Wild bees in viticultural landscapes:

Effects of vineyard inter-row management and viticultural landscape complexity on the diversity, abundance and functional traits of wild bees

Rare observation of a female wild bee (*Lasioglossum* sp.) foraging on a grapevine flower

DOCTORAL THESIS

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Affidavits

I hereby declare that I am the sole author of this work. No assistance other than that which is permitted has been used. Ideas and quotes taken directly or indirectly from other sources are identified as such.

Sophie Kratschmer

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Abstract

Vineyards can provide habitats for a range of beneficial organisms, especially if the inter-row space is covered with vegetation. In practice, vineyards are often intensively managed by frequent application of pesticides and soil tillage. The conversion of (semi-) natural habitats to vineyards results in landscape simplification. Wild bees are important pollinators of wild plants and crops but intensive agricultural management decreases floral resources and suitable nesting sites.

This thesis examines the effects of field and landscape parameters on wild bee communities in vineyards across Europe (AT, ES, FR, RO). Wild bees were sampled in 63 vineyard inter-row transects comprising three vegetation management intensities which resulted in either bare soil, temporary vegetated or permanently vegetated inter-rows. Floral resources were estimated by flower coverage along each transect. The landscape in a 750m radius around each vineyard was analysed to conclude landscape diversity indices and the relative proportion of landscape structures.

In European vineyards, wild bee diversity and abundance increased with higher floral resource availability, which was in turn related to the positive effect of low vegetation management intensity. Eusocial species benefitted from undisturbed soil conditions in permanently vegetated inter-rows, while solitary species were less sensitive to inter-row disturbances. Furthermore, higher landscape diversity compensated the negative effect of low floral resource availability on the eusocial bee abundance in inter-rows across Europe. In AT, the increased proportion of forests benefitted eusocial species, while high amounts of solitary trees was beneficial for solitary wild bees. Maintaining diverse floral resources, reducing inter-row vegetation management intensity, and preserving landscape elements (e.g. solitary trees) are key points to enhance wild bee diversity in viticultural landscapes.

Keywords: Apiformes, pollination, ecosystem services, floral resource availability, tillage, mixed regression models, Shannon Landscape Diversity Index, pollen analysis

Zusammenfassung

Weingärten können Lebensräume für Tiere und Pflanzen darstellen vor allem, wenn sie extensiv bewirtschaftet werden und die Fahrgassen begrünt sind. Weinbau kann aufgrund des hohen Pestizideinsatzes, häufiger Bodenbearbeitung und der Umwandlung von naturnahen Habitaten in Weingärten als intensive Landnutzung charakterisiert werden. Wildbienen sind wichtige Bestäuber von Wild- und Kulturpflanzen. Intensive Landnutzung reduziert ihr Futterangebot und zerstört Nisthabitate.

Diese Dissertation erforscht, wie sich Feld- und Landschaftsparameter auf die Wildbienengemeinschaften in Europas Weingärten (AT, ES, FR, RO) auswirken. Wildbienen wurden mittels Transektmethode in 63 Fahrgassen erhoben. Die Fahrgassenbewirtschaftungsintensitäten resultierten in offenem Boden, temporär- oder dauerbegrünten Fahrgassen. Das Blütenangebot wurde durch Schätzung der Blütendeckung am Transekt ermittelt. Landschaftsstrukturen wurden im 750 m Radius jedes Weingartens kartiert und die Landschaftsdiversität sowie Proportionen verschiedener Landschaftsstrukturen errechnet.

Ein steigendes Blütenangebot in europäischen Weingärten wirkte sich stark positiv auf die Wildbienendiversität und Abundanz aus und stand mit dem positiven Effekt extensiver Fahrgassenbewirtschaftung im Zusammenhang. Eusoziale Arten profitierten von ungestörten Bodenverhältnissen in dauerbegrünten Fahrgassen und vom steigenden Waldanteil. Negative Auswirkungen eines geringen Blütenangebotes auf die Abundanz eusozialer Arten wurden durch hohe Landschaftsdiversität der Umgebung ausgeglichen. Solitäre Arten reagierten weniger sensibel auf Störung der Fahrgassen und profitierten von der steigenden Anzahl an Einzelbäumen. Das Etablieren eines hohen Blütenangebotes, die Extensivierung der Fahrgassenbewirtschaftung und die Erhaltung von Landschaftsstrukturen (z.B. Einzelbäume) sind die wichtigsten Eckpunkte um Wildbienendiversität in Weinbaulandschaften zu fördern.

Stichwörter: Apiformes, Ökosystemdienstleistungen, Bodenbearbeitung, gemischte Regressionsmodelle, Shannon Landschaftsdiversität Index, Pollenanalyse

1. Introduction

While the beginning date of the Anthropocene is still in debate, the permanent impact of humans' activities on earth's ecosystems is evident (Zalasiewicz et al., 2006). Beside many abiotic indicators, the biotic change is considered an indicator of the Anthropocene, because for example the extinction rates of vertebrates accelerated dramatically since the mid-18th century (Waters et al., 2016). By now, 195 States are legally bound to implement the framework of the Convention on Biological Diversity into national biodiversity strategies and action plans to encounter the loss of biodiversity and degradation of related ecosystem services (United Nations, 1992). The negative effect of the current global change on insect diversity and abundance has received more attention in the last decade. A recent study showed a decline of up to 82 % in flying insect biomass in German nature reserves over 27 years (Hallmann et al., 2017). Further, it has been pointed out that Hymenopteran taxa are among the strongest decreasing insect orders (Galetti et al., 2014; Sánchez-Bayo and Wyckhuys, 2019).

About 87.5 % of the world's angiosperm species (Ollerton et al., 2011) and 85 % of the 107 global leading crop varieties depend, at least to some extent, on animal pollination. This corresponds to an estimated 5-8 % of the global crop production with an annual market value of 235-577 billion USD. Over 90 % of the animal pollinated leading crops are visited by bees (IPBES, 2016). Beside many other insect taxa, bees are most important pollinators of many wild plants because their nutrition during all life stages depends on pollen and nectar, which is mainly collected from flowers. A certain degree of flower constancy of generalist wild bee species, or even a high specialization of some wild bee taxa on foraging pollen from closely related plant taxa, guarantees the relocation of pollen from one plant individual to another individual of the same species and thus pollination (Westrich, 2018).

1.1. Wild bee ecology and pollination in agro-ecosystems

There is scientific consensus about the complementary pollination efficiency of wild and honey bees (e.g. Brittain et al., 2013; Isaacs et al., 2017). In contrast to over 20.000 known wild bee species globally (Scheuchl and Willner, 2016) honey bees and a few other bee species (e.g. some bumble bees, stingless bees and a few solitary bees) are managed pollinating insects. High wild bee diversity and abundance increase the pollination performance (quantity and quality of fruit set and yield) of crops like for example apples (Földesi et al., 2015; Mallinger and Gratton, 2015), coffee (Klein et al., 2003) or sweet cherry (Holzschuh et al., 2012) – to name just a few. Further, pollination efficiency is also strongly associated with functional trait diversity (Fontaine et al., 2006; Fründ et al., 2013; Garibaldi et al., 2015) and these functional traits are closely related to habitat requirements.

Wild bees are central place foragers. The females establish their nests at a fixed location and collect pollen and nectar for their offspring within a species-specific activity range, which is related to body size, specifically to the size of the wing muscles in the thorax (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007; Zurbuchen et al., 2010). The majority of wild bee species in Europe excavate nests in the soil (ground-nesting) and therefore demand open ground patches for nest establishment. Species that utilize pre-existing cavities or gnaw tunnels into plant material (above-ground nesting) require vertical structures such as plant stems, (natural) walls or deadwood elements. Depending on the species, pollen is collected from different plant taxa (polylectic wild bees) or only from closely related or single plant taxa (oligolectic wild bees). Nest establishment and resource collection is either done by each female on its own (solitary species) or organised in groups with division of tasks in egg-laying females and worker bees who collect resources (eusocial species; e.g. bumble bees, some Halictidae species). Apart from that, there are brood parasitic species, which depend on the occurrence of the host species because females lay their eggs into the nest of these host species (Scheuchl and Willner, 2016; Westrich, 2018).

