> Delabre	-	threatened	AR	-	3
<i>Lithospermum arvense</i> L.	-	-	-	-	10
<u><i>Medicago coronate</i> (L.) Bortal.</u>	5	-	TR	-	1
<i>Orlaya daucoïdes</i> (L.) Greuter	3	threatened common	R	-	2
<i>Papaver argemone</i> L.	-	threatened common	AC	decreasing	4
<i>Papaver dubium</i> L.	-	-	-	-	14
<u><i>Papaver hybridum</i> L.</u>	-	threatened common	AR	decreasing	1
<i>Papaver rhoeas</i> L.	-	-	-	-	52
<i>Polycnemum majus</i> Braun	-	-	-	-	1
<i>Ranunculus arvensis</i> L.	-	-	-	-	7
<i>Roemeria hybrida</i> (L.) DC.	3	-	TR*	rare	2
<u><i>Salsola kali</i> L.</u>	5	-	TR	-	3
<i>Scandix pecten-veneris</i> L.	-	-	-	-	1
<u><i>Sclerochloa dura</i> (L.) P. Beauv.</u>	-	-	TR*	-	3
<i>Valerianella coronata</i> (L.) DC.	-	-	-	-	4
<i>Velezia rigida</i> L.	3	-	TR*	decreasing	1
<u><i>Vicia narbonensis</i> L.</u>	3	-	-	-	1
<i>Vicia pannonica</i> Crantz.	-	-	-	-	21
<i>Vicia peregrina</i> L.	-	-	AR	decreasing	15
<i>Viola tricolor</i> ssp. <i>arvensis</i> (Murray) Gaudin	-	-	-	-	1

landscape context, neither for the contrast of low-intensity to intermediate ( $\beta_{LI}$ ) nor for the contrast of intermediate to high-intensity vineyards ( $\beta_{IH}$ ). There was, however, a marginal significant effect ( $p = 0.0561$ ,  $d.f. = 2.42$ ,  $F = 3.0876$ ) of landscape context on  $\gamma$ -diversity (species of all plots united at one site), with marl landscape having the highest mean  $\gamma$ -diversity (76.4 species) compared to limestone (63.1) and sand landscape (72.9).

The scan for target species showed that the majority of rare or threatened taxa in our plots belong to the group of cereal weeds (Table 5). The analysis of the  $\alpha$ -diversity of cereal weeds in vineyards using the stratification of plots and the data on historical land use (Figure 3) shows a higher number of cereal

weed species on the embankment and margins of the vineyards than inside. More cereal weed species have been found in low-intensity vineyards than in high-intensity vineyards. There is a conspicuous effect of the former cereal cultivation on cereal weed diversity. These relations were significant (Kruskal-Wallis test, for habitat types,  $p = 0.0063$ ; for intensity of agriculture,  $p = 0.0003$ ; for landscape context,  $p = 0.0067$ ; for former cultivation type,  $p = 0.0006$ ). Yong vineyards were less frequent for the high-intensity vineyard types ( $N = 2$ ) compared to intermediate and low-intensity vineyards ( $N = 6$ ); they were also more frequent in the sand ( $N = 5$ ) and marl landscapes ( $N = 1$ ) compared to the limestone landscape ( $N = 1$ ).



