



HAL
open science

Vegetation management intensity and landscape diversity alter plant species richness, functional traits and community composition across European vineyards

Rea M. Hall, Nicole Penke, Monika Kriechbaum, Sophie Kratschmer, Vincent Jung, Simon Chollet, Muriel Guernion, Annegret Nicolai, Françoise Burel, Albin Fertil, et al.

► **To cite this version:**

Rea M. Hall, Nicole Penke, Monika Kriechbaum, Sophie Kratschmer, Vincent Jung, et al.. Vegetation management intensity and landscape diversity alter plant species richness, functional traits and community composition across European vineyards. *Agricultural Systems*, 2020, 177, pp.102706. 10.1016/j.agsy.2019.102706 . hal-02365699

HAL Id: hal-02365699

<https://univ-rennes.hal.science/hal-02365699>

Submitted on 15 Jul 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

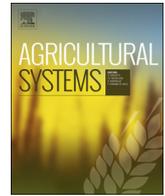
L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



ELSEVIER

Contents lists available at ScienceDirect

Agricultural Systems

journal homepage: www.elsevier.com/locate/agsy

Vegetation management intensity and landscape diversity alter plant species richness, functional traits and community composition across European vineyards

Rea M. Hall^{a,*}, Nicole Penke^b, Monika Kriechbaum^b, Sophie Kratschmer^b, Vincent Jung^c, Simon Chollet^c, Muriel Guernion^c, Annegret Nicolai^c, Françoise Burel^c, Albin Fertil^c, Ángel Lora^d, Rafael Sánchez-Cuesta^d, Gema Guzmán^e, Jose Gómez^e, Daniela Popescu^{f,g}, Adela Hoble^g, Claudiu-Ioan Bunea^g, Johann G. Zaller^h, Silvia Winter^{a,b,**}

^a Institute of Plant Protection, University of Natural Resources and Life Sciences Vienna (BOKU), Vienna, AT, Austria

^b Institute for Integrative Nature Conservation Research AND ^h Institute for Zoology, University of Natural Resources and Life Sciences Vienna (BOKU), Vienna, AT

^c Université de Rennes 1, CNRS, ECOBIO (Ecosystèmes, biodiversité, évolution) - UMR 6553, Rennes, France

^d University of Cordoba, Department of Forestry Engineering, Cordoba, Spain

^e Institute for Sustainable Agriculture, Spanish National Research Council (CSIC), Cordoba, Spain

^f SC JIDVEI SRL, Research Department, Jidvei, Romania

^g University of Agriculture Science and Veterinary Medicine Cluj Napoca, Romania

^h Institute for Zoology, University of Natural Resources and Life Sciences Vienna (BOKU), Austria

ARTICLE INFO

Keywords:

Agroecology
Tillage
Herbicides
Cover crops
Landscape
Ecosystem services

ABSTRACT

Land-use intensification at the field and landscape scale is a strong driver for declining biodiversity and ecosystem service provision. Vineyards are characterised by non-productive inter-rows, which could potentially host diverse plant communities. Mulching, tillage or herbicides are used to mitigate the competition between vines and the inter-row vegetation. As plant species with the same set of functional traits will respond similarly to environmental filters like management measures, knowledge about plant trait–environment-relations can be used to predict community and ecosystem processes which are essential for preserving ecosystem services like soil erosion mitigation. We hypothesized that higher vegetation management intensity reduces plant (functional) diversity, changes functional traits and community composition.

Across Europe, four viticultural regions in Austria, France, Spain and Romania, which comprised 78 vineyards differing in vegetation management intensity (bare soil, temporary and permanent vegetation cover), were selected for sampling vascular plant diversity. Around each vineyard, the surrounding landscape composition and landscape diversity was investigated within a 750 m radius. Rao's quadratic entropy as a measure of functional diversity was calculated based on a selection of plant functional traits. The effects of management and landscape variables on species richness, functional traits, functional diversity and vegetation cover were analysed by generalized linear mixed models and random forests (RF). Furthermore, plant community composition was analysed with non-metric multidimensional scaling (NMDS).

Higher management intensities resulted in lower species richness, functional diversity and vegetation cover. The country with the related divergent edaphoclimatic conditions was a significant factor affecting most diversity and functional trait parameters, whereas landscape diversity increased plant species richness only slightly. Vegetation management intensity had the highest explanatory power for species richness, functional diversity and most functional traits according to RF analysis. Consequently, plant functional traits like a higher coverage of ruderals and annuals could be clearly related to bare soil management. Furthermore, the type of cover crops influenced the relationship between annual and perennial plant species, Grime plant strategy types and species diversity. Accordingly, NMDS showed a separation between permanent vegetation cover and bare soil vineyards. The overall positive effect of extensive management and the use of diverse cover crops or

* Corresponding author at: Institute of Plant Protection, University of Natural Resources and Life Science Vienna (BOKU), Gregor Mendel Straße 33, 1180 Vienna, Austria.

** Corresponding author at: Institute of Plant Protection, University of Natural Resources and Life Sciences Vienna (BOKU), Gregor Mendel Straße 33, 1180 Vienna, Austria.

E-mail address: rea.hall@boku.ac.at (R.M. Hall).

<https://doi.org/10.1016/j.agsy.2019.102706>

Received 14 February 2019; Received in revised form 21 July 2019; Accepted 17 September 2019

Available online 01 November 2019

0308-521X/ © 2019 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license

(<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

spontaneous vegetation in vineyard inter-rows should be better implemented in agricultural policies to support both, biodiversity and ecosystem provision.

1. Introduction

Land-use change is a strong global driver for the loss of biodiversity, ecosystem functioning and service provision decline (e.g. Foley et al., 2005; Green et al., 2005; Kleijn et al., 2009). Particularly agricultural intensification was shown to reduce plant species richness leading to simplified community structures, and thus to a decline in ecosystem stability and resilience which are both important factors for maintaining essential ecosystem services (Tilman, 1999; Báez and Collins, 2008; Tilman et al., 2014). Nevertheless, our current understanding of the ecological interdependencies between biodiversity and ecosystem services, particularly in agricultural landscapes, is still limited (Bommarco et al., 2013). A meta-analysis showed that increasing plant diversity promoted most ecosystem services, i.e. provisioning, regulating services like erosion control and supporting ecosystem services like a higher diversity of primary consumers (Balvanera et al., 2006). However, studies in arable fields or vineyards were missing in that quantitative review.

Two alternative approaches have been suggested to reduce negative effects of intensive agricultural land use on biodiversity: the land sparing versus the land sharing (also called wildlife- or nature-friendly farming) approach (Green et al., 2005). In the land sparing approach, production and conservation areas are separated for maximising yields on agricultural land and biodiversity on semi-natural areas, whereas in the land sharing approach the intensity of agricultural land use is reduced to meet both, production and conservation goals (Green et al., 2005). The latter approach is similar to the ecological intensification approach which aims at linking high productivity with minimized negative impacts on the environment by decreasing the anthropogenic inputs for optimized ecosystem service provision (Bommarco et al., 2013).

The controversy between the land sparing versus land sharing approach could be reconciled in permanent crop systems like vineyards which are commonly characterised by non-productive inter-rows between the vine rows. Furthermore, most wine growers aim at producing high quality wines with regulations limiting the yield. Vineyard inter-

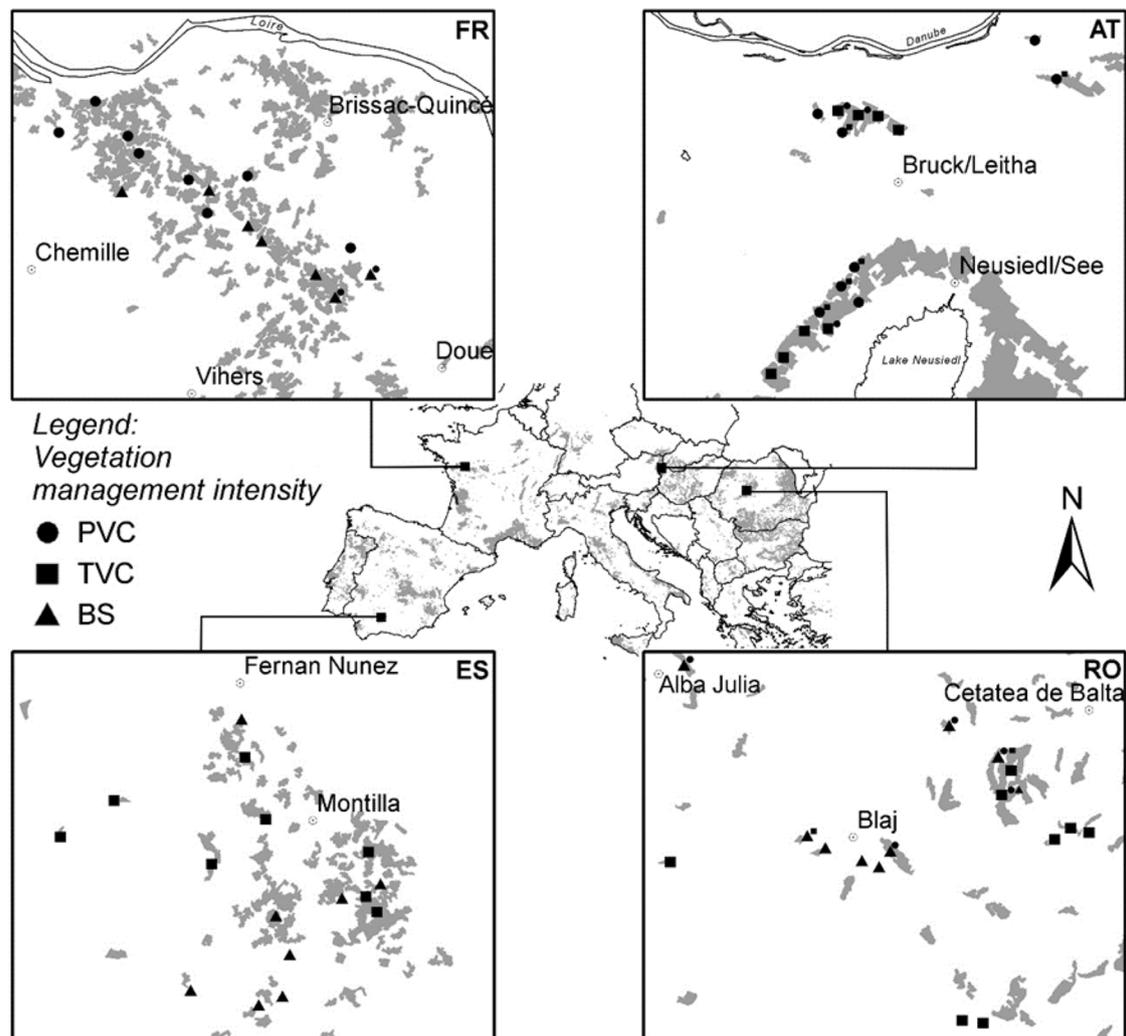


Fig. 1. Locations of study areas in France (FR), Austria (AT), Spain (ES) and Romania (RO) in relation to the wine growing area according to CORINE land cover. The symbols denote the vegetation management intensity (PVC = permanent vegetation cover, TVC = temporary vegetation cover, and BS = bare soil) of the studied vineyards, smaller symbols identify neighbouring vineyards with differential vegetation management intensity if more than one vineyard per landscape circle was studied.

rows could offer habitats for plant and animal species (Kehinde and Samways, 2014a; Shields et al., 2016) and consequently increase biodiversity and ecosystem service provision if extensive vegetation management practices were applied (Winter et al., 2018). However, only few studies considered the effect of the surrounding landscape matrix on biodiversity and ecosystem service provision in vineyards (Kehinde and Samways, 2014b; Kehinde et al., 2018) which would be required for an integrated assessment of the land use effects (Tschamtko et al., 2005).