During the last decades it has been shown that wild bees are threatened by intensive agricultural management (Kennedy et al., 2013; Kremen et al., 2002). Landscape simplification due to increasing field size, the use of high pesticide quantities, frequent soil tillage and the reduction of floral resources are amongst other interlinked factors which deteriorate habitat quality for wild bees (Goulson et al., 2015). However, wild bee species composition is differently affected by environmental disturbances (Carrié et al., 2017; Hopfenmüller et al., 2014) because, as mentioned above, different functional traits require certain habitat characteristics (Williams et al., 2010). Wild bee diversity and abundance are enhanced by increased quantity and quality of floral resources (Williams et al., 2015) and increased landscape heterogeneity (Andersson et al., 2013), which is linked to higher proportions of semi-natural areas in agricultural landscapes (Nicholson et al., 2017).

1.2. Vineyard management, biodiversity and ecosystem services

Vineyards cover about 7.6 million hectares worldwide (OIV, 2018) and are often intensively managed. As in other agro-ecosystems, this includes frequent applications of pesticides (most importantly fungicides), soil tillage and habitat fragmentation due to increasing field size or conversion of (semi-) natural habitats to vineyards (Merenlender, 2000; Nicholls et al., 2008). Grapevine is a perennial crop with relatively wide inter-row spaces, which may be covered with spontaneous vegetation or seeded cover crops. This inter-row vegetation is managed by winegrowers by mulching, tillage, herbicide application or a combination thereof, to mitigate potential water and/or nutrient competition between the vines and “weeds” (Pardini et al., 2002). The intensity of this inter-row management varies across wine-growing areas according to local pedological and climatic conditions as well as to irrigation facilities. At low management intensity, the inter-rows may be comparable with wildflower strips or field margins in agricultural landscapes and can be a suitable habitat for a range of plant and animal species that provide ecosystem services (ES). For example, vineyard inter-rows can provide habitats for invertebrates that provide pest control (Nicholls et al., 2008) or cover crops in the inter-row enhance soil fertility (Winkler et al., 2017) and prevent soil erosion especially on hilly terrain, which is characteristic for many viticulture areas (Montanarella, 2005; Viers et al., 2013). The maintenance of characteristic viticultural landscape structures like hedges, riparian areas, extensively managed grasslands or solitary trees enhance biodiversity and related ES (reviewed in Viers et al., 2013). Further, high landscape diversity in wine-growing areas provides a high aesthetic value for tourism (Hervé et al., 2018). However, in many regions landscape structures have been removed to facilitate work efficiency with agricultural machinery (Eichhorn et al., 2006).

Grapevine (*Vitis vinifera* L.) is self-pollinated, therefore insect pollination plays usually only a minor role for grape yield (Cabello Saenz et al., 1994). Bees occasionally collect pollen from grapevine, but the grapevine flower is not very attractive to bees because it is rather small, green and provides no nectar (Vorwohl, 1977). However, biodiversity-friendly managed vineyards and viticultural landscapes that include mosaics of (semi-) natural elements can provide habitats for wild bees (Kehinde and Samways, 2012; Kehinde and Samways, 2014a). As a consequence, viticulture can contribute to resilient pollination services for other crops and (wild-) plants by enhancing wild bee diversity (Bartomeus et al., 2013). Further, by improving habitats for pollinators other ES like biological pest control, soil protection or landscape aesthetics can be enhanced too (Wratten et al., 2012). From the socio-economic point of view, the establishment of habitats for wild bees in vineyards can be used for marketing, because winegrowers experience an increased consumer demand for eco-friendly produced wine (Schütte and Bergmann, 2019). Despite these benefits, the meta-analysis included in this thesis revealed a knowledge gap about the effects of vineyard inter-row management on wild bees and pollination services. Studies evaluating the impact of vineyard inter-row management and landscape structures on wild bees have not yet been carried out in Europe.

2. Aims and publications of the thesis

This thesis aims to evaluate the effects of viticultural ecosystem parameters at different spatial scales on wild diversity, abundance and functional traits. The field scale is represented by the vineyard inter-rows, where the vegetation management and the floral resource availability are the key variables. Regarding the landscape scale, different landscape structures and landscape diversity are considered the key variables.

In this thesis I focus on the following research questions:

a) What are the most important field scale parameters (vegetation management, floral resource availability) and landscape scale parameters (landscape diversity landscape structures) affecting wild bee diversity, abundance and functional traits in vineyard inter-rows?
b) Can increased landscape diversity compensate possible negative effects of intensive vegetation management and/or low floral resource availability on wild bee diversity, abundance and functional traits in vineyard inter-rows?
c) What are preferred pollen resources for wild bees in viticultural landscapes and is grapevine pollen an important food resource?
d) Do vineyard inter-rows provide habitat for rare wild bee species?

Based on the results of this thesis, management recommendations on how to support wild bees in vineyard inter-rows are provided. Winegrowers are therefore able to contribute to wild bee diversity promotion in the agro-ecosystem, which is a key factor for resilient pollinator communities and thus sustainable pollination of entomophilous (i.e. insect pollinated) crops and wild plants.

To answer the research questions two core publications (I, II) and three further publications (III, IV, V) are included in the result chapters of this thesis. Additionally, chapter four is extended with unpublished (preliminary) results to assess the preferred pollen resources of wild bees in vineyard inter-rows. Further, the last result chapter describes rare wild bee species documented in the inter-rows and evaluates their occurrence in the context of site characteristics. Hereinafter, references to the respective publications are given by Latin numbers as follows:

I 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. doi: 10.1016/j.agee.2018.07.018.

II Kratschmer, S., Pachinger, B., Schwantzer, M., Paredes, D., Guzmán, G., Goméz, J.A., Entrenas, J.A., Guernion, M., Burel, F., Nicolai, A., Fertil, A., Popescu, D., Macavei, L., Hoble, A., Bunea, C., Kriechbaum, M., Zaller, J.G., Winter, S. (2019): Response of wild bee diversity, abundance and functional traits to vineyard inter-row management intensity and landscape diversity across Europe. *Ecology and Evolution*, 9, 4103-4115. doi: 10.1002/ece3.5039

III 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. *Journal of Applied Ecology*, 1–12. doi: 10.1111/1365-2664.13124.

IV Kratschmer, S.*, Petrović, B.*, Curto, M., Meimberg, H., Pachinger, B. (resubmitted): Pollen availability for the Horned Mason Bee (*Osmia cornuta*) in regions of different land use and landscape structures, *Ecological Entomology*.
* Authors contributed equally

V Ebmer, A.W., Kratschmer, S., Pachinger, B. (2016): *Lasioglossum* (*Lasioglossum*) *laterale* (Brullé, 1832) (Hymenoptera: Apidae), eine seltene mediterrane Halictidae, neu für Österreich. *Beiträge zur Entomofaunistik*, 17, 77-83.

3. Summary of methods

This chapter provides an overview of this thesis' methods and includes important figures and tables referring to respective details in the core publications (I, II). Because the methods of pollen analyses are only partly included in manuscript IV, a detailed method description is provided in section 3.6. Further, publications about pollinators/wild bees in vineyards were included in a meta-analysis, which assessed the effects of vegetation management intensity on biodiversity and ecosystem services in vineyards (III).

3.1. Study sites

The research for this thesis was conducted in viticultural areas (Fig. 1) in Austria (I), France, Romania and Spain (II) covering three European climate zones (Mediterranean, temperate oceanic and temperate continental). In total, 63 vineyards were investigated: 15 vineyards in France and 16 vineyards in Austria, Romania and Spain each. The study sites were chosen according to different inter-row vegetation management intensities (I, II). Winegrowers were interviewed to gather information about inter-row management practices and whether they used seed mixtures or allowed spontaneous vegetation to establish inter-row vegetation cover. In the case of sown cover crops they were asked which plant taxa are included and which seed mixture brand was used.