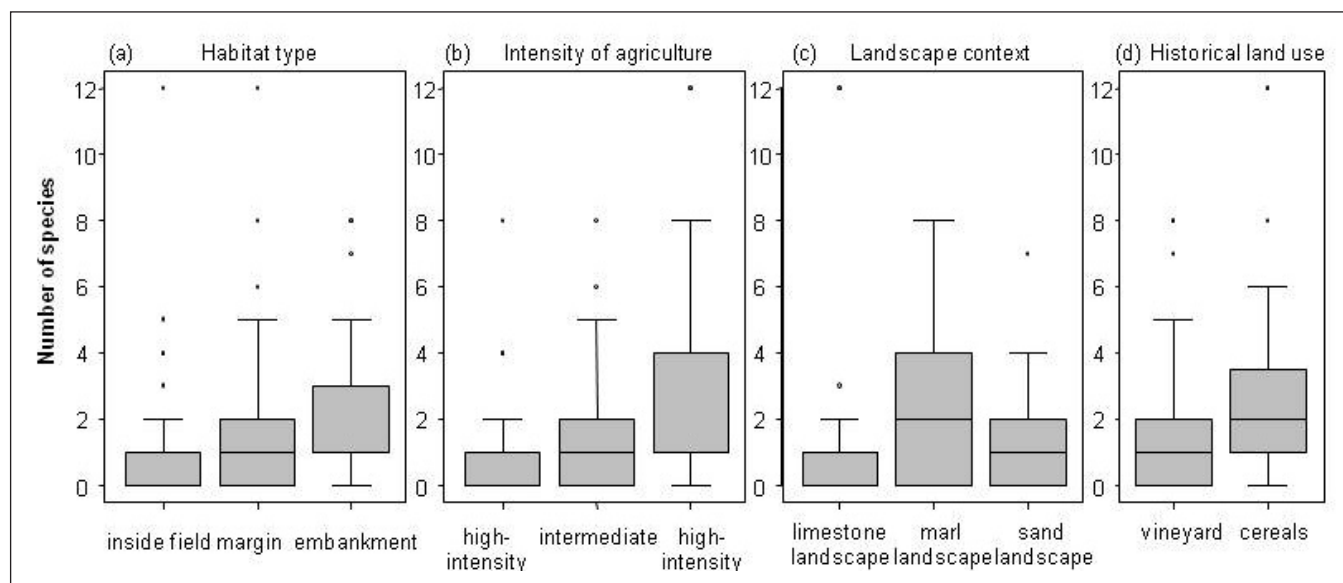


Figure 3 – Number of cereal weed species in the studied plots according to habitat type, intensities of agriculture, landscape context and the former cultivation type;  $N = 45$  for each box, except for vineyards,  $N = 111$  and cereals  $N = 24$ .

## Discussion

### $\alpha$ -Diversity

First, the analysis of different levels of  $\alpha$ -diversity showed that, in this order, habitat types, intensity of agriculture and landscape context determine plot scale  $\alpha$ -diversity of vascular plants in vineyard landscapes (Table 3, Figure 2). The high importance of vineyard margins and embankments for plant diversity is in line with the higher arable plant diversity found for arable field edges (Marshall 1989; Dutoit *et al.* 1999; Roschewitz *et al.* 2005; Gabriel *et al.* 2006). This has been associated with lesser use of fertilizers, herbicides (Schneider *et al.* 1994; Robinson & Sutherland 2002; Fried *et al.* 2008) but can also stem from dispersal between these adjacent communities (Turnbull *et al.* 2000). However, in very low-intensity systems diversity inside fields can be equally important than in margins (Dutoit *et al.* 1999). Dispersal to sink populations in suboptimal habitats offers an explanation how habitat mosaics with interspecific differences in population growth rates can contribute to local  $\alpha$ -diversity at their boundaries (Turnbull *et al.* 2000). It has to be noted that the shape of our sampling units is varying in a systematic way from more elongate to more quadratic when passing from embankments to the vineyard interior. One would expect that this has a

decreasing effect on diversity. However effect of habitat type on diversity held also true in a field trial with fixed shape. We therefore think that we only slightly overestimated the effect of habitat type on  $\alpha$ -diversity of vascular plants in vineyards.

Second, we observed a decline in  $\alpha$ -diversity with increasing intensity of agriculture (Table 3, Figure 2). This contrasts with the findings of Maillet (1992) who observed a higher diversity in high-intensity, non-ploughed systems. However, vineyard practices changed since the work of Maillet and management types diversified, including organic agriculture, use of grass lanes in vineyards and the spread of exclusive herbicide use without ploughing (Maillet 1992). All these changes may have altered the relationship towards what we observe today. A similar decrease for  $\alpha$ -diversity with management intensity (=  $\gamma$ -diversity in small scale studies) has been documented when comparing organic and conventional fields (Hyvönen *et al.* 2003; Roschewitz *et al.* 2005; Gabriel *et al.* 2006). The difference in  $\alpha$ -diversity with increasing intensity of agriculture is similar to the decline from field edges to centre in the high-intensity vineyards studied here. This reflects again the importance of management intensity for species decline at several scales in agro-ecosystems (Schneider *et al.* 1994; Robinson & Sutherland 2002).

Third, we demonstrated that landscape contexts had significant effects on  $\alpha$ -diversity (Table 3, Figure 2). The 'marl landscape' with the highest  $\alpha$ -diversity is richer in non-arable land and has a more intense and diverse land use, with few vineyards. The lowest diversity was found in the 'limestone landscape' with vineyards as dominant land use. The higher diversity in a more diverse landscape can be related to higher levels of dispersal due more diverse adjacent habitats (Turnbull *et al.* 2000). Maillet (1992) already showed that a large part of the regional flora grows in vineyards, hence recruitment limitation may be less important. This may thus be interpreted as evidence for larger species pools (Zobel 1997) and lower dispersal limitation for (Turnbull *et al.* 2000) in these areas. Alternatively, bedrock type which in our example was correlated to landscape context can influence  $\alpha$ -diversity (Fried *et al.* 2008).