Besides biotic and abiotic constraints across European agro-ecosystems, management is one major driver for biodiversity and plant community composition in vineyards (Lososová et al., 2003; Kazakou et al., 2016). Management regimes alter environmental filters that determine which species pools are assembled into local communities (Díaz et al., 1998; Booth and Swanton, 2002; Kazakou et al., 2016). As plant species with the same set of functional traits will respond similarly to environmental drivers, knowledge about plant trait–environment-relations can be used to predict community and ecosystem processes which are essential for preserving ecosystem functions and services (Noble and Gitay, 1996; Díaz and Cabido, 1997; Kahmen and Poschod, 2004; Díaz et al., 2007). Certain management practices may even increase ecosystem disservices, i.e. ecosystem functions with negative effects for human well-being, like an increased cover of competitive weed species resulting from filtering out other plant community members by e.g. frequent applications of the same herbicide (Owen et al., 2008). Nevertheless, bare soil management is still a common practice for reducing the competition between inter-row vegetation and vines for water and nutrients in rainfall-deficient regions without irrigation (Pardini et al., 2002; Ripoche et al., 2011).

As management affects the processes of community assembly rather than species diversity directly (cf. Mayfield et al., 2010), it is important to study the consequences for functional traits and species diversity simultaneously. The common assumption that declines in species richness results in losses of functional trait diversity (Kazakou et al., 2016) which result in an overall loss of ecosystem functions and services might not always hold in different systems and communities (e.g. Mayfield et al., 2010).

Certain filters may lead to a diversification or convergence of plant functional traits, e. g. plant strategy type convergence resulting in a larger proportion of faster growing species as response to periodic soil tillage (Grime, 2006; Kazakou et al., 2016). On the other hand, a certain level of disturbance (e.g. mowing, infrequent tillage or a combination of both) promotes the coexistence of diverse traits and associated species by reducing the vigour of highly competitive plant species (Grime, 2006). The current promotion of vegetation cover in vineyard inter-rows with agri-environmental schemes for reducing soil erosion could also lead to trait convergence by filtering out therophytes which benefit

from soil tillage (Lososová et al., 2003). Furthermore, the increasing use of cover crop mixtures which usually consist of a small set of grass or legume species may also lead to a shift in plant communities consisting of a narrower range of plant traits in comparison to spontaneous vegetation. Whereas numerous studies (i. e. Pardini et al., 2002; Tesic et al., 2007; Giese et al., 2014) focused on the economic effect of cover crops in general (vine growth regulation and quality improvement as substitute for cost- and time-consuming mechanical pruning), only few studies investigated the influence of different cover crop types on biodiversity (Baumgartner et al., 2008; Sanguankee and León, 2011; Steenwerth et al., 2016).

To the best of our knowledge, no study investigated the effects of inter-row vegetation management and landscape diversity on plant species richness, functional traits and functional diversity in several wine growing regions. Thus, we examined the effects of vegetation management in four European wine growing regions across a west-east transect. We expected that management intensification will lead to a reduction in species richness, functional diversity and consequently to a shift to plant communities which are dominated by competitive weeds. Furthermore, we hypothesized that an increasing proportion of semi-natural elements and higher landscape diversity increased plant species and functional diversity, e.g. through spill-over effects from semi-natural habitats (Mania et al., 2015; Nascimbene et al., 2016).

2. Material and methods

2.1. Study regions

The study regions form a west-east European transect (see Fig. 1) starting in southern Spain in the Montilla-Moriles wine growing region (Andalusia), to western France in the Loire Valley (Coteaux-du-Layon in Anjou), eastern Austria Carnuntum and Neusiedler See-Hügelland wine regions (Lower Austria and Burgenland) to the Târnave wine growing region in Transylvania in Romania (Alba county). The climate varies from summer-dry Mediterranean in Spain to oceanic in France and temperate continental in Austria and Romania. Climate data (mean annual temperature and total annual precipitation for 2016) for the investigated vineyards were obtained from spatial downscaling based on European climate data (Moreno and Hasenauer, 2016). The landscape in the study regions is characterised by a mix of vineyards with other forms of agricultural land use (mostly arable land use in Austria or olive groves in Spain) and semi-natural elements (SNE). All investigated vineyards (with the exception of 7 out of 16 vineyards in Spain which received deficit drip irrigation) were rainfed.

Table 1

Geographical location of study regions within four European countries and respective management type per study region and the mean (\pm SD) proportion of vineyards, other types of agriculture and semi-natural elements (SNE) within the landscape circle. The overall number of studied vineyards per study region increased due to the inclusion of neighbouring vineyards with different management types within one landscape circle in Austria and Romania.

Country	GPS coord. of study region	Prop. of vineyards	Prop. of other agriculture	Prop. of SNE	Management type (no. of studied vineyards)	Details of management
Austria	47°97'N, 16°73' E	26.67 \pm 15.83	27.54 \pm 16.98	34.60 \pm 20.52	TVC (13) PVC (12)	Tillage in every second inter-row† Mulching
France	47°23'N, 0°42' E	35.40 \pm 19.70	13.10 \pm 17.11	43.73 \pm 16.28	BS (6) PVC (10)	Herbicides (on average twice a year) Mulching
Romania	46°13'N, 24°06' E	34.52 \pm 19.14	17.94 \pm 16.63	42.10 \pm 13.82	BS (8) TVC (9)	Tillage Tillage in every second inter-row†
Spain	37°35'N, 4°38' W	23.93 \pm 13.86	60.16 \pm 14.29	9.29 \pm 3.46	PVC (6) BS (8) TVC (8)	Mulching Tillage* Temporary vegetation cover during the winter season, later removed by herbicides or tillage

† other inter-row mulched * in one vineyard, tillage is sometimes replaced by herbicides; PVC = permanent vegetation cover, TVC = temporary vegetation cover; BS = bare soil.

2.2. Study design and vineyard management

In each country, we investigated the effects of two to three different vegetation management intensities representing the most common management practices in each study region (see Table 1). The management intensities were defined as: (i) bare soil management (BS) by either frequent soil tillage (Spain and Romania) or herbicide use (France and partly in Spain, mostly non-selective glyphosate) in every inter-row, (ii) temporary vegetation cover (TV) by tillage in every second inter-row (Austria and Romania) or temporary vegetation cover during the winter season in Spain and (iii) permanent vegetation cover (PV) without any soil tillage in the last four years consisting of spontaneous or a mix of spontaneous and cover crop species. Management intensity reflects disturbance frequency among commercial vineyards, including common local management strategies (tillage, herbicide use, mulching) in the respective study regions. Overall, 78 vineyards were studied.

Inter-row vegetation consisted mainly of spontaneous vegetation, only one vineyard with permanent vegetation cover was sown with cover crop mixtures in the last 10 years in France, four in Spain (all temporary vegetation cover, three of them with *Hordeum vulgare*) and three in Romania (all temporary vegetation cover). In Austria cover crop mixtures were regularly seeded in vineyards with temporary vegetation cover ($n = 12$) and less frequently also in vineyards with permanent vegetation cover ($n = 4$).

Most vineyards were managed conventionally, except for one in Spain (temporary vegetation cover), three in Austria (2 permanent and 1 temporary vegetation cover) and one in Romania (permanent vegetation cover) which were managed organically. With the exception of five vineyards which applied the traditional goblet method in Spain (bare soil management), vines were trained in the trellis system in all other vineyards.

Vineyards were located in the center of landscape circles with 750 m radius, overall, 16 landscape circles were established in each country (in France 15). Several countries (especially Austria, Romania and France) contained additional, adjacent vineyards in the center of the landscape circle differing in vegetation management intensity.

2.3. Vegetation survey

Vegetation surveys were performed at the beginning of the vegetation period (April-May for all countries but Spain, where sampling started in December) and once in summer (June-July for all countries

but Spain, there vegetation was recorded in February and March before winegrowers removed the vegetation) on four 1 m² plots in the center of one vineyard inter-row. The overall vegetation cover, litter and bare soil cover were recorded at each sampling date. In addition, the coverage of each vascular plant species was estimated with the scale of Londo (1976). Vegetation data were aggregated across both sampling dates.

2.4. Landscape analysis

Landscape mapping was performed within a 750 m radius around each studied vineyard, land cover types were defined according to the EUNIS habitat type classification (EEA, 2016) in the field in 2015 (AT) or 2016 (ES, FR, RO). Field mapping was based on national datasets for the latter countries (AT: Nutzflächenkartierung and INVEKOS data – BMLFUW, 2012; ES: SIGPAC, 2011; FR: IGN, 2012). ArcGIS 10.2 (ESRI, 2013) was used for digitising spatial datasets, and converting them to raster data. Further, the proportion of SNE (semi-natural elements) and vineyards per landscape circle as well as the distance between each study plot and the closest SNE was calculated. The following landscape structures were considered SNE: woodlots, grassland, pastures, extensively managed orchards (excluding intensive olive orchards), fallows, crop fields, hedges, grass strips, unsealed paths and roads, built-up areas, heathland, river bodies, and wetlands. The Shannon landscape diversity index (SHDI) was calculated with FRAGSTATS 4.2 (McGarigal et al., 2012).

2.5. Plant functional trait analysis

Plant traits allow to compare disturbance regimes across different plant communities within the chosen European transect. In order to identify in which way vegetation management intensity and landscape properties affect plant communities in vineyards an analysis linking different functional plant traits (Table 2) with the given environmental conditions through species abundance data (3-data-matrices) was chosen.

Continuous traits (dry matter, leaf area and dry matter per fresh matter) were obtained from TRY global plant trait database, version 4 which was released in July 2017 (see Appendix S1 in the online supplementary material for full list of references; www.try-db.org; Kattge et al., 2011). For each species and trait the mean of all TRY single, best estimate and mean values with an error risk below 4 were averaged (cf. Kattge et al., 2011).

Table 2

Information on the traits used and the rationale for their selection (N = number of trait data available for sampled plant species).

Traits	N	Rationale for parameter selection and comments
Specific leaf area (SLA)	196	The SLA is the ratio of leaf area to dry mass and can be related to resource economy, with higher values associated with faster growth (Kazakou et al., 2016)
Leaf dry-matter content (LDMC) (g/g)	181	LDMC is a measure of tissue density; higher values are related to slower biomass production which is characteristic for slow growing species (Gross et al., 2007)
Plant height (cm)	220	Plant height influences competition and the resistance to disturbance (Mayfield et al., 2010)
Life span (annual/perennial)	220	High disturbance frequency is expected to decrease the coverage of perennial species, this however depends on the type (tillage, herbicide use) of disturbance and the storage organ of the perennial species. Due to the low number of respective taxa, biennial species were assigned to perennial species.
Storage organ (seeds/belowground storage)	218	The type of storage organ provides additional information to life span, in the sense that disturbance might not affect perennial plant species with belowground storage organs. Plant species were categorized due to their predominant storage mechanism in the groups “seeds” which represent all plants without any storage organs and “belowground storage” comprising plant species with rhizoms, storage roots, belowground runners and bulbs.
Pollination mode (wind/selfing)	217	Pollination mode is not only related to certain species groups but also to certain selective filters in the habitat (pollinator abundance, floral diversity etc.). As boundaries between the pollination mode are blurry, plants were categorized according to their predominant pollination mode in insect- or wind-pollinated or selfing plants.
Grime strategy (c, r, s and mixed-forms)	219	The C-S-R model classifies plants in respect to their response to stress and disturbance in three groups (Grime et al., 1988) which results in competitive (low stress and disturbance), stress-tolerators (high stress and low disturbance), ruderals (low stress and high disturbance) and plants which can be considered mixed types, e.g. CSR.

Categorical traits were obtained from BiolFlor Database version 1.1 (www.floraweb.de; Klotz et al., 2002), Botanischer Informationsknoten Bayern (<http://daten.bayernflora.de>; Lippert and Meierott, 2014) the Natural Resource Conservation Service (Natural Resources Conservation Service, 2018; www.plants.usda.gov), Weed Science Society of America (Weed Science Society of America, 2018; wssa.net), Flora Ibérica (www.floraiberica.es; Castroviejo et al., 1993) as well as from literature (Ellenberg et al., 1992; Hunt et al., 2009; Sell and Murell, 2006).

3. Data analysis

Data analysis and graphical visualisation of the results was performed using software R, Version 3.4.4 (R Core Development Team, 2018) including the R packages *vegan* (Oksanen et al., 2018), *FD* (Laliberté et al., 2015), *lme4* (Bates et al., 2018), *DHARMA* (Hartig, 2018), *MuMIn* (Bartoň, 2018), *corrplot* (Wei et al., 2017), and *AICcmodavg* (Mazerolle, 2017).