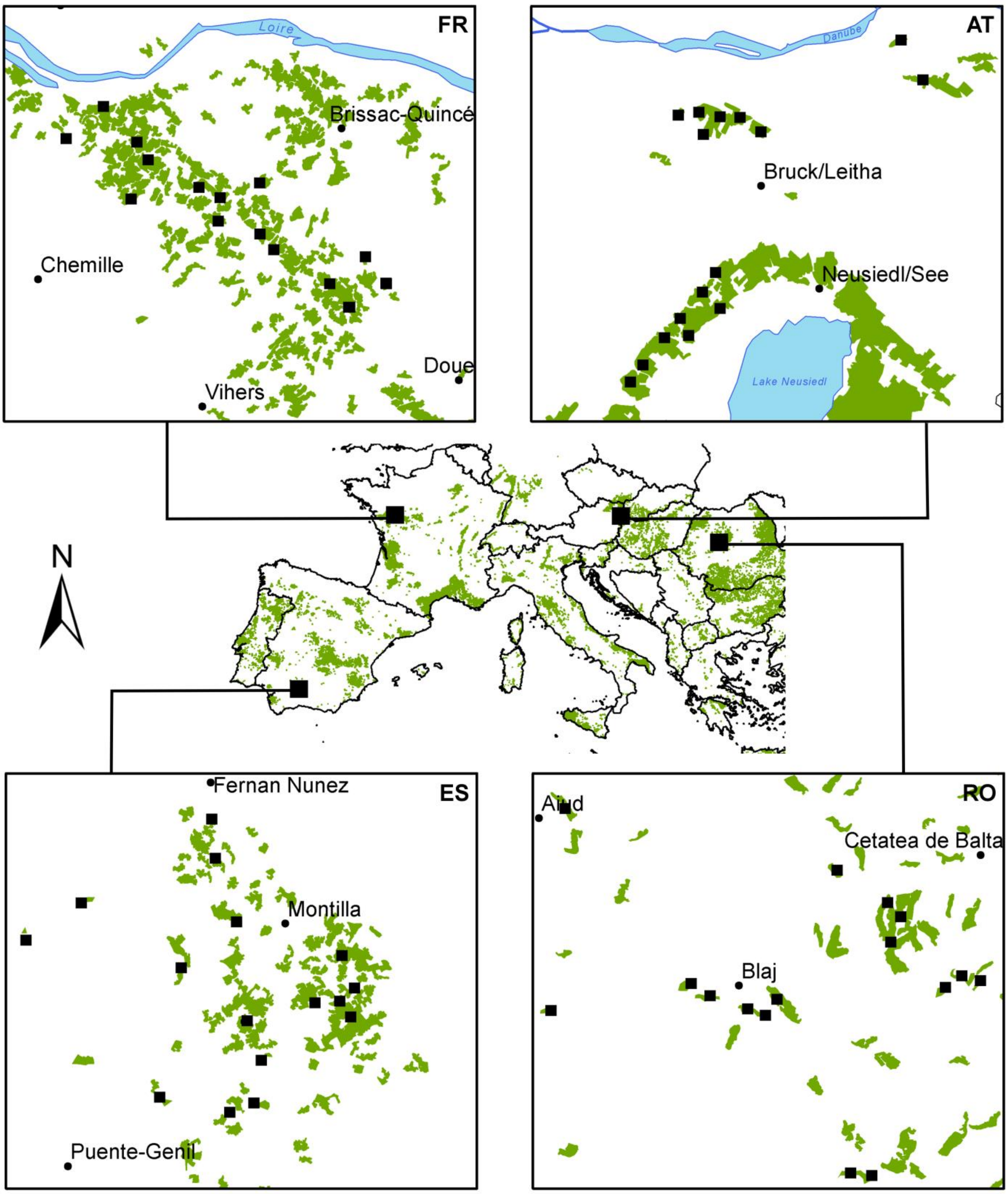

Fig. 1 Maps of studied viticultural areas across Europe. FR: Loire Valley, AT: Carnuntum and Neusiedler See-Hügelland, RO: Târnave and ES: Montilla Moriles. Green shading: Viticultural areas according to CORINE land cover (EEA 2017). Squares: Location of studied vineyards and viticultural.

3.2. Wild bee sampling

Wild bees were sampled by hand-netting along an inter-row transect, which was allocated in two neighbouring inter-rows and covered a total area of 200 m^2. In order to adjust to the different inter-row widths (1.5-3.0 m), the transect lengths ranged between 67 and 133 m. Each inter-row transect was sampled five times in 2016 in each country (II) and additionally in 2015 in Austria (I). During the 15 min. transect walk per sampling event, each wild bee individual was caught with an aerial-net. Bumble bees and honey bees were identified in the field and released after the sampling event, the other bees were identified in the laboratory. Sampling dates among the countries were synchronized to grapevine phenology (first budburst, first flower buds, full florescence, pea-sized berries and beginning of maturation) to adapt to the different climatic zones (II). In Austria sampling started in April and ended in August in each year (I). Each sampling round was done within 3-5 days in the respective months. To assess the importance of grapevine as floral resource for wild bees, an additional transect walk (15 min/transect) was done during the full florescence of grapevine. These transects were located at the same position as the inter-row transects but the length was standardized to 100 m per vineyard and the grapevine flowers were inspected for wild bees.

Functional traits of wild bees (I, II; Table 1) were selected according to their possible response to inter-row management, floral resource availability and landscape parameters. Information about functional traits (nesting type, sociality, lecty) was gathered from literature (Scheuchl and Willner, 2016) or expert’s assessment. As a proxy for activity range and body size the inter-tegular distance (ITD in mm) was measured (Greenleaf et al., 2007) from 1-5 specimens from each species per country and averaged per species. The ITD is measured by the distance between the bases of the tegulae at the dorsal side of the bee’s thorax (Cane, 1987).

Table 1 Wild bee functional traits, sociality was defined according to Michener (2007). ITD = Inter-tegular distance

Trait	**Variable types**	**Definition**	**Rationale for selection**
Nesting type	Ground-nesting	Majority of wild bee species in Europe excavate nests in the ground.	Interlinked with habitat requirements (e.g. bare compact ground or pre-existing cavities), which alter bee diversity, abundance and community composition.
	Above-ground nesting	Nesting in pre-existing cavities, plant stems, dead wood (incl. *Bombus* spp.)	
	Parasitic	♀ lay their eggs in nests of specific host species	Less efficient pollinators (Garibaldi et al., 2015) but indicate vital host populations (Hudson et al., 2006).
Sociality	Solitary	Nest establishment and resource collection by each ♀ alone	Type of sociality could result in shorter (solitary) or longer seasonal activity (eusocial) and may affect duration in which a species is pollinating. Affected by vegetation management due to nesting type.
	Eusocial	Division of tasks: egg-laying ♀ and ♀ that collect resources (e.g. bumble bees, some Halictidae species)	
	Parasitic	See above	See above
Body size	ITD (mm)	The shortest linear distance measured between the wing tegulae across the dorsal thorax (Cane, 1987).	Strongly related to the flying distance of a species (i.e. the distance, a female can fly to collect pollen and nectar) and affected by landscape features (Gathmann and Tscharntke 2002; Greenleaf et al. 2007; Zurbuchen et al. 2010)
Lecty	Polylectic	Pollen generalists: Pollen is collected from different plant taxa but species can show a certain degree of flower constancy.	A greater variety of plants is visited to collect pollen and nectar.
	Oligolectic	Pollen specialists: Pollen is collected from closely related or single plant taxa.	Morphological adaption to respective flower structure; occurrence of host plant is relevant.

3.3. Inter-row vegetation management

The inter-row vegetation is controlled by shallow tillage (AT, ES, RO) or herbicide application (FR). Occasionally, Spanish winegrowers used herbicides additionally to tillage. Across all countries, three different inter-row vegetation management intensities were identified (II; Table 2): (1) Permanently vegetated inter-rows (Fig. 2a) were not tilled for at least five years prior to 2015 and the vegetation was mulched 1-5 times per year. (2) In temporary vegetated vineyards either every second inter-row (AT, RO; Fig. 2b) or every inter-row during the dry season (ES; Fig. 2c) was tilled. (3) In bare soil vineyards frequent soil tillage (ES, RO; Fig. 2d) and/or herbicide application (ES, FR) leaves almost no inter-row vegetation during the growing period. Considering the untilled inter-row in temporary vegetated vineyards, the vegetation coverage (%) was estimated twice a year in four 1x1 m sub-plots per inter-row (II), to obtain a quantitative measure for the tillage intensities.

Table 2 Mean (± SD) vegetation coverage (%) per vegetation management intensity, method of vegetation management and number of management events per year. Number of landscape circles mapped corresponds to the number of vineyards sampled per country. Mean (± SD) Shannon landscape diversity index (SHDI) per country.