### $\beta_1$ -Diversity

The  $\beta_1$ -diversity among different habitats in vineyards was influenced by landscape context (Table 4). In the marl landscape, the floristic differences between the different habitats (field margins, centres and embankments) were greater than in *e.g.* limestone landscapes. This can be due to the higher land use and geological diversity in this landscape context. Moreover, a higher  $\gamma$ -diversity in the marl landscape (see results section), can contribute a larger pool of species for the habitats in marl landscapes to differentiate. The absence of statistical interaction of the landscape effect on  $\alpha$ -diversity with intensity of agriculture or habitat type, suggests that the effect of landscape context did not differ among specific habitats or management types. There are, however, differences in species composition which can be attributed to differences in soil factors (Saatkamp *et al.* 2007).

Heterogeneous landscapes provide more species to fit into different habitats than monotonous landscapes (Roschewitz *et al.* 2005). This landscape level effect enhanced diversity of the vineyard in general, without necessarily increasing the proportion of  $\beta_1$ -diversity on  $\gamma$ -diversity.

The change of  $\beta_1$ -diversity according to the characteristics of the surrounding landscapes questions the concept on transition zones between adjacent communities *via* the distinction of ecotones and ecoclines. In our

data, the presence of specialised species in the transition between two different habitats changed according to the landscape context. This implies that the difference between ecotones and ecoclines, which van der Maarel (1990) defined on the basis of presence or not of specialised species, depends on characteristics outside the system and not on characteristics of the transition system itself. In our data, similar transitions in terms of composition may be classified as either ecotones or ecoclines, depending on the surrounding landscape. The consistency of these definitions should be followed up in landscapes with contrasting diversity.

The analysis of  $\alpha$ -diversity discussed above is complementary for the understanding in this context: high-intensity fields have much less species than low-intensity. This means that only very few specialised species can maintain populations in the centre of intensively managed vineyards and consequently this vegetation is quite different from the surroundings. The low diversity of high intensity fields does not contribute significantly to the total number of species: there was no significant difference in absolute  $\beta_1$ -diversity among fields of different management types (Table 4), similar to studies from arable fields (Roschewitz *et al.* 2005; Gabriel *et al.* 2006). Therefore, the low  $\alpha$ -diversity found here suggests that management intensity should be reduced if plant diversity and pollinator services are important goals (Gabriel *et al.* 2006).

### $\beta_2$ - and $\gamma$ -diversity

There was no effect of landscape context on  $\beta_2$ -diversity and only a tendency towards higher  $\gamma$ -diversity in the marl landscape. Since  $\beta_2$ -diversity is reflecting the differences among vineyards of different management types, we think that landscape context does not influence how differently managed vineyards differ floristically among each other. Concerning  $\gamma$ -diversity, we think that the tendency to higher values in marl landscapes can be related to their higher land use and geological diversity. However, our data suggest, that this higher  $\gamma$ -diversity is not mediated by between vineyards  $\beta_2$ -diversity but by a higher floristic difference among habitats ( $\beta_1$ -diversity) within vineyards.

## Species of conservation interest

In Table 5, we identified a set of rare and threatened plants that are of high conservation interest by scanning Red Data Books and floristic works (Girerd 1991; Jauzein 1995; Montégut 1997; Verlaque & Filosa 1997; Roux & Nicolas 2001). It is astonishing at first sight, that most species of high conservation value in vineyards are better known as cereal field specialist. However, these have been identified as conservation targets at several occasions (e.g. Fried *et al.* 2009). The analysis of their diversity in the same schemes as the entire flora showed that they are influenced by the same factors than entire flora  $\alpha$ -diversity. This finding is in contradiction to other works in similar agro-ecosystems (Roschewitz *et al.* 2005). The analysis of recent historical factors such as cereal cultivation complemented the interpretation of this species group of conservation interest: the highest number of cereal weeds are found on vineyards with recent cereal cultivation and show the persistence of these species after land use changes.

## Conclusions

Contrasts between habitats are sharper in diverse landscapes due to supplementary species, and in high-intensity vineyards due to stronger habitat specificities. Low-intensity systems offer an increased  $\alpha$ -diversity and may have also indirect effects on rare plant conservation the study system (Gibson *et al.* 2006). They can serve as source sites for the maintenance of plant diversity in the surrounding landscapes. However, since  $\alpha$ -diversity and  $\beta$ -diversity varied according to landscape contexts in our work, not all landscapes may be suited in a similar way for the conservation of high plant diversity or high numbers of rare plants.

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