First, species accumulation curves (SAC) for each country with respect to the vegetation management intensity were calculated, using 999 random permutations in the “*specaccum*” function in R package *vegan* (Gotelli and Colwell, 2001; Oksanen et al., 2018). SAC are not only used to estimate the number of species but are also an indicator of adequacy of the sampling as the accuracy of prediction improves as a SAC approaches a plateau (Thompson et al., 2003). Due to the use of different cover crop types and varying site characteristics vineyards cannot be described as a single vegetation/habitat type. Thus, additionally SACs were calculated for each vineyard separately.

Besides the vascular species richness per subplot, the Shannon diversity index (H) was calculated using R package *vegan* (Oksanen et al., 2018).

We selected Rao’s quadratic entropy FDQ (Rao, 1982; Champely and Chessel, 2002) as functional divergence index (calculation with the R package “*FD*” developed by Laliberté et al., 2015). This index calculates the pairwise abundance-weighted variance between all species and it can operate with a mixed set of categorical and continuous variables (Lepš et al., 2006). FDQ was calculated on species level on basis of the continuous and categorical traits.

Prior to analysis, data exploration (collinearity, outlier detection, and dispersion of response variables) was executed following Zuur et al. (2010). Data analysis was conducted in two steps: First, the importance of landscape and management parameters on species richness, functional diversity and species traits (Table 3) were assessed by conditional Random Forests (R package “*party*”, Hothorn et al., 2006; Strobl et al., 2009). For each response variable a Random Forest with 1000 trees was grown and the number of randomly chosen predictor at each tree’s node accounted for the square root of total predictors ($m_{\text{try}} = 3$; Puech

et al., 2014).

In the second step, generalized linear mixed models (GLMM) were constructed including random effects due to the nested sampling design of plots within vineyards and vineyards nested within landscape circles. For discrete count data (e. g. species richness) the Poisson and for continuous response variables the Gaussian error structure was selected. For modelling response variables with proportion data like vegetation cover and other relative coverage rates (annuals, perennials, Grime-strategists etc.) GLMM with beta distribution were chosen (R package “*glmmTMB*”, Magnusson et al., 2018), as those variables are typically asymmetric, and thus Gaussian-based approximation for testing can be quite inaccurate, usually leading to huge overdispersion (Cribari-Neto and Zeileis, 2010). As collinearity of explanatory variables can lead to wrong parameter estimation, predictors with $\text{cor} \geq 0.5$ were excluded from analysis in the same model. In this case, variables with higher single explanatory power were chosen for calculating the models. Additionally, the variance inflation factor (VIF), as measure of independency of predictors was calculated using R package “*car*” (Fox et al., 2018). Variables were removed from analysis in the same GLMM when $\text{VIF} > 5$ indicating high collinearity between predictor variables (Zuur et al., 2010). Models were selected by comparing the second order Akaike Information Criterion value (AICcvalue) corrected for small sample sizes. To identify the most parsimonious model based on the lowest AICc value we computed the AIC differences (ΔAICc) between the different candidate models (Posada and Buckley, 2004). As a rough rule Burnham and Anderson (2002) proposed that models for which $\Delta\text{AICc} \geq 2$ receive substantial support as the chance of the smaller AICc value being correct lies at approx. 73%. In order to account for the different vegetation management intensity levels in the case study region, the fixed factor “country” was always included in the model selection process.

For analysing the most important traits characterising community structure and to detect possible relations between vegetation management intensity, landscape parameters and plant communities a non-metric multidimensional scaling (NMDS) was computed with the R package “*vegan*” (Oksanen et al., 2018). Contrary to other ordination techniques that rely on Euclidean distances, i.e. Principal Coordinates Analysis, NMDS uses rank orders on basis of a Bray-Curtis dissimilarity calculation, which is invariant to changes in units and therefore can accommodate a variety of different kinds of data (Paliy and Shankar, 2016). Due to two extreme outliers two plots from vineyard no. 14 in Spain were removed from NMDS analysis.

Table 3

Overview of dependent and explanatory variables and variable type which were used for GLMM selection and random forest creation.

Dependent variables	Variable type
Species richness	Discrete
Shannon diversity index	Continuous
Vegetation cover	Continuous proportion (0-100)
Categorical plant traits (life span, storage organ, pollination mode, Grime strategy type)	Continuous proportion of relative coverage of respective plant trait (for levels see Table 2)
Continuous plant traits (leaf area, SLA, LDMC, plant height)	Continuous (community weighted means – CWM; for more information see Table 2)
Rao’s quadratic entropy	Continuous
Explanatory variables	Variable type
Vegetation management intensity	Categorical (bare soil, temporary vegetation cover, permanent vegetation cover)
Country	Categorical (Austria, France, Romania, Spain)
Covercrop presence	Binomial (yes / no)
Covercrop type	Categorical (grass, mixture, non)
Proportion of semi-natural elements	Continuous proportion (0-100)
Landscape Diversity	Continuous
Proportion of vineyards	Continuous proportion (0-100)
Distance to semi-natural elements	Continuous

4. Results

4.1. Vegetation cover

Vegetation cover was highest in vineyards with permanent vegetation being 66.3% higher than in bare soil vineyards (see also Fig. 2). Cover crops (grasses + mixtures) were most frequently seeded (80%) in vineyards with temporary vegetation cover. Seed mixtures accounted for the highest mean vegetation cover of $79.4 \pm 13.7\%$ compared to non-seeded vineyards ($58.8 \pm 33.6\%$) and vineyards with grasses as cover crops ($67.4 \pm 25.0\%$). Furthermore, there were big differences between countries: Spanish vineyards showed the overall lowest mean vegetation cover ($38.0 \pm 29.1\%$) which could not be only linked to the high vegetation management intensity but also to the average annual temperature which was highest in Spain ($18.0 \pm 0.3^\circ\text{C}$). The lowest average annual temperature of $10.8 \pm 0.3^\circ\text{C}$ was observed in Romania. However, Austrian vineyards accounted for the highest mean vegetation cover of $80.3 \pm 12.5\%$ (average annual temperature: $11.7 \pm 0.2^\circ\text{C}$). Across all vineyards, the lowest vegetation cover ($4.8 \pm 3.7\%$) was observed in the herbicide treated vineyards in France, the highest mean coverage rate was observed in Romanian and Austrian vineyards with permanent vegetation cover ($84.5\% \pm 7.1\%$).

4.2. Species richness

All species accumulation curves (SAC) calculated for each country with respect to the vegetation management intensity plateaued and

revealed a direct impact of the vegetation management intensity on the number of species in the vineyards. Furthermore, the SACs calculated for each single vineyard showed a plateau effect of sampling between 3 and 4 plots indicating accuracy of the sampling (Fig. S1 and S2 in the supplementary material).

In total, 220 different plant species comprising 37 plant families were recorded in the vineyard inter-rows across all countries. The most frequent plant family was the Asteraceae family with 43 recorded species followed by the Poaceae family (34 species) which accounted for the overall mean highest coverage of $11\% \pm 2.2$ across all sampled vineyards.

The highest species richness of 108 vascular plant species was found in Romanian vineyards (mean \pm SD: 14.8 ± 4.1), followed by Austria (102 species; 14.0 ± 4.1), France (75 species, 11.6 ± 4.2), and Spain (47 species, 6.6 ± 4.3). Random forests (RF; Table S1 in the supplementary material) revealed that the factor vegetation management intensity had the strongest impact on the species richness (random permutation test; $P = 0.002$). This was confirmed by GLMMs (see Table 4) which further showed that species richness in the vineyards was best explained by the management factors (intensity and the type of cover crop) as well as by interactions between landscape diversity and country (see Fig. 3).

No notable differences in species richness were detected between vineyards with temporary or permanent vegetation cover but bare soil vineyards showed 38.8% fewer species (mean: 8.8 ± 5.5) than permanently vegetated vineyards (mean: 14.4 ± 4.4), irrespective if bare soil conditions were created by herbicide application or tillage (Fig. S3

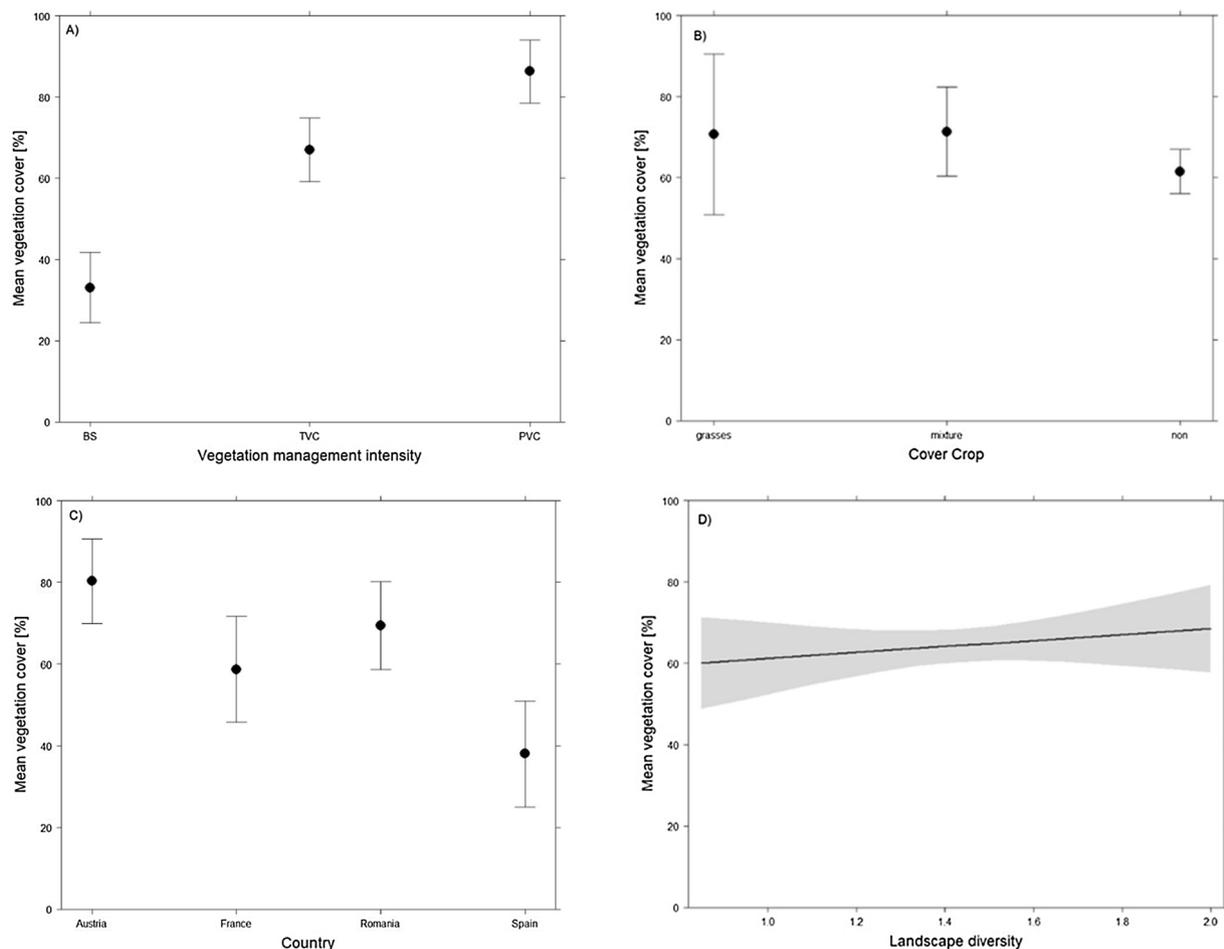


Fig. 2. Effect plots of the most parsimonious GLMM displaying mean vegetation cover in vineyard inter-rows in four different countries in response to (A) vegetation management intensity (BS = bare soil, TVC = temporary vegetation cover and PVC = permanent vegetation cover), (B) cover crop type, (C) countries and (D) Shannon landscape diversity index. Error bars/grey shading: 0.95 confidence intervals.

Table 4

Summary of AICc values used for model selection of dependent variables; number of estimated explanatory parameters and parameter combinations = 41 (AICc = Second order Akaike Information Criterion, $\Delta AICc$ = difference between AICc to the next most parsimonious model, R^2_m = marginal R², R^2_c = conditional R²).