Country	**Vegetation coverage (%) and no. of vineyards**			**Vegetation management**		**No. Land-scape circles**	**SHDI**
	Permanent vegetation	**Temporary vegetation**	**Bare soil**	**Method**	**Events / year**		
AT	82.7 ± 11.5 n = 7	82.9 ± 14.5 n = 9	n = 0	Tillage	1-3	16	1.6 ± 0.3
ES	n = 0	56.1 ± 23.8 n = 8	19.9 ± 19.6 n = 8	Tillage and/or Herbicides	1-4	16	1.3 ± 0.2
FR	96.4 ± 2.9 n = 8	n = 0	21.1 ± 19.6 n = 7	Herbicides	1-4	15	1.5 ± 0.2
RO	63.6 ± 13.7 n = 4	63.5 ± 15.6 n = 7	35.1 ± 12.1 n = 5	Tillage	2-5	16	1.4 ± 0.3
All countries	84.4 ± 15.5 n = 19	68.3 ± 21.3 n = 24	22.9 ± 18.5 n = 20		1-5	63	1.4 ± 0.3

Fig. 2 Inter-row management intensities in vineyards across Europe. (a) Permanently vegetated (Austria; April 2016), (b) temporary vegetated by alternating tillage (Austria; June 2016), (c) temporary vegetated (Spain; March 2015) and (d) bare soil (Romania; May 2015).

3.4. Floral resource availability

Floral resource availability ("forage availability" in I) was visually estimated by the coverage of all flowering entomophilous plants at the respective sampling dates along each two adjacent inter-rows (I, II). For these estimates five category levels (<1 % = very low; 1-5 % = low; 5-25 % = medium; 25-50 % = high; 50-100 % = very high) were defined following an adapted DAFOR scale (Gardener, 2012). To ensure comparable estimates in vineyards across Europe, the samplers adjusted their estimations by discussions in the field prior to the sampling season. Further, the number of flowering plant taxa (mostly identified to species level) was documented to analyse flowering diversity (I).

3.5. Landscape survey

Landscape structures (Fig. 3, Table A.1 in I) around the centre of each inter-row transect were mapped within a 750 m radius (I, II). This radius was chosen to ensure a minimum distance of 1500 m between the studied vineyards, which covers the activity range of many wild bee species (Zurbuchen et al., 2010; Zurbuchen and Müller, 2012). The digitalization and calculation of the proportions of landscape structures in each landscape circle as well as the distances to the closest semi-natural element (SNE; I) were done with ArcGIS 10.2 (ESRI, 2013). Further, the SHDI (Shannon Landscape Diversity Index) of each landscape circle was calculated in FRAGSTATS 4.2 (McGarigal et al., 2012), to obtain a standardized parameter for landscape diversity across the countries (II, Table 2). This was also done because the viticultural landscapes across the countries showed different characteristics (Fig. 3). For example, olive orchards represented over 80 % of the agricultural areas mapped in Spain but were not present in any other country. Further, the proportion of SNE, wood and artificial elements (e.g. villages, towns) differed significantly among the countries (Kruskal-Wallis tests: SNE: $\chi^2 = 29.69$; df = 3; $p \leq 0.001$, wood: $\chi^2 = 28.13$; df = 3; $p \leq 0.001$; artificial elements: $\chi^2 = 11.62$; df = 3; $p = 0.008$).

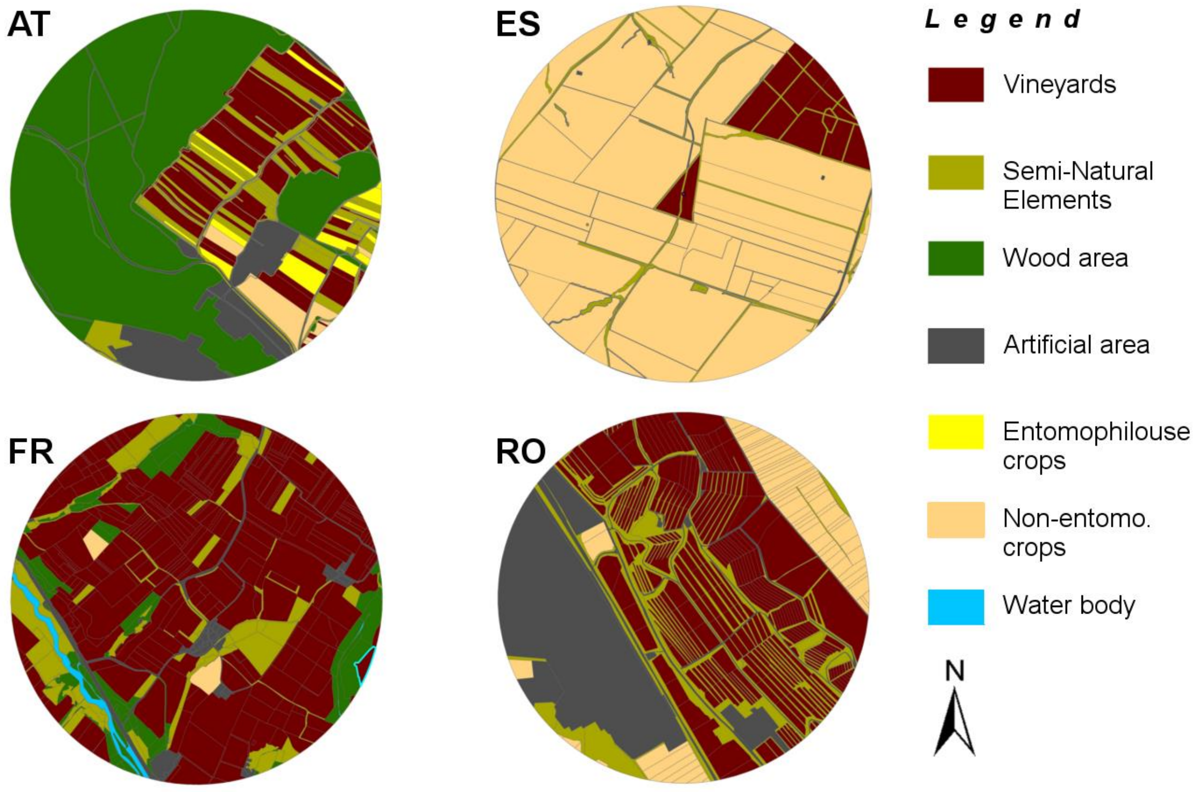

Fig. 3 Examples for different landscape settings in viticultural areas across Europe. The proportions of different landscape structures (e.g. arable land, semi-natural elements or artificial areas) varied to cover the range of complex and simple landscapes per country.

3.6. Pollen analysis

To assess preferred pollen foraging plants for wild bees in vineyards, pollen analyses were done from Austrian samples. During field work in Austria, wild bees with pollen loads were collected in separate jars to avoid pollen sample contamination between wild bee individuals. Before pinning a specimen, a pollen sample was taken from each of these individuals. Half of the pollen load (Westrich, 1986) was scraped off with the insect pin, which was later used for pinning this specimen, and stored in a 2 ml tube. Each sample that was analysed further was homogenised with 1.0-1.5 ml ethanol (96 %). The amount of alcohol varied to obtain similar dense samples on the microscope slide. Using a new disposable pipette for each sample, 1-2 drops of the mixed sample were applied on a microscope slide. The first samples were embedded in undyed glycerine gelatine which hampered pollen identification due to low contrast of the exine structures (outside layer of a pollen grain). Therefore, the following samples where embedded in fuchsine dyed glycerine (V), which also allows moving pollen grains under the microscope for identification (Jones, 2012). Using a light microscope (magnification: 400x, 600x), it is not possible to identify pollen to species level in many cases, therefore, pollen with similar exine structures are aggregated to pollen types or groups (Beug, 2015). “Pollen types” group plants of a higher taxonomic level, whereas in “pollen groups” plant species/genera from different families are combined due to their similar morphological appearance (e.g. the *Sorbus*-group includes 13 Rosaceae genera but also the genus *Lycium*). Table A1 in the appendix shows the identified pollen types and groups from the samples and gives further information about plant taxa included in the respective type or group according to Beug (2015). For some Asteraceae pollen the determination of a pollen type or group was not possible, therefore these pollen grains were attributed to two main categories Asteraceae tubiliflorae (Fig. 4b) and Asteraceae liguliflorae (Fig. 4c) which are easily recognisable by the exine structure. Per sample, 300 pollen grains were counted by attributing them to the pollen types identified. (AGES, 2016; AutPal, 2016; Beug, 2015). In total, 207 samples were taken from bees and the pollen of 44 samples (14 undyed; 30 dyed) was identified and counted.