Diversity indices	Best model	AICc	$\Delta AICc$	R^2_m	R^2_c
Species richness	Null model: vineyard/circle	1,673.0	–	0.44	0.84
	country * landscape diversity + vegetation management intensity + cover crop type	1,603.2	0.00		
	vegetation management intensity * country + cover crop type	1,605.6	2.4		
Shannon diversity index (H)	Null model: vineyard/circle	296.1	–	0.37	0.77
	country + vegetation management intensity	273.0	0.0		
	country + cover crop type	275.0	2.0		
Rao's quadratic entropy (RaoQ)	Null model: vineyard/circle	–1,677.2	–	0.00	0.71
	Cover crop type	–1,671.0	6.24		
Continuous plant traits					
CWM of specific leaf area (SLA)	Null model: vineyard/circle	2,180.9	–	0.25	0.58
	country * landscape diversity + vegetation management intensity + cover crop type	2,121.2	0.0		
	country * landscape diversity + cover crop type	2,123.2	2.1		
CWM of leaf dry matter content (LDMC)	Null model: vineyard/circle	–1,425.0	–	0.49	0.79
	vegetation management intensity + country	–1,446.0	0.0		
	vegetation management intensity	–1,438.6	7.4		
CWM of plant height	Null model: vineyard/circle	2,461.8	–	0.37	0.72
	country * cover crop type + vegetation management intensity + landscape diversity	2,371.5	0.0		
	country * landscape diversity + management system + cover crop type	2,375.3	3.8		
Categorical plant traits					
Relative coverage of annuals	Null model: vineyard/circle	0.05	–	0.50	0.85
	vegetation management intensity * country	–30.6	0.0		
	vegetation management intensity + country	–27.7	2.9		
Relative coverage of perennials	Null model: vineyard/circle	–102.6	–	0.50	0.85
	vegetation management intensity + country	–141.2	0.0		
	vegetation management intensity * country	–136.3	4.9		
Relative coverage of r-strategists	Null model: vineyard/circle	–163.2	–	0.47	0.77
	management intensity + cover crop presence	–213.9	0.0		
	vegetation management intensity + cover crop type	–209.0	4.9		
Relative coverage of c-strategists	Null model: vineyard/circle	–149.7	–	0.47	0.74
	vegetation management intensity + country	–191.2	0.0		
	vegetation management intensity * country	–186.7	4.5		
Relative coverage of csr-strategists	Null model: vineyard/circle	–288.3	–	0.23	0.75
	country	–294.8	0.0	0.29	0.74
	vegetation management intensity + country	–293.0	1.8		
Relative coverage of plants with belowground storage organs	Null model: vineyard/circle	–186.3	–	0.49	0.87
	vegetation management intensity + country	–222.4	0.0		
	vegetation management intensity	–215.7	6.7		
Relative coverage plants with seeds as storage organs	Null model: vineyard/circle	–226.1	–	0.57	0.91
	vegetation management intensity * country	–264.4	0.0		
	vegetation management intensity + country	–262.5	1.9		
Relative coverage of selfing plants	Null model: vineyard/circle	–121.7	–	0.47	0.78
	vegetation management intensity + cover crop type	–158.8	0.0		
	vegetation management intensity * cover crop type	–157.0	1.8		
Relative coverage of wind pollinated plants	Null model: vineyard/circle	–127.0	–	0.32	0.76
	vegetation management intensity + cover crop type	–144.0	0.0		
	vegetation management intensity	–142.1	2.3		
Mean vegetation cover					
Mean vegetation cover	Null model: vineyard/circle	2,573.8	–	0.67	0.93
	vegetation management intensity * country + cover crop type + landscape diversity	2,429.4	0.00		
	vegetation management intensity * country + cover crop type	2,433.6	4.22		

in supplementary material). Overall, tilled vineyards showed a mean number of 11.2 (\pm 5.5) species. In the herbicide treated bare soil vineyards the average species richness was only 6.6 (\pm 2.9). The most abundant species in these vineyards was *Poa annua* with a 91.2% higher mean coverage than in all other vineyards, followed by *Taraxacum officinale* agg. (+ 50.6%) and *Convolvulus arvensis* (+ 8.9%).

Nevertheless, the lowest species richness (mean: 4.2 \pm 4.1) was found in vineyards with grasses as cover crops which were dominated by *Hordeum vulgare* and *Festuca rubra* agg. Contrary, the establishment of cover crop mixtures (mean: 13.6 \pm 4.2) as well as spontaneous vegetation cover (mean: 12.3 \pm 5.5) lead to an increase in species richness (see Fig. 3).

These results were also depicted in Shannon diversity index (see Fig. S3B) which was lowest in herbicide treated bare soil vineyards (mean: 1.0 \pm 0.4) and highest in vineyards with permanent vegetation cover

(mean: 1.8 \pm 0.4) which was similar to vineyards with temporary vegetation cover (mean: 1.7 \pm 0.5).

4.3. Functional traits and community structure

The NMDS (see Fig. 4) analysis revealed differences in the species assemblages along the management gradient, indicating that bare soil management through intensive tillage promoted therophytes typical for ruderal habitats like *Stellaria media* and *Brassica nigra* as well as weedy species like *Echinochloa crus-galli*, whereas bare soil management through herbicide application favoured the establishment of disturbance-tolerant grasses like *Poa annua* as well as weeds with belowground storage organs like *Elymus repens*, *Convolvulus arvensis* or *Taraxacum officinale* agg (see Fig. S8 in the supplementary material). Contrary, vineyards with permanent vegetation cover were

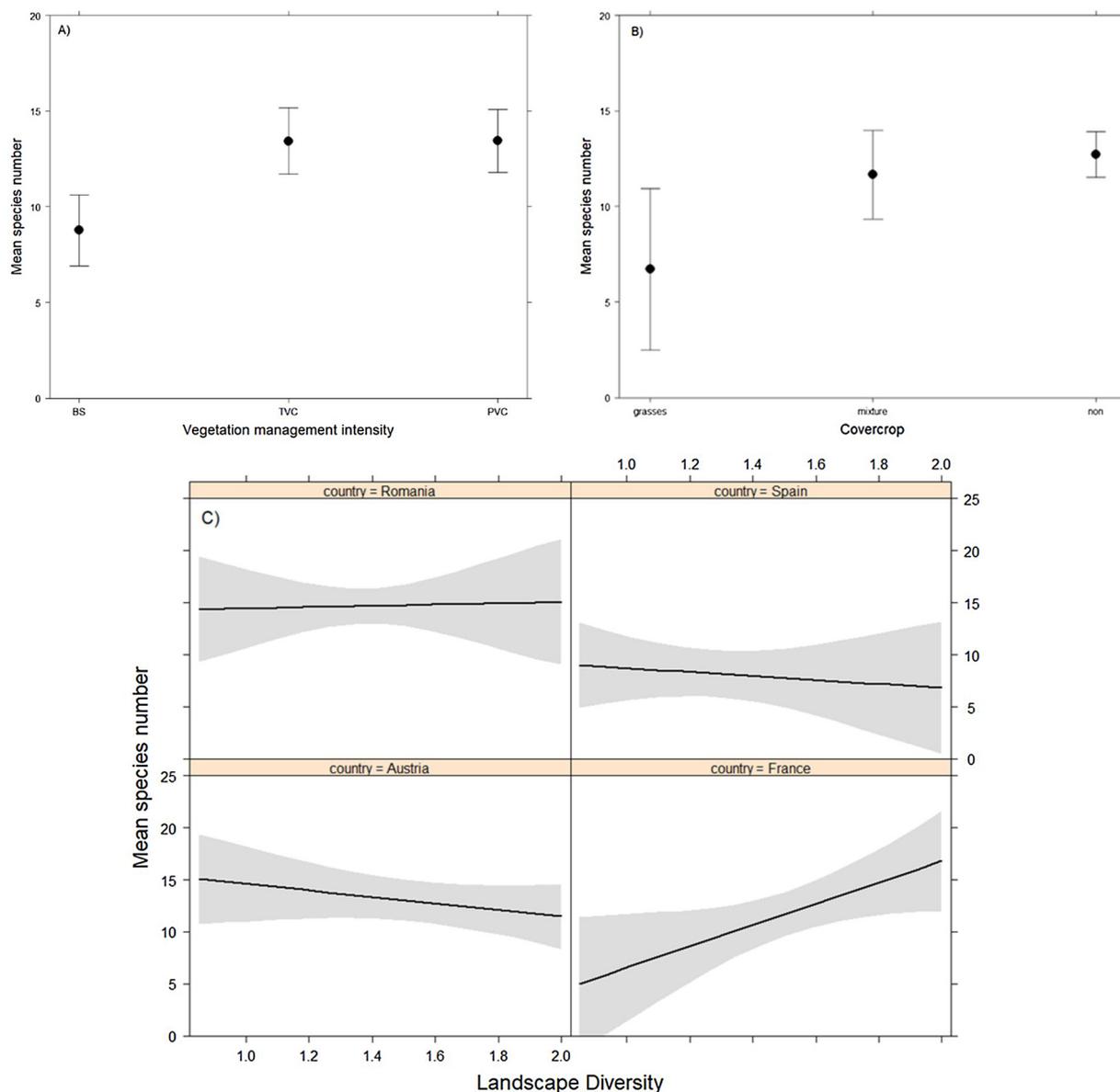


Fig. 3. Effect plots of the most parsimonious GLMM displaying plant species richness in vineyard inter-rows in four different countries in response to (A) vegetation management intensity (BS = bare soil, TVC = temporary vegetation cover and PVC = permanent vegetation cover), (B) cover crop type and (C) interactions between countries and Shannon landscape diversity index. Error bars/grey shading: 0.95 confidence intervals.

characterised by typical perennial grassland species like *Holcus lanatus* and *Lolium perenne* which clearly increased with lower management intensities (97.8% higher coverage rate in vineyards under permanent vegetation compared to bare soil management). Thus, as confirmed by RF, specific plant traits and even life strategies of plants could be clearly associated with the vegetation management intensity. A higher disturbance frequency resulted in a higher specific leaf area (SLA) and lower leaf dry matter content (LDMC).

Categorical traits, particularly Grime life strategy, storage traits as well as pollination strategies in plant communities were also influenced by the vegetation management intensity according to NMDS, RF, and GLMM (Table 4, Figs. 5–7). Across all vineyards, c- and csr-strategist were most abundant in vineyards with permanent vegetation cover, whereas r-strategists showed a 85.6% higher relative coverage in bare soil vineyards, compared to vineyards with lower disturbance frequency (see Figs. 5–7). This association could be confirmed by the GLMM which revealed that the relative coverage of r-strategists was best explained by the factors vegetation management intensity and the use of cover crops: In vineyards with spontaneous vegetation cover the

share of ruderal species was 65.6% higher than in vineyards cultivated with grasses as cover crops and 53.1% higher than in vineyards with cover crop mixtures.

Annual species were clearly more abundant in bare soil vineyards (mean relative cover of $83.7 \pm 44.7\%$) than in vineyards with permanent vegetation cover ($25.1 \pm 22.6\%$). Particularly, in bare soil inter-rows with high tillage frequencies the share of annual species was 20.8% higher than in herbicide treated bare soil vineyards and 67.7% higher than in vineyards with permanent vegetation cover (Fig. S4 in supplementary material).

Permanent vegetation cover resulted in the highest relative coverage of perennial species (75.8 ± 25.0). On country level, vineyards in Spain accounted for the highest mean cover of 85.8% of annual species, whereas Austrian vineyards showed the exact opposite with a comparably low coverage of 26.4% of annual species. Similarly, Spanish vineyards were dominated by plants without storage organs which propagated exclusively by seeds (relative coverage of 84.3 ± 25.4), whereas Austrian vineyards were dominated by plant species with belowground storage organs.

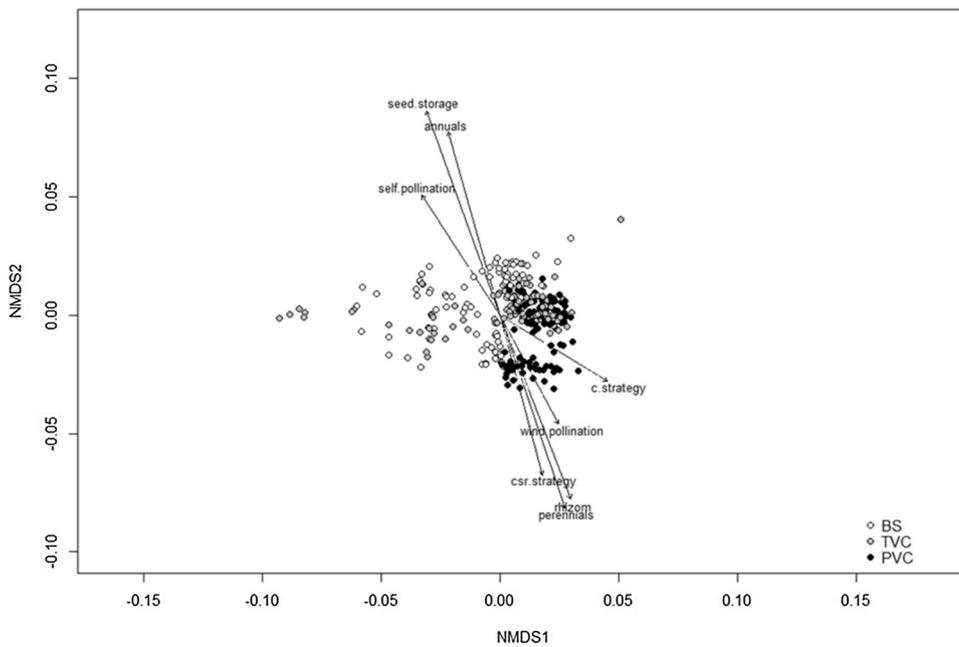


Fig. 4. Non-metric multi-dimensional scaling (NMDS) ordination of plant community composition displaying the plots with their associated management intensity (white: BS = bare soil, grey: TVC = temporary vegetation cover and black: PVC = permanent vegetation cover). The vectors show the significant functional traits associated with the community composition.

There was a 62.6% higher share of predominantly self-pollinating and cleistogamous plants like *Bromus sterilis*, *Hordeum murinum*, or *Poa annua* in vineyards under bare soil management, particularly under herbicide treatment. Herbicide treated vineyards accounted for 55.6% more self-pollinators than tilled vineyards and 73.6% more than vineyards with permanent vegetation cover. Vineyards with permanent vegetation cover promoted wind-pollinated species like *Lolium perenne* or *Dactylis glomerata*. In addition, GLMM revealed a strong impact of the seeded cover crop type: In vineyards that were seeded with grasses the share of self-pollinating species was 52.5% higher than in vineyards seeded with cover crop mixtures which showed a 48.1% higher share of wind-pollinated species.

As a consequence of the above mentioned results, RF showed that functional divergence measured by Rao's quadratic entropy (RaoQ) was also best described by the factor vegetation management intensity (random permutation value; $P = 0.002$) followed by the factors country and distance to SNE. Plant communities in frequently disturbed vineyards showed a 21.6% reduced functional divergence than vineyards with permanent vegetation cover. This indicates a reduced dissimilarity among functional characteristics of the species in bare soil

vineyards which can be associated with lower stability of these plant communities.

5. Discussion

Plant functional diversity, functional traits, species richness and community composition primarily responded to inter-row vegetation management, i.e. tillage, herbicide use and the sowing of cover crops or the maintenance of spontaneous vegetation. These results conform to other studies which investigated different management effects in vineyards within single wine growing regions across the world (Gago et al., 2007; Baumgartner et al., 2008; Bagella et al., 2014; Kazakou et al., 2016; Steenwerth et al., 2016).

5.1. Vegetation cover

Vegetation cover increased with decreasing vegetation management intensity and the use of cover crop mixtures (see Fig. 2). These findings confirm the results from Kazakou et al. (2016), who found the highest above-ground biomass in vineyards with cover crops followed by

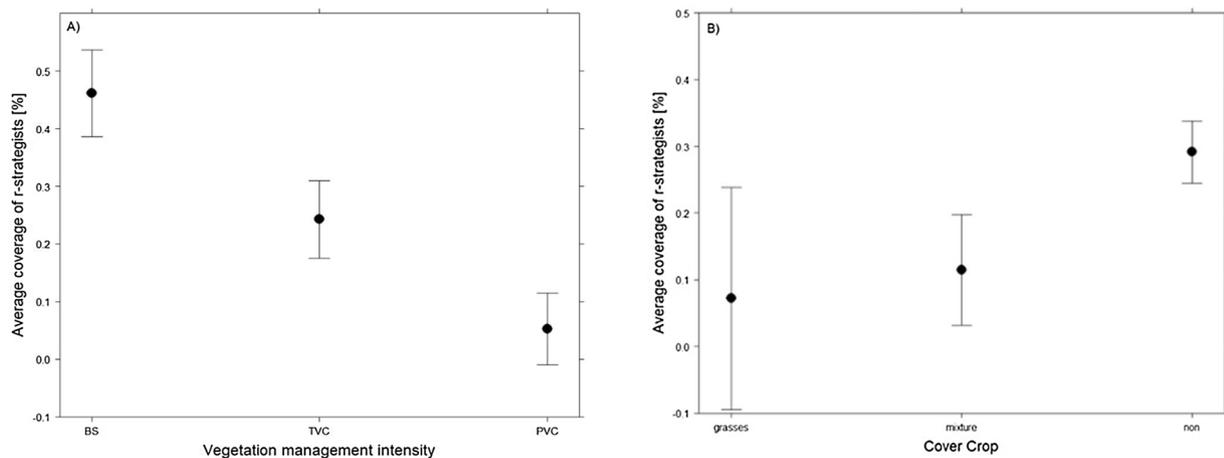


Fig. 5. Effect plots of the most parsimonious GLMM displaying relative coverage of r-strategists in vineyard inter-rows in four different countries in response to (A) vegetation management intensity (BS = bare soil, TVC = temporary vegetation cover and PVC = permanent vegetation cover) and (B) cover crop type. Error bars: 0.95 confidence intervals.

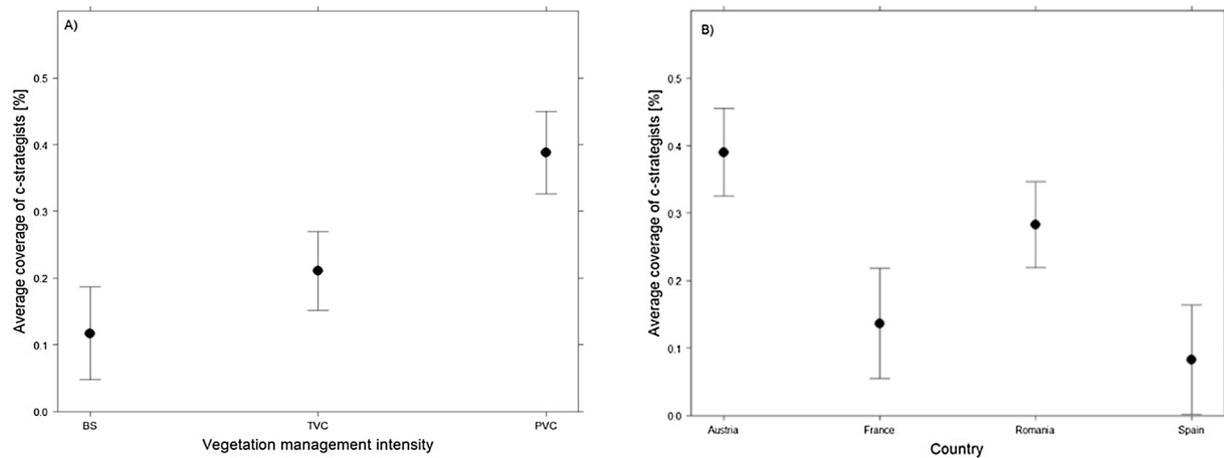


Fig. 6. Effect plots of the most parsimonious GLMM displaying relative coverage of c-strategists in vineyard inter-rows in four different countries in response to (A) vegetation management intensity (BS = bare soil, TVC = temporary vegetation cover and PVC = permanent vegetation cover) and (B) country. Error bars: 0.95 confidence intervals.

vineyards with spontaneous vegetation cover. Even though there is a large environmental gradient across the four countries, the average annual temperature and the total annual precipitation could not explain the effect of the different countries in the best GLMMs. The highest average annual temperature was observed in Spanish vineyards which also showed the lowest mean vegetation cover. However, these vineyards were also subject to the highest vegetation management intensity. In all other countries average annual temperature and total precipitation were similar, whereas big differences in the mean vegetation cover were observed that could be related to the vegetation management intensity in these countries. A recent meta-analysis also showed that climate zone and irrigation were not the main factors limiting the beneficial effects of extensive vegetation management for biodiversity and ecosystem service provision (Winter et al., 2018). However, actual rainfall distribution and temperature during the growing season are important factors influencing grape yield and must quality, especially if deficit irrigation cannot be applied in dry climates (Ruiz-Colmenero et al., 2011).

5.2. Management and landscape effects on plant species richness

Across all countries, the vegetation management intensity was the most important variable influencing species richness. Vineyards with bare soil inter-rows showed the lowest number of species (see Fig. 3),

particularly those under herbicide treatment (see Fig. S3 and Sanguaneko and León, 2011). Species richness of vineyards with temporary vegetation cover did not differ significantly from those with permanent vegetation cover. Moderate rates of soil disturbance disrupt competitive hierarchies by increasing mortality rates of rosulate and reptant perennials which benefit from frequent mowing (Nascimbene et al., 2013) and by offering open space for the recruitment of less competitive species (Gago et al., 2007; “intermediate disturbance hypothesis”, Grime, 1973; Connell, 1978).

Besides the vegetation management intensity, another variable affecting species diversity in vineyards was the presence and the type of cover crops (see Fig. 3), particularly in vineyards with temporary (61% seeded) or permanent (18% seeded) vegetation cover. The overall lowest species richness was recorded in vineyards with grasses as cover crops in comparison to vineyards with cover crop mixtures or spontaneous vegetation cover (cf. Baumgartner et al., 2008). Cover crops are used to improve ecosystem service provision, however, in most cases the diversity of the cover crop mixture is very low and therefore the use of cover crops might rather hinder the establishment of “weeds” from the soil seed bank than increase plant biodiversity (Baumgartner et al., 2008; Sanguaneko and León, 2011; Steenwerth et al., 2016). The present study confirmed that vineyards with spontaneous vegetation cover exhibited higher species richness than high biomass cover crops (Gago et al., 2007; Smith et al., 2015; Kazakou et al., 2016) which was even

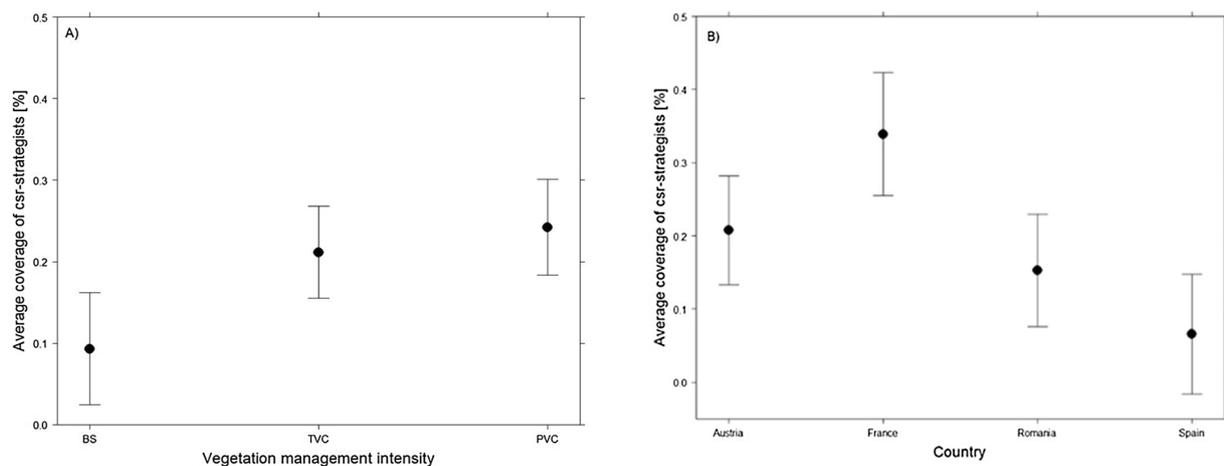


Fig. 7. Effect plots of the most parsimonious GLMM displaying relative coverage of csr-strategists in vineyard inter-rows in four different countries in response to (A) vegetation management intensity (BS = bare soil, TVC = temporary vegetation cover and PVC = permanent vegetation cover) and (B) country. Error bars: 0.95 confidence intervals.

lower than those of the herbicide treated vineyards. In an Italian study, the use of herbicides in conventional vineyards was identified as the main factor reducing species richness in conventional vineyards (Nascimbene et al., 2013). These findings go in accordance with other studies (Scursoni et al., 2006; Owen, 2008; Vencill et al., 2012) indicating that herbicides with the same mode of action exert a high selection pressure on plant populations and communities that can lead to a shift to herbicide-tolerant, often noxious weed communities. However, herbicides can also disrupt competitive community structures, thereby creating open space where other species can establish (Wilmanns, 1993).