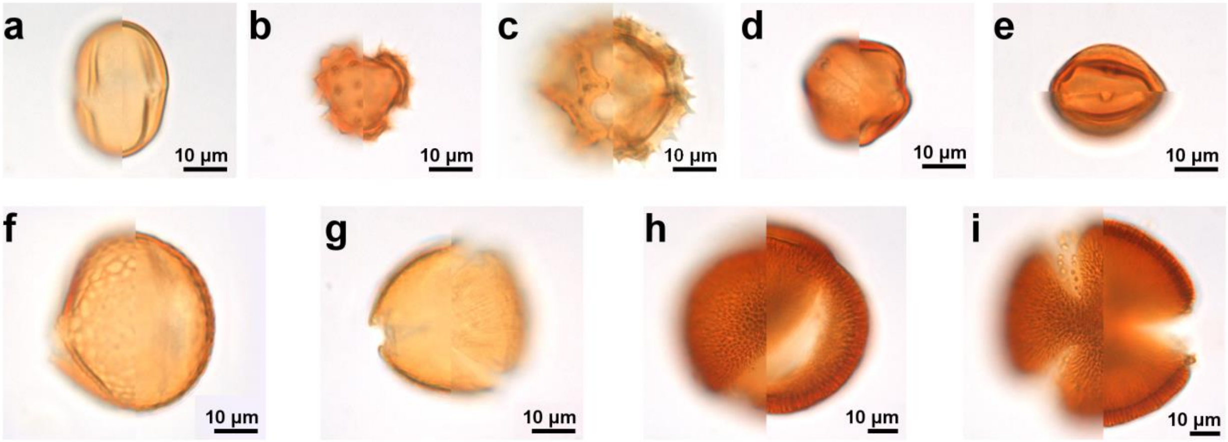

Fig. 4 Pollen from plant species representing different pollen types or species: a) *Robinia pseudoacacia* (equatorial view); b) *Senecio*-type (Asteraceae tubiliflorae; polar view); c) *Crepis*-type (Asteraceae liguliflorae; equatorial view); d) *Vitis vinifera* (polar view); e) *Vitis vinifera* (equatorial view); f) *Trifolium pratense*-type (equatorial view); g) *Sorbus*-group (polar view); h) *Convolvulus arvensis* (equatorial view); i) *Convolvulus arvensis* (polar view). Pictures show two optical layers and spatial orientation (equatorial, polar view) which are most important for pollen identification.

Additionally to the samples taken from wild bees in vineyards, trap nests (Fig. 5) for *Osmia cornuta*, a wild bee species often used for pollination in orchards (e.g. Bosch, 1994), were installed close to four sampled inter-rows in spring 2016 (IV). Further trap nests were mounted in regions of different land use (agricultural region, village-structured region, urban region) to analyse the effects of land use and landscape structures on pollen resource availability for *Osmia cornuta*. The pollen richness (i.e. number of different pollen types) in these trap nests was assessed by pollen analysis as described above. To analyse how the reproduction success is affected by land use the number of brood cells in each trap nest was counted (IV).

Fig. 5 Trap nest setting for evaluation of pollen resources of *Osmia cornuta* in different land use regions. The wooden box includes the trap nest (left inside the box) and a starter colony of eight *Osmia cornuta* cocoons (little white box with hole on the right side).

3.7. Data analysis

To analyse the effects of the most important field and landscape scale parameters on wild bee diversity, abundance and functional traits in vineyard inter-rows two different regression approaches were applied. In the first publication, generalised linear mixed models (GLMMs) were used to analyse the temporal non-independent observations within the same vineyards of the two year survey in Austria (I). For each response variable (Table 3) Poisson error distributed model sets were formulated which included the combination of the study year and month as random factor (N = 10) and different combinations of non-collinear field and landscape parameters as predictor variables (Table 3). Model selection was based on AICc (Motulsky and Christopoulos, 2003), considering a cut-off at Δ *AICc* > 2 to decide whether a model was more likely to be correct compared to next best model. According to this selection, the most parsimonious models per response variable were summarized by model averaging using the Zero Method because the focus was to determine the effect size of the variables (Grueber et al., 2011; Nakagawa and Freckleton, 2011). For these statistics the R-packages “lme4” (Bates et al., 2015), “DHARMa” (Hartig, 2017), “AICcmodavg” (Mazerolle, 2016), “arm” (Gelman et al., 2016) and “MuMIn” (Barton, 2016) were used. In the second publication the response variables (Table 3) were aggregated across all sampling events per vineyard and predictors (Table 3) were averaged if necessary (e.g. vegetation cover). Based on an information theoretic approach (Burnham and Anderson, 2002) a model set of 10 Poisson or Gaussian (only for models with ITD as response) error distributed GLMs for each response variable was formulated. To assess whether increased landscape diversity compensate negative effects of intensive vegetation management and/or floral resource availability, models with interaction terms were included (Table 3 in II). Model selection was done as described above. Additionally to the R-packages cited above the package “effects” (Fox, 2003) was used to plot the results of the GLMs.

The wild bee community across inter-row management regimes (I) and countries (II) was analysed by Detrended Correspondence Analysis (DCA; I) and Principal Component Analysis (PCA, II) based on aggregated abundance data per species and vineyard (R-packages “vegan” Oksanen et al., 2017). Significantly related functional traits to the species assemblage were assessed by first calculating community weighted means (CWMs) per trait and vineyard (I, II; R-package “FD”

Laliberté et al., 2015). Then the CWMs were fitted onto the species assemblage results of the DCA (I) and PCA (II) by vector fitting based on random permutations (n = 999; Oksanen, 2015). Similarly, field and landscape variables were fitted onto the DCA to analyse significant relations to functional traits (I). The results of the PCA (II) built the baseline for further inclusion of functional traits as response variables (Table 3) in the GLMs.

A detailed analysis of the most important field and landscape parameters for the wild bee abundance per functional trait and per four pre-selected wild bee species, was done for the Austrian bee community. The selection of the four species was based on their high/moderate abundance and their functional traits: *Lasioglossum marginatum* (99 individuals) represented a polylectic, eusocial and ground nesting species. *Bombus lapidarius* (40 individuals) was selected as a polylectic, eusocial and above-ground nesting species. *Andrena ovatula* (28 individuals) represented a solitary, ground nesting and polylectic species preferring Fabaceae. Two solitary and ground nesting *Systropha* species (*S. curvicornis* – 24 individuals, *S. planidens* – 2 individuals) represented strictly oligolectic species. Random Forests (RF; I) were computed with the R-package “party” (Hothorn et al., 2006; Strobl et al., 2008, 2007). With this recursive partitioning method, the calculation of a conditional variable importance was done based on one RF with 500 trees for each response variable (Table 3).

Pollen samples from wild bees in vineyard inter-rows were analysed qualitatively by comparing the proportions of different pollen types from different seasons (spring and summer) and locations in the vineyard (inter-row and grapevine flower). Pollen types which represented less than 1% were aggregated, because they are probably not related to pollination or pollen foraging behaviour (Westrich, 1986). Unidentified pollen was excluded from analysis. A similar approach was chosen for the analyses in manuscript IV. Further, the effects of landscape structures and land use regions on pollen richness in *Osmia cornuta* trap nests were assessed by RF and Poisson error distributed GLMMs as described above and using the already cited R-packages.

Rare wild bee species were evaluated by literature research and expert’s evaluation with focus on the Austrian wild bee fauna. A description of the rare species is given in chapter 4.4 and extends the short information presented in the core publications (I, II).

Table 3 Response and predictor variables used in the different statistical analysis of the publications (displayed by Latin numbers according to references in chapter 2).

Statistical method Variables	GLMM	GLM	DCA	PCA	RF
Response variables					
Number of wild bee species					
Total	I	II			
Per sociality type		II			
Wild bee abundance					
Total	I		I	II	
Per sociality type		II			I
Per nesting type					I
Per lecty type					I
Per species (*Andrena ovatula*, *Bombus lapidarius*, *Lasioglossum marginatum*, *Systropha* spp.)					I
CWM of sociality, nesting type, lecty type			I	II	
CWM of Inter-tegular distance		II	I	II	
Number of pollen types and brood cells	IV				IV
Total abundance of pollen types per trap nest				IV	
Predictor variables					
Field scale					
Vegetation management intensity	I		I		I
Mean vegetation coverage (%)		II			
Floral resource availability	I	II			I
Number of flowering plant species	I				I
Landscape scale (per landscape circle)					
SHDI	I	II	I	II	I
Mean slope	I				I
Landscape structures % (e.g. SNE, woods, vineyards, crops, artificial structures)	I; IV		I		I; IV
Number of solitary trees	I		I		I
Distance to the next SNE (m)	I		I		I
Land use region					IV

Notes: GLMM=Generalised linear mixed model; GLM=Generalised linear model; AICc=Second order Akaike's information criterion; DCA=Detrended Correspondence Analysis; PCA=Principal Component Analysis; CWM=Community Weighted Mean; SNE=Semi-natural element; SHDI=Shannon Landscape Diversity index; Land use regions (IV): Agricultural-, viticultural-, village-structured- and urban region,

4. Publications & Results

4.1. The two-year study from Austria

In Austria 84 wild bee species and 493 individuals were documented during two study years (2015, 2016). Increasing floral resource availability affected the total species richness and abundance positively and was, according to the RF, the most important field scale parameter for most functional traits. Permanently vegetated inter-rows had a weak negative effect on the total wild bee species richness and abundance compared to inter-rows with temporary vegetation cover. Regarding the surrounding landscape, wild bee richness and abundance was positively affected by increasing proportions of artificial areas, woods and the increasing distance to the next SNE.

Wild bee communities were clustered by the inter-row management intensities. Eusocial wild bees were significantly positively correlated to permanently vegetated inter-rows and the proportion of woods, which was also determined an important landscape variable by RF. Solitary wild bees benefited from temporary vegetated inter-rows and an increasing amount of solitary trees around the vineyards. The body size increased with the higher proportion of insect pollinated crops and the landscape diversity was identified as the most important variable for the variation in wild bees' body size in vineyard inter-rows by the RF.

The eusocial, polylectic and ground nesting *Lasioglossum marginatum* was the most abundant species. The landscape diversity and the proportion of enthomophilous crops were the most important predictors for this species' abundance in vineyards. For *Bombus lapidarius* which is also eusocial but nests above-ground, the flowering plant diversity in the vineyards and the proportion of entomophilous crops in the landscape were the most improtant parameters. For the solitary and ground nesting species *Andrena ovatula* the proportion of wood, SNE, vineyards and non-entomophilous crops at the landscape scale and the floral resource availability at the field scale were found to be the most important predictors. The two solitary and ground nesting *Systropha* species are highly specialized and forage solely on *Convolvulus* (preferably on *C. arvensis*; Scheuchl and Willner, 2016). Only landscape scale parameters (SHDI and number of solitary trees) appeared to be important for the abundance of those species in vineyards.

Core Publication I: Kratschmer et al. (2018) AEE 266, 142-152

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*. Elsevier, 266, 142-152. doi: 10.1016/j.agee.2018.07.018.

Viticultural landscape with solitary trees and hedges in Austria (Neusiedler See-Hügelland viticultural region; April 2015)

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Tillage intensity or landscape features: What matters most for wild bee diversity in vineyards?

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ABSTRACT

Vineyard inter-rows can provide habitats for a range of plant and animal species especially when covered with vegetation. However, frequent tillage results in the degradation of habitat quality and the provision of biodiversity-based ecosystem services. Wild bees are important pollinators of crops and wild plants and depend on both, floral resources and suitable nesting sites, which are influenced by the landscape configuration.

We examined effects of field and landscape parameters on wild bee species' richness, abundance and functional traits in Austrian vineyards over two years using Generalised Linear Mixed models, Detrended Correspondence Analysis and Random Forests. Alternating tillage was compared with no tillage in two inter-rows per vineyard. Forage availability in these inter-rows was estimated by flower coverage at each sampling date, and landscape features were analysed within a radius of 750 m around the vineyards.

Across all vineyards we found 84 wild bee species with a mean abundance (± SD) of 29 (± 16.6). Forage availability had the strongest positive effect on wild bee diversity and abundance. In comparison to no tillage, alternating tillage slightly increased wild bee diversity and abundance. Eusocial wild bees were more abundant in untilled inter-rows, whereas solitary wild bees were more closely associated with alternating tilled vineyards. At the landscape scale, the percentage of artificial areas (mostly villages) and distance to semi-natural elements raised wild bee diversity and abundance. The proportion of woodland increased the abundance of wild bees, in particular of eusocial taxa. Solitary wild bee abundance was enhanced by the number of solitary trees.

Pollination provided by wild bees in viticultural areas can be enhanced by maintaining a diversity of different soil management strategies to improve forage availability in vineyards. Furthermore, semi-natural elements such as fallows or solitary trees providing floral resources and nesting habitat should be preserved within viticultural landscapes.

1. Introduction

In agroecosystems, a large proportion of pollination services are provided by wild bees (Klein et al., 2007). The monetary value of insect pollination to agriculture was estimated at about 150 billion Euro worldwide (Gallai et al., 2009). Intensive agriculture is deteriorating habitat quality at different spatial scales (Kennedy et al., 2013) by increasing local disturbance and reducing landscape complexity. Parallel decrease of pollinators and insect-pollinated plants were observed in two european countries (Biesmeijer et al., 2006).

Pollination performance (quantity and quality of fruit set and yield) of certain crops has been linked to wild bee species richness (Holzschuh et al., 2012; Klein et al., 2003; Mallinger and Gratton, 2015) and to functional diversity (Fontaine et al., 2006; Garibaldi et al., 2015). Because of certain adaptations, like the activity of bumble bees at relatively low temperatures or oligolectic foraging behaviour, wild bees can

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be more efficient in pollinating wild plants or crops compared to honey bees (e.g. Mallinger and Gratton, 2015, reviewed in Klein et al., 2007). There is a consensus about the complementary pollination efficiency of wild and honey bees (Brittain et al., 2013; Greenleaf and Kremen, 2006; Isaacs et al., 2017).

Wild bees are central place foragers, depending on floral resources (pollen and nectar) and suitable nesting sites (e.g. sparsely vegetated ground, stems, dead wood, cavities) within species-specific flying distances (Westrich, 1989a). Wild bee diversity has been shown to be affected by farming practices and landscape composition (Andersson et al., 2013; Kleijn and van Langevelde, 2006), and is closely related to the proportion and distance of semi-natural elements (SNE) (Le Féon et al., 2013; Morandin and Kremen, 2013). In viticultural areas, fallows, hedgerows, natural grasslands, solitary (fruit) trees as well as stone and loess walls may be beneficial SNEs for wild bees. These elements can provide nesting habitats and floral resources for wild bees and, over a larger spatial scale, enhance pollination in intensively managed farmland (Albrecht et al., 2007). Thus, pollination services are altered by management practices on the field and landscape scale (Connelly et al., 2015; Cusser et al., 2016; and reviewed in Kennedy et al., 2013).

The cultivation of vine dates back to the Mesolithic Age and originated in the Caspian Sea region and later spread from Greece to Middle Europe (Bauer et al., 2013). Today, vineyards cover about 7.6 million hectares worldwide (OIV, 2018). Vineyards are restricted to climate types of comparatively dry and warm/hot summers which also support several thermophilic species. Vine (*Vitis vinifera* L.) is mainly self-pollinated, insect and wind pollination play a minor role for grape yield (Cabello Saenz et al., 1994). Although observations exist of honey bees foraging on vine, the plant flowers a relatively short time, thus offers very limited pollen resources and no nectar for bees (Vorwohl, 1977).

Winegrowers manage potential water and nutrient competition between inter-row vegetation and vines by tilling, mulching or through the application of herbicides (Pardini et al., 2002). At low management intensity, the inter-row space between the vines is covered with spontaneous vegetation or cover crops, which can provide floral resources for wild bees and nesting habitats especially for ground-nesting species. It has been shown that strategies to support pollinators enhances overall biodiversity and associated ecosystem services like biological pest control, soil and water protection, and soil erosion (Wratten et al., 2012). So far, no significant effect of organic versus conventional vineyard management or natural habitats in the surrounding landscape on wild bee species richness and abundance has been reported (Kehinde and Samways, 2014a, 2014b, 2012). Knowledge about how soil tillage affects wild bees is scarce compared to other management parameters (Ullmann et al., 2016; Williams et al., 2010). A meta-analysis revealed a knowledge gap of how pollinators respond to management intensity (i.e. tillage frequencies) in vineyards (Winter et al., 2018).