In comparison to vineyard management, landscape diversity or proportion of semi-natural elements were less important parameters in the statistical models explaining species diversity. In contrast, Nascimbene et al. (2016) showed that the location of vineyards in landscapes with a high proportion of semi-natural habitats (> 40%) significantly increased plant species richness in comparison to crop landscapes with less than 30% semi-natural habitats. Mania et al. (2015) also found a significant increase of plant species richness of vineyards in response to adjacent semi-natural habitat size and type. In the current study, the landscape circles containing the lowest of proportion of SNE (9% on average) were located in Spain. Considering the plant species richness in the different wine growing regions across Europe, Spanish vineyards were also the least diverse in contrast to the Romanian and Austrian. This could be attributed to the lowest overall landscape diversity, the highest vegetation management intensity and the lowest vegetation cover which both could be linked to the extreme summer temperature. Despite a share of 44% of SNE in the landscape circles in France, the species richness in these vineyards was only slightly higher than those in the Spanish vineyards, implicating only a small effect of SNE on the species diversity in vineyards.

5.3. Filtering function of management on functional plant traits and community composition

Results indicated that an increase in vegetation management intensity led to a significant change in plant community structure (see Fig. 4) and thus, to a shift in plant traits. Tillage in bare soil inter-rows led to an increased cover of typical annual species which can germinate and establish throughout the vegetation period (no pronounced seasonality) like *Stellaria media* (Wilmanns, 1993) as well as troublesome weeds like *Echinochloa crus-galli*. These species were favoured by tillage which creates suitable sites for seed germination and contributes to the spread of near-surface roots and rhizome propagules by mechanical disturbance (Boström and Fogelfors, 1999; Gago et al., 2007; Koning et al., 2019). In contrast, herbicide treatment (mainly by glyphosate) promoted common perennial species like *Taraxacum officinale* agg. (Gago et al., 2007), *Convolvulus arvensis* or *Elymus repens* (DeGennaro and Weller, 1984; Monteiro et al., 2012) which have belowground storage organs from which they can resprout after herbicide treatment (DeFelice and Kendig, 1993).

The most abundant plant families were Asteraceae and Poaceae, which accords with an Italian (Mania et al., 2015) and a Portuguese study (Monteiro et al., 2012). Differences in the species assemblages along the management gradient indicated that high management intensities promoted therophytes which are typical for ruderal habitats, whereas vineyards with low soil disturbance frequencies were characterised by hemicryptophytes and phanerophytes requiring less disturbed habitats (Lososová et al., 2003; Kahmen and Poschlod, 2008; Monteiro et al., 2012). Typical or characteristic plant species of vineyards like vegetatively propagating geophytes also benefit from moderate soil tillage or rare herbicide treatments (Wilmanns, 1993). Plant strategy types and their associated traits according to Grime (1977) are also clearly related to the vegetation management intensity with a higher share of csr-strategists with decreasing intensity (see Fig. 7). Csr-strategists usually have intermediate growth rates, are more tolerant to

cutting through morphological adaption like rosette formation or short growth, and have biennial to perennial life spans (Grime, 1979).

Pollination traits, storage mechanisms and life span characteristics, all properties which can be associated to the strategy types, showed the strongest response to the management regime (see Table 4 and Fig. S4-S6 in supplementary material). Vineyards with high disturbance frequency were dominated by annual species which mainly invested their resources in seed production. Moreover, these species are more likely to be self-pollinators, particularly at highly disturbed sites where pollinators or other individuals of the same species are scarce (Barrett, 2010). On the other hand, lower disturbance frequencies promoted the establishment of perennial species with storage roots or rhizomes which were mostly wind pollinated species. This linkage of storage and pollination traits to life span and strategy type was also confirmed by studies based on continuous functional traits (SLA, LDMC and plant height) showing that plant life span, storage forms and type of pollination are closely linked to morphological properties (Grime, 1973; Vandewalle et al., 2014; Koning et al., 2019). This is also true for the present study, revealing that most continuous traits related to plant growth performance (LDMC, SLA and plant height) could be linked to the management regime. SLA was highest in bare soil vineyards, indicating higher photosynthetic capacity, higher growth rates and generally faster turnover of plant parts which permits flexible response to disturbance (Westoby et al., 2002; Pfestorf et al., 2013; Májeková et al., 2014; Kazakou et al., 2016), a characteristic feature of ruderal species (Grime et al., 1988).

The interpretation of LDMC is similar, though inverse than for SLA. High LDMC (and thus low-SLA) species tend to achieve longer average leaf life spans which require extra structural strength causing lower growth rates - typical traits of perennial species (Westoby et al., 2002; Louault et al., 2005). Therefore, results showed that LDMC decreased with increasing disturbance frequency which was due to the reduced abundance of perennial species in the intensively managed vineyard inter-rows. In contrast to other studies (Louault et al., 2005; Pfestorf et al., 2013; Vandewalle et al., 2014), vegetation management intensity only had a minor influence on the community weighted means of plant height, which has direct implications for the competitive situation within a community.

Summarizing all these results in the functional divergence index (RaoQ) revealed that the vegetation management intensity was the most important variable influencing functional diversity. With increasing vegetation management intensity reduced dissimilarity among species was detected, indicating the dominance of a few species. Kazakou et al. (2016) also found that intensive tillage decreased whereas spontaneous vegetation cover increased functional richness, indicating a high degree of niche differentiation and low resource competition in vineyards. There is considerable evidence for the existence of positive correlations between the taxonomic diversity of plant communities and community stability which is one of the most important factors for providing essential ecosystem services (Tilman, 1999; Báez and Collins, 2008; Tilman et al., 2014). Plant communities comprising of species with dissimilar traits (or asynchronous traits according to Hector et al., 2010) react differently to environmental drivers and, thus are more resilient. This indicates that these asynchronous communities can buffer or withstand for example disturbances with less changes in structure and processes than more synchronous communities do (Morecroft et al., 2016). In the present study, the highest diversity levels were found in vineyard-inter-rows with low disturbance frequencies. A good predictor for the dissimilarity of traits in these vineyards was the larger abundance of csr-strategists as functional diversity is assumably closer related to ecosystem stability or resilience than species richness (Morecroft et al., 2016).

5.4. Implications for ecosystem services in relation to plant-soil interactions

Our results showed that extensive vegetation management

increased vegetation cover in vineyard inter-rows. High vegetation cover increases erosion mitigation, carbon sequestration (Ruiz-Colmenero et al., 2013; Biddoccu et al., 2016; Guzmán et al., 2019), wild bee diversity, abundance and related pollination services (Kratschmer et al., 2018), and the aesthetic appreciation of vineyards (Hervé et al., 2018). Vineyards with high above-ground biomass production also showed the largest benefits for soil-related ecosystem service provision (Guzmán et al., 2019).

Cover crops in vineyards are used as ecological management tool to improve soil structure, mitigate soil erosion, control weeds, increase soil fertility and pest control, enhance biodiversity and to regulate excessive vine growth and grape vigor, thus improving grape quality (Baumgartner et al., 2008; Giese et al., 2014; Muscas et al., 2017; Garcia et al., 2018). However, there is a trade-off between the provision of those ecosystem services and conservation goals, particularly when species-poor grass mixtures are used as cover crops that have the competitive strength to outcompete and/or suppress the establishment of therophytes (Lososová et al., 2003; Monteiro et al., 2008, 2012). Ecosystem disservices like a high proportion of noxious weeds were not associated with low or medium intensity disturbance.

Vegetation cover, biomass and plant diversity are important drivers of below-ground ecosystem processes by influencing the faunal, microbial biomass and soil organic matter dynamics (Buchholz et al., 2017). Vegetation in vineyards also provides food and structure for many arthropod taxa (Altieri et al., 2005) which influences pest control by providing habitats for natural enemies of vine pests (Nicholls et al., 2000; Danne et al., 2010).

5.5. Implications for sustainable vineyard and landscape management

Intensive vegetation management resulting in bare soil significantly reduced species and functional diversity in comparison to temporary or permanent vegetation management (cf. Winter et al., 2018). Furthermore, the intensive use of herbicides and high tillage frequency in vineyard inter-rows resulted in the lowest overall vegetation cover and species diversity, whereas infrequent tillage did not significantly decrease species diversity in comparison to permanent vegetation cover. In addition, specialist ruderal species which are adapted to infrequent soil tillage are threatened throughout Europe (Richner et al., 2015) and might therefore be promoted by temporary vegetation cover management. Consequently, sustainable vineyard management clearly benefits from low intensity disturbance which increases vegetation cover and biodiversity.

The positive effect of semi-natural elements and landscape diversity for sustainable viticulture was not clearly demonstrated in the current study; nevertheless, other studies showed a strong positive effect of nearby semi-natural elements on vineyard biodiversity (Mania et al., 2015; Nascimbene et al., 2016). This discrepancy could be related to the type of the semi-natural elements, as grass dominated habitat types showed a significantly lower species richness in comparison to large woodlots (Mania et al., 2015) or species-rich dry grasslands (Nascimbene et al., 2016). For the involved European case study region, the land sharing approach (cf. Green et al., 2005) seems to be more effective for maintaining biodiversity in vineyards. This could be related to the types of the semi-natural elements nearby which could in general not be classified as species-rich habitat types.

6. Conclusion

In the sense of ecological intensification (Bommarco et al., 2013), vegetation cover contributes to agricultural productivity and ecosystem service provision. However, vegetation cover in inter-rows needs to be carefully designed to reduce possible trade-offs between biodiversity and ecosystem service provision, as some studies revealed negative effects of seeded cover crops on biodiversity in comparison to the spontaneous vegetation originating from the soil seed bank or adjacent

habitat types. Consequently, agri-environmental policies within the Common Agricultural Policy of the European Union need to be transformed, as some countries like Austria oblige wine growers to seed cover crop mixtures in order to receive agri-environmental compensation payments for reducing erosion, increasing soil fertility and carbon sequestration (BMLFUW, 2016). Policies encouraging farmers not to use herbicides would also contribute to increasing biodiversity and related ecosystem service provision. Nevertheless, cover crop management (frequency and timing of tillage or mulching and the choice of cover crops) needs to be adapted to local edaphoclimatic conditions to mitigate the competition for soil water to balance wine production with regulating ecosystem services and biodiversity provision.

Acknowledgements

This study was funded by the European BiodivERsA project VineDivers (www.vinedivers.eu) through the BiodivERsA/FACCE JPI (2013-2014 joint call) for research proposals, with the national funders: Austrian Science Fund (grant number I 2044-B25 FWF), French National Research Agency (ANR), Spanish Ministry of Economy and Competitiveness (MINECO), Romanian Executive Agency for Higher Education, Research, Development and Innovation Funding (UEFISCDI) and Federal Ministry of Education and Research (BMBF/Germany). We would like to thank all winegrowers who provided information regarding vineyard management and provided access to their vineyards as study sites. The study has been supported by the TRY initiative on plant traits (<http://www.try-db.org>). The TRY initiative and database is hosted, developed and maintained by J. Kattge and G. Bönisch (Max Planck Institute for Biogeochemistry, Jena, Germany). TRY is currently supported by DIVERSITAS/Future Earth and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agry.2019.102706>.