This study investigates the effects of field (soil tillage, forage availability) and landscape parameters on wild bee species' richness, abundance and traits in vineyards and discusses the consequences for pollination services in viticultural landscapes. The objectives were (i) to evaluate the most important field and landscape parameters and how they affect wild bee richness and abundance in vineyards, and (ii) to analyse how wild bee traits and representative species interact with field and landscape parameters.

2. Methods

2.1. Study sites

The study sites were located in two Eastern Austrian viticultural areas (Fig. 1), in Carnuntum (48° 04′ N, 16° 47′ E, province of Lower Austria) and Neusiedlersee-Hügelland (47° 54′ N, 16° 41′ E, province of Burgenland). The rainfed vineyards are spread over the small to medium scaled agricultural landscape and consist of small parcels (0.4–1.0 ha) with trellis systems on plain or hilly terrain. Besides vineyards, arable fields and other landscape features, like SNE, woods or villages, characterize the landscape. The climate is continental. In 2015 the average temperature was 11.5 °C and annual precipitation was 508 mm, while in 2016 the average temperature was lower (11.1 °C) and the annual precipitation was 636 mm (ZAMG, 2017).

We selected a total of 16 vineyards, each embedded in a landscape circle of a 750 m radius and investigated each vineyard during two consecutive years (2015 and 2016). The 750 m radius was chosen to ascertain a minimum distance of 1500 m between the studied vineyards which covers the foraging distance of different wild bee species (Zurbuchen et al., 2010). The vineyards ranged in age from 6 to 58 years (years of establishment until 2016). The cultivated vines comprised different red (Zweigelt, Blue Frankish, Blue Portuguese) and white varieties (Grüner Veltliner, Welschriesling, White Burgundy, Chardonnay, Muscatel). The studied vineyards differed in the applied inter-row tillage regime: No tillage, when the last tillage event was performed five or more years ago and resulted in permanent vegetation cover. Alternating tillage was defined as tillage in every second inter-row one to three times annually and resulted in temporal vegetation cover. In 2015, eight vineyards were untilled and eight were alternatingly tilled. In 2016 one untilled vineyard was surprisingly tilled in early spring and therefore was excluded from analysis. We decided to include an alternatingly tilled, neighbouring vineyard in the analysis for 2016 instead, which was also subject of soil and plant investigations in the same project (Fig. 1).

2.2. Sampling procedure

Wild bees were sampled with a semi-quantitative standard transect method by establishing 200 m^2 transects along inter-rows. The length of each transect was adapted to the width of the respective inter-row which ranged between 1.5 and 2 m across the studied vineyards. To detect possible effects of alternating tillage, each transect was split up into two parts: one 100 m^2 transect was established in the vegetated inter-row, the other in the neighbouring inter-row with soil tillage. Sampling dates were adjusted to the vine's phenology because the phenological stages (first leave buds, first flower buds, full florescence, berries have pea size and begin of maturation; Bauer et al., 2013) comply with wild bee sampling recommendations which should be conducted monthly from April to September (Schindler et al., 2013). This resulted in five transect walks in every vineyard between April (first leave buds) and August (begin of maturation of grapes) in both study years. Each sampling campaign was done within 2–3 days with sunny and nearly windless weather conditions and temperatures above 15 °C. Except for bumble bees (*Bombus*) and honey bees (*Apis mellifera*), which were identified and counted in the field, all other wild bee individuals were collected during a 15 min transect walk using a sweep-net, and identified to species level in the lab (Amiet, 1996; Amiet et al., 2010, 2007, 2004, 2001, 1999; Gokcezade et al., 2010; Mauss, 1994; Scheuchl, 2006, 2000; Schmid-Egger and Scheuchl, 1997), using the nomenclature according to Gusenleitner et al. (2012). Further, nests from ground-nesting wild bees were documented qualitatively if such observations occurred during sampling. Floral resources in the inter-rows (as a proxy for forage availability) were recorded at each sampling date along each transect. The flower coverage of all momentarily flowering entomophilous plants was visually estimated on each sampling event in five classes (< 1% = very low; 1–5 % = low; 5–25 % = medium; 25–50 % = high; 50–100 % = very high) following an adapted DAFOUR scale (Gardener, 2012). Similarly, the number of those entomophilous flowering plant species was documented.

Bees' functional traits (Table 1) and their relation to pollination efficiency and fruit set (De Palma et al., 2015; Fontaine et al., 2006; Garibaldi et al., 2015) were obtained from a literature search (Greenleaf et al., 2007; Scheuchl and Willner, 2016; Westrich, 1989b). To estimate the activity range of species we measured the inter-tegular-distance (ITD) of 1–5 individuals per species according to Cane (1987)

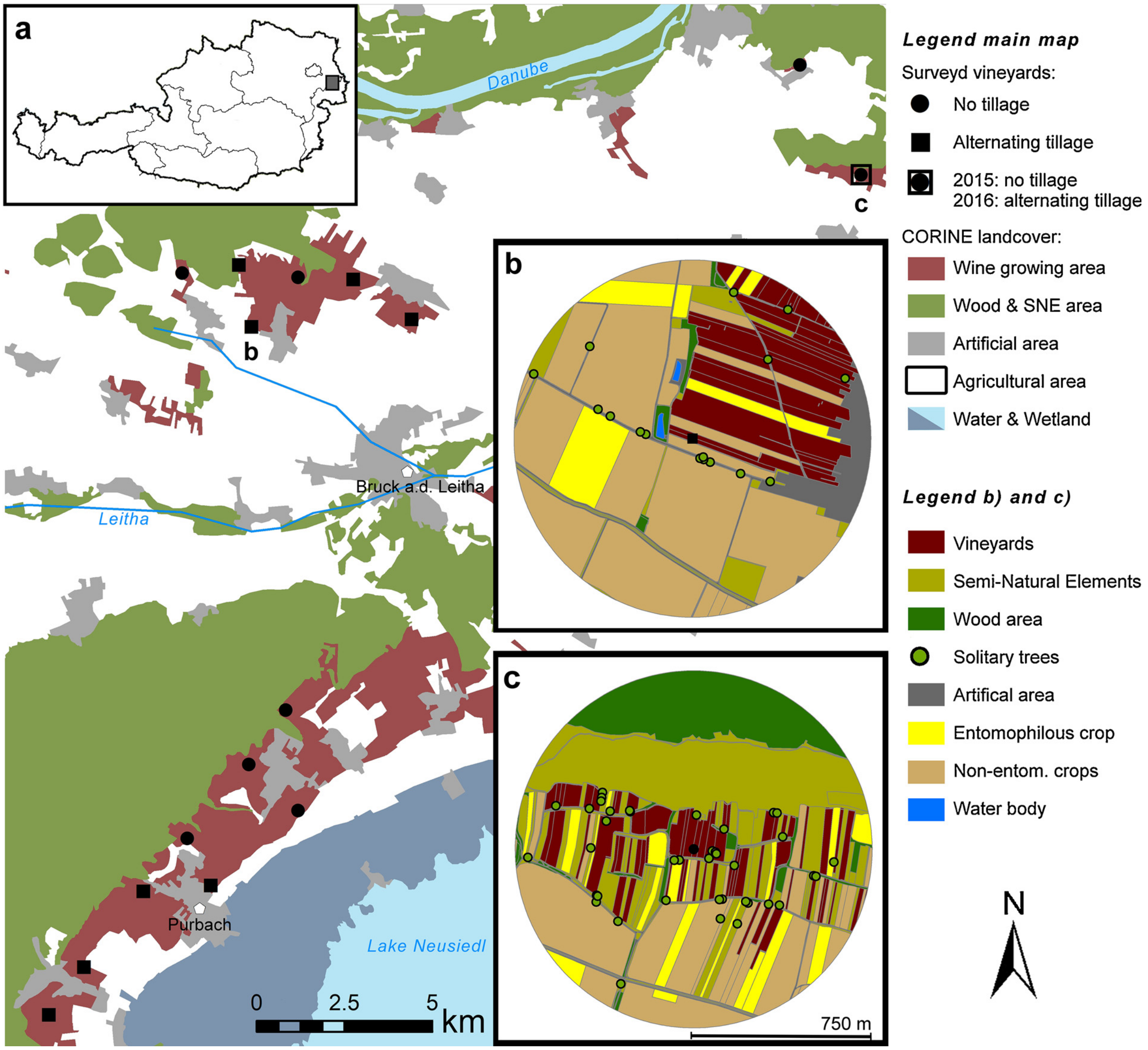

Fig. 1. Location of study area in (a) Eastern Austria in the viticultural areas Carnuntum (north of the Leitha) and Neusiedlersee-Hügelland (south of the Leitha river). Main map with locations of the studied vineyards including respective tillage regime, expansion of wine growing-, wood-, SNE-, artificial-, agricultural area, water and wetland according to CORINE land cover (Umweltbundesamt GmbH, 2016). Detailed examples of (b) a simplified and (c) a structured landscape circle including the mapped habitat classifications (see Table A.1 for details).