References

- Altieri, M.A., Ponti, L., Nichols, C.I., 2005. Manipulating vineyard biodiversity for improved insect pest management: case studies from northern California. *Int. J. Biodivers. Sci. Manage.* 1, 1–13. <https://doi.org/10.1080/17451590509618092>.
- Báez, S., Collins, S.L., 2008. Shrub invasion decreases diversity and alters community stability in Northern Chihuahuan Desert Plant Communities. *PlosOne* 3 (6), e2332. <https://doi.org/10.1371/journal.pone.0002332>.
- Bagella, S., Filigheddu, R., Caria, M.C., Girlanda, M., Roggero, P.P., 2014. Contrasting land uses in Mediterranean agro-silvo-pastoral systems generated patchy diversity patterns of vascular plants and below-ground microorganisms. *CR Biol.* 337, 717–724. <https://doi.org/10.1016/j.crvi.2014.09.005>.
- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* 9 (10), 1146–1156.
- Barrett, S.C.H., 2010. Review: understanding plant reproductive diversity. *Philos. Trans. Biol. Sci.* 365, 99–109.
- Bartoň, K., 2018. MuMIn – Multi-Model Inference. R Package Version 1.42.1. Retrieved from: <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., 2018. lme4 - Linear Mixed-effects Models Using 'Eigen' and S4. R Package Version 1.1-17. Retrieved from: <http://lme4.r-forge.r-project.org/>.
- Baumgartner, K., Steenwerth, K.L., Veilleux, L., 2008. Cover-crop systems affect weed communities in a California vineyard. *Weed Sci.* 56, 596–605. <https://doi.org/10.1614/ws-07-181.1>.
- Biddoccu, M., Ferraris, S., Opsi, F., Cavallo, E., 2016. Long-term monitoring of soil management effects on runoff and soil erosion in sloping vineyards in Alto Monferrato (North-West Italy). *Soil Tillage Res.* 155, 176–189.
- BMLFUW (Federal Ministry for Agriculture, Forestry, Environment and Water Management), 2012. Bundesministerium Für Land- Und Forstwirtschaft, INVEKOS-GIS. Abteilung II/4, Direktzahlungen & INVEKOS. URL: <https://www.bmlfuw.gv.at/land/direktzahlungen/Invekos.html> (Accessed 29.09.2016).
- BMLFUW (Federal Ministry for Agriculture, Forestry, Environment and Water Management), 2016. ÖPUL 2015 – Das Agrar-Umweltprogramm Bis 2020.
- Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. *Trends Ecol. Evol.* 28 (4), 230–238.

- Booth, B.D., Swanton, C.J., 2002. Assembly theory applied to weed communities. *Weed Sci.* 50, 2–13.
- Boström, U., Fogelfors, H., 1999. Type and time of autumn tillage with and without herbicide at reduced rates in southern Sweden. 2. Weed flora and diversity. *Soil Tillage Res.* 50, 283–293.
- Buchholz, J., Querner, P., Paredes, D., Bauer, T., Strauss, P., Guernion, M., Scimia, J., Cluzeau, D., Burel, F., Kratschmer, S., Winter, S., Potthoff, M., Zaller, J.G., 2017. Soil biota in vineyards are more influenced by plants and soil quality than by tillage intensity or the surrounding landscape. *Sci. Rep.* 7, 17445.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Inference: A Practical Information-theoretic Approach 1st Edition*. Springer, New York.
- Castroviejo, S., Aedo, C., Cirujano, S., Laínz, M., Montserrat, P., Morales, R., Muñoz Garmendia, F., Navarro, C., Paiva, J., Soriano, C. (Eds.), 1993. *Flora iberica 3*. CSIC, Madrid, Real Jardín Botánico Retrieved from: http://www.floraiberica.es/PHP/generos_lista.php.
- Champely, S., Chessel, D., 2002. Measuring biological diversity using Euclidean metrics. *Environ. Ecol. Stat.* 9, 167–177.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- Cribari-Neto, F., Zeileis, A., 2010. Beta Regression in R. *J. Stat. Softw.* 34 (2).
- Danne, A., Thomson, L.J., Sharley, D.J., Penfold, C.M., Hoffmann, A.A., 2010. Effects of native grass cover crops on beneficial and pest invertebrates in Australian vineyards. *Environ. Entomol.* 39 (3), 970–978.
- DeFelice, M.S., Kendig, A., 1993. Control of Perennial Broadleaf Weeds in Missouri Field Crops. University of Missouri Extension, pp. 487.
- DeGennaro, F.P., Weller, S.C., 1984. Differential susceptibility of field bindweed (*Convolvulus arvensis*) biotypes to glyphosate. *Weed Sci.* 32, 472–476.
- Díaz, S., Cabido, M., 1997. Plant functional types and ecosystem function in relation to global change: a multiscale approach. *J. Veg. Sci.* 8, 463–474.
- Díaz, S., Marcelo, C., Casanoves, F., 1998. Plant functional traits and environmental filters at a regional scale. *J. Veg. Sci.* 9, 113–122.
- Díaz, S., Lavorel, S., Chapin, F.S., Tecco, P.A., Gurvich, D.E., Grigulis, K., 2007. Functional diversity – at the crossroads between ecosystem functioning and environmental filters. In: Canadell, J., Pataki, D.E., Pitelka, L.F. (Eds.), *Terrestrial Ecosystem in a Changing World*. Springer, Berlin, pp. 79–91.
- EEA (European Environment Agency), 2016. *EUNIS Habitat Type*. (Accessed 29 September 2017). <http://eunis.eea.europa.eu/habitats.jsp>.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1992. *Zeigerwerte Von Pflanzen in Mitteleuropa*. *Scripta Geobotanica* 18 (2).
- ESRI, R., 2013. *ArcGIS Desktop: Release 10*. Environmental Systems Research Institute, CA.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. *Science* 309, 570–574.
- Fox, J., Weisberg, S., Price, B., Adler, D., Douglas, B., Baud-Bovy, G., Bolker, B., Ellison, S., Firth, D., Friendly, M., Gorjanc, S., Heiberger, R., Laboissiere, R., Maechler, M., Monette, G., Murdoch, D., Nilsson, H., Ogle, D., Ripley, B., Venables, W., Walker, S., Winsemius, D., Zeileis, A., R-Core, 2018. *car – Companion to Applied Regression*. R Package Version 3.0-0. Retrieved from: <https://cran.r-project.org/web/packages/car/car.pdf>.
- Gago, P., Cabaleiro, C., Garcia, J., 2007. Preliminary study of the effect of soil management systems on the adventitious flora of a vineyard in northwestern Spain. *Crop. Prot.* 26 (4), 584–591.
- García, L., Celette, F., Gary, C., Ripoche, A., Valdés-Gómez, H., Metay, A., 2018. Management of service crops for the provision of ecosystem services in vineyards: a review. *Agric. Ecosyst. Environ.* 251, 158–170.
- Giese, G., Velasco-Cruz, C., Roberts, L., Heitman, J., Wolf, T.K., 2014. Complete vineyard floor cover crops favorably limit grapevine vegetative growth. *Sci. Hortic.* 170, 256–266.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391.
- Green, R.E., Cornell, S.J., Scharlemann, J.P., Balmford, A., 2005. Farming and the fate of wild nature. *Science* 307 (5709), 550–555.
- Grime, J.P., 1973. Vegetation classification by reference to strategies. *Nature* 250, 26–31.
- Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111 (982), 1169–1194.
- Grime, J.P., 1979. Plant strategies and vegetation processes. *Biol. Plant.* 23 (4) 254–254.
- Grime, J.P., Hodgson, J.G., Hunt, R., 1988. *Comparative Plant Ecology: a Functional Approach to Common British Species*. Springer.
- Grime, J.P., 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *J. Veg. Sci.* 17 (2), 255–260.
- Gross, N., Nash Suding, K., Lavorel, S., 2007. Leaf dry matter content and lateral spread predict response to land use change for six subalpine grassland species. *J. Veg. Sci.* 18 (2), 289–300.
- Guzmán, G., Cabezas, J.M., Sánchez-Cuesta, R., Lora, Á., Bauer, T., Strauss, P., Winter, S., Zaller, J.G., Gómez, J.A., 2019. A field evaluation of the impact of temporary cover crops on soil properties and vegetation communities in southern Spain vineyards. *Agric. Ecosyst. Environ.* 272, 135–145.
- Hartig, F., 2018. *DHARMA – Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models*. R Package Version 0.2.0. Retrieved from: <https://cran.r-project.org/web/packages/DHARMA/DHARMA.pdf>.
- Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., Scherer-Lorenz, M., Spehn, E.M., Bazeley-White, E., Weilenmann, M., Caldeira, M.C., Dimitrakopoulos, P.G., Finn, J.A., Huss-Danell, K., Jumpponen, A., Mulder, C.P.H., Palmberg, C., Pereira, J.S., Simantziouras, A.S.D., Terry, A.C., Troumbis, A.P., Schmid, B., Loreau, M., 2010. General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology* 91 (8), 2213–2220.
- Hervé, M.E.T., Boudes, P., Cieslik, C., Montebault, D., Jung, V., Burel, F., Cluzeau, D., Winter, S., Nicolai, A., 2018. Landscape Complexity Perception and Representation in a Wine-growing Region With the Designation of Origin in the Loire Valley (France): a Cultural Ecosystem Service? *Renewable Agriculture and Food Systems*. Cambridge University Press, pp. 1–13. <https://doi.org/10.1017/S1742170518000273>.
- Hothorn, T., Buehlmann, P., Dudoit, S., Molinaro, A., Van Der Laan, M., 2006. Survival ensembles. *Biostatistics* 7 (3), 355–373.
- Hunt, R., Hodgson, J.G., Thompson, K., Bungener, P., Dunnett, N.P., Askew, A.P., 2009. A new practical tool for driving a functional signature for herbaceous vegetation. *Appl. Veg. Sci.* 7 (2), 163–170.
- IGN (Institut Géographique National), 2012. Layers: “végétation”, “RPG (Référentiel Parcellaire Géographique)”, “Cadastre”.
- Kahmen, S., Poschlod, P., 2004. Plant functional trait responses to grassland succession over 25 years. *J. Veg. Sci.* 15 (1), 21–32.
- Kahmen, S., Poschlod, P., 2008. Effects of grassland management on plant functional trait composition. *Agric. Ecosyst. Environ.* 128, 137–145.
- Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., et al., 2011. TRY - a global database of plant traits. *Glob. Chang. Biol.* 17, 2905–2935.
- Kazakou, E., Fried, G., Richarte, J., Gimenez, O., Violle, C., Metay, A., 2016. A plant trait-based response-and-effect framework to assess vineyard inter-row soil management. *Bot. Lett.* 163 (4), 373–388.
- Kehinde, T., Samways, M.J., 2014a. Insect–flower interactions: network structure in organic versus conventional vineyards. *Anim. Conserv.* 17, 401–409. <https://doi.org/10.1111/accv.12118>.
- Kehinde, T., Samways, M.J., 2014b. Management defines species turnover of bees and flowering plants in vineyards. *Agric. For. Entomol.* 16 (1), 95–101.
- Kehinde, T., von Wehrden, H., Samways, M., Klein, A.M., Brittain, C., 2018. Organic farming promotes bee abundance in vineyards in Italy but not in South Africa. *J. Insect Conserv.* 22, 61–67.
- Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E.D., Clough, Y., Díaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovács, A., Marshall, E.J.P., Tschamtké, T., Verhulst, J., 2009. On the relationship between farmland biodiversity and land-use intensity in Europe. *Proc. R. Soc. Lond., B, Biol. Sci.* 276 (1658), 903–909.
- Klotz, S., Kühn, I., Durka, W., 2002. *BIOFLOR - eine datenbank zu biologisch-ökologischen merkmalen der gefäßpflanzen in Deutschland*. Schriftenreihe Für Vegetationskunde. Bd. 38. Bundesamt für Naturschutz, Bonn.
- Koning, L.A., de Mol, F., Gerowitt, B., 2019. Effects of management by glyphosate or tillage on the weed vegetation in a field experiment. *Soil Tillage Res.* 186, 79–86.
- Kratschmer, S., Pachinger, B., Schwantzer, M., Paredes, D., Guernion, M., Burel, F., Nicolai, A., Strauss, P., Bauer, T., Kriechbaum, M., Zaller, J.G., Winter, S., 2018. Tillage intensity or landscape features: what matters most for wild bee diversity in vineyards? *Agriculture, Ecosystems & Environment* 266, 142–152.
- Laliberté, E., Legendre, P., Shipley, B., 2015. Measuring Functional Diversity (FD) From Multiple Traits, and Other Tools for Functional Ecology. *FD Package*. R Package Version 1.0-12. Retrieved from: <https://cran.r-project.org/web/packages/FD/FD.pdf>.
- Lepš, J., de Bello, F., Lavorel, S., Berman, S., 2006. Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia* 78, 481–501.
- Lippert, W., Meierott, L., 2014. *Kommentierte Artenliste Der Farn- Und Blütenpflanzen Bayerns*. Selbstverlag der Bayerischen Botanischen Gesellschaft, München, S., pp. 1–408.
- Londo, G., 1976. The decimal scale for relevés of permanent quadrats. *Vegetatio* 33, 61–64.
- Lososová, Z., Danihelka, J., Chytrý, M., 2003. Seasonal dynamics and diversity of weed vegetation in tilled and mulched vineyards. *Biologia* 58, 49–57.
- Louault, F., Pillar, V.D., Aufrère, J., Garnier, E., Soussana, J.F., 2005. Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. *J. Veg. Sci.* 16, 151–160.
- Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Benthem, K., Bolker, B., Brooks, M., 2018. *glmmTMB – Generalized Linear Mixed Models Using Template Model Builder*. R Package Version 0.2.2.0. Retrieved from: <https://cran.r-project.org/web/packages/glmmTMB/glmmTMB.pdf>.
- Májeková, M., De Bello, F., Doležal, J., Lepš, J., 2014. Plant functional traits as determinants of population stability. *Ecology* 95 (9), 2369–2374.
- Mania, E., Isocrono, D., Pedullà, M.L., Guidoni, S., 2015. Plant Diversity in an intensively cultivated vineyard agro-ecosystem (Langhe, North-West Italy). *South Afr. J. Enol. Vitic.* 36 (3), 378–388.
- Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S., Vesk, P.A., 2010. What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Glob. Ecol. Biogeogr.* 19 (4), 423–431.
- Mazerolle, M.J., 2017. *AICcmodavg: Model Selection and Multimodel Inference Based on (Q)AIC(c)*. R Package Version 2.1-1. Retrieved from: <https://cran.r-project.org/web/packages/AICcmodavg/AICcmodavg>.
- McGarigal, K., Cushman, S.A., Ene, E., 2012. *FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps*.
- Monteiro, A., Caetano, F., Vasconcelos, T., Lopes, C.M., 2012. Vineyard weed community dynamics in the Dão winegrowing region. *Ciência e Técnica Vitivinícola* 27 (2), 73–82.
- Monteiro, A., Lopes, C.M., Machado, J.P., Fernandes, N., Araújo, A., 2008. Cover cropping in a sloping, non-irrigated vineyard: I - Effects on weed composition and dynamics. *Ciência e Técnica Vitivinícola* 23, 29–36.
- Morecroft, M.D., Bealey, C.E., Scott, W.A., Taylor, M.E., 2016. Interannual variability,

- stability and resilience in UK plant communities. *Ecol. Indic.* 68, 63–72.
- Moreno, A., Hasenauer, H., 2016. Spatial downscaling of European climate data. *Int. J. Climatol.* 36 (3), 1444–1458.
- Muscas, E., Cocco, A., Mercenaro, L., Cabras, M., Lentini, A., Porqueddu, C., Nieddu, G., 2017. Effects of vineyard floor cover crops on grapevine vigor, yield, and fruit quality, and the development of the vine mealybug under a Mediterranean climate. *Agric. Ecosyst. Environ.* 237, 203–212.
- Nascimbene, J., Marini, L., Ivan, D., Zottini, M., 2013. Management intensity and topography determined plant diversity in vineyards. *PLoS One* 8 (10), e76167.
- Nascimbene, J., Zottini, M., Ivan, D., Casagrande, V., Marini, L., 2016. Do vineyards in contrasting landscapes contribute to conserve plant species of dry calcareous grasslands? *Sci. Total Environ.* 545, 244–249.
- Natural Resources Conservation Service, 2018. The PLANTS Database. Retrieved from: United States Department of Agriculture, Retrieved from. www.plants.usda.gov.
- Nicholls, C.I., Parella, M.P., Altieri, M.A., 2000. Reducing the abundance of leafhoppers and thrips in a northern California organic vineyard through maintenance of full season floral diversity with summer cover crops. *Agr For Entomol* 2, 107–113. <https://doi.org/10.1046/j.1461-9563.2000.00054.x>.
- Noble, I.R., Gitay, H., 1996. A functional classification for predicting the dynamics of landscapes. *J. Veg. Sci.* 7, 329–336.
- Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szocs, E., Wagner, H., 2018. *Vegan: Community Ecology Package*. R Package Version 2.5-2. Retrieved from: <https://cran.r-project.org/web/packages/vegan/vegan.pdf>.
- Owen, M.D., 2008. Weed species shifts in glyphosate-resistant crops. *Pest Manag. Sci.* 64 (4), 377–387.
- Paliy, O., Shankar, V., 2016. Application of multivariate statistical techniques in microbial ecology. *Mol. Ecol.* 25 (5), 1032–1057.
- Pardini, A., Faiello, C., Longhi, F., Mancuso, S., Snowball, R., 2002. Cover crop species and their management in vineyards and olive groves. *Adv. Hortic. Sci.* 16, 225–234.
- Pestorf, H., Weiß, L., Müller, J., Boch, S., Socher, S.A., Prati, D., Schöningh, I., Weisser, W., Fischer, M., Jeltsch, F., 2013. Community mean traits as additional indicators to monitor effects of land-use intensity on grassland plant diversity. *Perspect. Plant Ecol. Evol. Syst.* 15, 1–11.
- Posada, D., Buckley, T.R., 2004. Model selection and model averaging in phylogenetics: advantages of akaike information criterion and bayesian approaches over likelihood ratio tests. *Syst. Biol.* 53 (5), 793–808.
- Puech, C., Baudry, J., Joannon, A., Poggi, S., Aviron, S., 2014. Organic vs. Conventional farming dichotomy: does it make sense for natural enemies? *Agric. Ecosyst. Environ.* 194, 48–57.
- Rao, C.R., 1982. Diversity and dissimilarity coefficients: a unified approach. *Theor. Popul. Biol.* 21, 24–43.
- R Core Development Team, 2018. *A Language and Environment for Statistical Computing*. Vienna, Austria. Retrieved from. <https://www.r-project.org/>.
- Richner, N., Holderegger, R., Linder, H.P., Walter, T., 2015. Reviewing change in the arable flora of Europe: a meta-analysis. *Weed Res.* 55, 1–13.
- Ripoche, A., Metay, A., Celette, F., Gary, C., 2011. Changing the soil surface management in vineyards: immediate and delayed effects on the growth and yield of grapevine. *Plant Soil* 339 (1-2), 259–271.
- Ruiz-Colmenero, M., Bienes, R., Marques, M.J., 2011. Soil and water conservation dilemmas associated with the use of green cover in steep vineyards. *Soil Tillage Res.* 117, 211–223.
- Ruiz-Colmenero, M., Bienes, R., Eldridge, D.J., Marques, M.J., 2013. Vegetation cover reduces erosion and enhances soil organic carbon in a vineyard in the central Spain. *Catena* 104, 153–160.
- Sanguankeeo, P.P., León, R.G., 2011. Weed management practices determine plant and arthropod diversity and seed predation in vineyards. *Weed Res.* 51, 404–412. <https://doi.org/10.1111/j.1365-3180.2011.00853.x>.
- Scursoni, J., Forcella, F., Gunsolus, J., Owen, M., Oliver, R., Smeda, R., Vidrine, R., 2006. Weed diversity and soybean yield with glyphosate management along a north-south transect in the United States. *Weed Sci.* 54, 713–719.
- Sell, P., Murrell, G., 2006. *Flora of Great Britain and Ireland 4th edition*, Cambridge.
- Shields, M.W., Tompkins, J.M., Saville, D.J., Meurk, C.D., Wratten, S., 2016. Potential ecosystem service delivery by endemic plants in New Zealand vineyards: successes and prospects. *PeerJ* 4, e2042. <https://doi.org/10.7717/peerj.2042>.
- S.I.G.P.A.C.-, 2011. *Consejería De Agricultura Pesca Y Desarrollo Rural*. Junta de Andalucía. <http://www.juntadeandalucia.es/agriculturaypesca/sigpac/index.xhtml> (Accessed 07 June 2017).
- Smith, R.G., Atwood, L.W., Pollnac, F.W., Warren, N.D., 2015. Cover-crop species as distinct biotic filters in weed community assembly. *Weed Sci.* 63, 282–295. <https://doi.org/10.1614/WS-D-14-00071.1>.
- Steenwerth, K., Orellana-Calderón, A., Hanifin, R.C., Storm, C., McElrone, A.J., 2016. Effects of various vineyard floor management techniques on weed community shifts and grapevine water relations. *Am. J. Enol. Vitic.* 67, 153–162. <https://doi.org/10.5344/ajev.2015.15050>.
- Strobl, C., Hothorn, T., Zeileis, A., 2009. *Party on! A New, Conditional Variable Importance Measure for Random Forest Available in the Party Package*. Technical Report 50, Department of Statistics. Retrieved from: University of Munich. <https://epub.uni-muenchen.de/9387/1/techreport.pdf>.
- Tesic, T., Keller, M., Hutton, R.J., 2007. Influence of vineyard floor management practices on grapevine vegetative growth, yield and fruit composition. *Am. J. Enol. Vitic.* 58, 1–11.
- Thompson, G.G., Withers, P.C., Pianka, E.R., Thompson, S.A., 2003. Assessing biodiversity with species accumulation curves; inventories of small reptiles by pit-trapping in Western Australia. *Austral. Ecol.* 28, 361–383.
- Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80 (5), 1455–1474.
- Tilman, D., Isbell, F., Cowles, J.M., 2014. Biodiversity and ecosystem functioning. *Annu. Rev. Ecol. Evol. Syst.* 45, 471–473.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecol. Lett.* 8 (8), 857–874.
- Vandewalle, M., Purschke, O., de Bello, F., Reitalu, T., Prentice, H.C., Lavorel, S., Johansson, L.J., Sykes, M.T., 2014. Functional response of plant communities to management, landscape and historical factors in semi-natural grasslands. *J. Veg. Sci.* 25, 750–759.
- Vencill, W.K., Nichols, R.L., Webster, T.M., Soteres, J.K., Mallory-Smith, C., Burgos, N.R., Johnson, W.G., McClelland, M.R., 2012. Herbicide resistance: toward an understanding of resistance development and the impact of herbicide-resistant crops. *Weed Science Special Issue* 2–20.
- Weed Science Society of America, 2018. *Composite Database of Weeds*. Retrieved from: <http://wssa.net/wssa/weed/composite-list-of-weeds/>.
- Wei, T., Simko, V., Levy, M., Xie, Y., Jin, Y., Zemla, J., 2017. *Corrplot – Visualization of a Correlation Matrix*. R Package Version 0.84. Retrieved from: <https://cran.r-project.org/web/packages/corrplot/index.html>.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.T., 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* 33, 125–159.
- Wilmanns, O., 1993. Plant strategy types and vegetation development reflecting different forms of vineyard management. *J. Veg. Sci.* 4 (2), 235–240.
- Winter, S., Bauer, T., Strauss, P., Kratschmer, S., Paredes, D., Popescu, D., Landa, B., Guzmán, G., Gómez, J.A., Guernion, M., Zaller, J.G., Batáry, P., 2018. Effects of vegetation management intensity on biodiversity and ecosystem services in vineyards: a meta-analysis. *J. Appl. Ecol.* 55, 2484–2495.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problem. *Methods Ecol. Evol.* 1, 3–14.