Table 1

Definitions and explanation of wild bees' functional traits used for trait analysis.

Trait	Variable types	Definition	Rationale for selection
Nesting type	Ground-nesting	Excavating nest in the ground	Interlinked with habitat requirements (e.g. bare compact ground or pre-existing cavities) which alter bee diversity and abundance
	Above-ground nesting	Nesting in pre-existing cavities, plant stems, dead wood (incl. *Bombus* spp.)	
	Parasitic	♀ lay their eggs in nests of specific host species	Less efficient pollinators (Garibaldi et al., 2015) but indicates vital host populations (Hudson et al., 2006)
Sociality	Solitary	♀ nests and breeds alone	Type of sociality could result in shorter (solitary) or longer seasonal activity (eusocial) and may affect duration in which a species is pollinating
	Eusocial	♀ nesting and breeding in colonies (unfertile workers and fertile females)	
ITD (mm)	Continuous Variable	The shortest linear distance measured between a wing tegulae across the dorsal thorax (Cane, 1987)	ITD is strongly related to foraging distance, e.g. species with ITD $<$ 1.5 mm just fly less than 50 m while large species with ITD $>$ 3 mm can visit locations over 1 km far away (Greenleaf et al., 2007). Increased activity range may contribute to pollination within a wider radius
Lecty	Polylectic	Pollen generalists: Foraging on plants of different families but can show a certain degree of flower constancy	A greater variety of plants may be pollinated
	Oligolectic	Pollen specialists: Only foraging on plants from the same genus or family	Effective pollination due to adaption

*ITD*Inter-tegular-distance in mm

Table 2
Candidate models for wild bee species richness and abundance used for model averaging.

Response	Fixed Factors	K	AICc	$\Delta AICc$	ω_i	LL	Dispersion	R^2m	R^2c
Wild bee species richness	Forage availability Artificial area %	6	539.75	0	0.46	−263.60	1.2045	0.56	0.65
	Tillage frequency Forage availability Artificial area %	7	540.27	0.52	0.35	−262.77	1.2050	0.56	0.65
	Forage availability Distance to SNE (m)	6	541.53	1.78	0.19	-264.49	1.2467	0.56	0.63
Wild bee abundance	Forage availability Distance to SNE (m) Wood area %	7	681.86	0	0.45	−333.56	2.0258	0.65	0.89
	Tillage frequency Forage availability Wood area % Artificial area %	8	682.73	0.87	0.29	−332.89	1.9619	0.64	0.90
	Tillage frequency Forage availability Distance to SNE (m) Wood area %	8	683.04	1.18	0.25	−333.04	2.0362	0.65	0.88

K Number of estimated parameters.
AICc Second order Akaike Information Criterion.
Δ AICc Difference between AICc to the next most parsimonious model.
ω_i Akaike's weight.
LL Laplace Likelihood.
R^2m R^2marginal.
R^2c R^2conditional.

with a digital microscope (Keyence VHX-5000). The activity range of species is known to increase when ITD increases (Greenleaf et al., 2007) and may be affected by the surrounding landscape. Since bumble bees were identified in the field, the ITD was measured from five individuals per species selected from the collection at BOKU (Vienna). The selection was limited to individuals sampled in eastern parts of Austria.

2.3. Landscape survey

Field mapping of landscape circles was performed in July 2015 following the EUNIS habitat type classification (European Environment Agency, 2016) and based on the Austrian land utilization mapping ("Nutzflächenkartierung"; INVEKOS data, BMLFUW, 2012). For landscape parameter analysis, landscape features were aggregated to eight habitat classes (Table A.1). Woods (which include woodlots and forests) were not included in SNE, because 46% of sampled species are related to open land habitats, while 25% species use woods or wood edges as habitats amongst others (Scheuchl and Willner, 2016). Therefore, only landscape features characteristic for open areas were pooled as SNEs (orchards, tree rows, natural grasslands, fallows, grass strips, field margins, hedgerows etc.; Table A.1) and the proportion of woods was treated as a separate habitat class (cf. Rollin et al., 2013). The proportions of habitat classes and the distance to SNE (m; Table A.2) were calculated in ArcGIS (ESRI, 2013). The Shannon landscape diversity index (SHDI) was computed based on raster data in FRAGSTATS 4.2 (McGarigal et al., 2012) and CHLOE (Boussard and Baudry, 2014), the latter software was also used for validation of the index. Further, the mean slope per landscape circle (Table A.2), representing a terrain factor, was calculated using a digital elevation model with a resolution of 10 m in ArcGIS.

2.4. Data analyses

Honey bees (*Apis mellifera*) were excluded from analysis because their occurrence and abundance was biased on nearby hives (cf. Kennedy et al., 2013), present close to some of the investigated vineyards. Because of the low number of observations in the category "very high" forage availability ($n = 5$) we decided to merge this category with the level "high", representing $> 50\%$ flower coverage in further analysis. This was also done to avoid deterioration of model quality due to influential observations in the level "very high". All statistical analyses were computed in R 3.3.2 (R Core Development Team, 2017; RStudio Team, 2015).

To check for spatial autocorrelation we conducted Moran's Test with the R package "ape" (Paradis et al., 2004) on the response variables species richness and abundance across the respective distances (m) between each vineyard, calculated with the Geographic Distance Matrix Generator V1.2.3 (Ersts, 2016). The distance between nearby vineyards ranged between 1501–3594 m. Neither significant autocorrelation among study sites for bee species richness ($P = 0.61$) nor abundance ($P = 0.73$) was found. Data exploration (collinearity, outlier detection, distribution of response variables) was accomplished according to Zuur et al. (2010). Predictors were expected to be collinear and thus not included in the same model if cor $\geq$ 0.3. Differences of species richness and abundance between the two viticultural areas (Neusiedlersee-Hügelland and Carnuntum) were tested with non-parametric Mann-Whitney U tests.

To analyse, which field (tillage regime, forage availability, number of flowering species) and/or landscape parameters (SHDI, proportion (%) of SNE, woods, vineyards, entomophilous crops, non-entomophilous crops, artificial/constructed entities, distance to SNE (m), number of solitary trees and mean slope) affect wild bee species richness and abundance in vineyards we formulated Generalized Linear Mixed Models (GLMMs) with a Poisson error distribution using the R package "lme4" (Bates et al., 2015). To account for the temporal non-independent observations within the same vineyard and to analyse both study years together the months (April to August) of each year ($N = 10$) were chosen as random factors. For each response variable a model set of 40 GLMMs was formulated by combining non-collinear field and landscape parameters.

Model selection was carried out by using the second order Akaike Information Criterion corrected for small sample size (AICc; Motulsky and Christopoulos, 2003). The cut-off to decide whether a model is more likely to be correct than the next best model was set at $\Delta AICc < 2$ (R package "AICcmodavg"; Mazerolle, 2016). This resulted in a set of three equally correct models for each response variable (Table. 2) and thus a high degree of model selection uncertainty (Burnham and Anderson, 2002). Therefore, model averaging was carried out using the so called Zero Method (Burnham and Anderson, 2002), as the focus was to determine which variables would have the strongest effect on wild bee diversity and abundance (Grueber et al., 2011; Nakagawa and Freckleton, 2011). The predictor variables in the model sets were found to be on different scales (i.e. percentage scale of landscape variables, metric scale of distance measurements, levels of categorical variables) and therefore standardized using Gelman's approach (R Package "arm" Gelman et al., 2016). Model averaging was done using the R Package "MuMIn" (Barton, 2016).

To analyse functional traits, community-weighted means (CWM) were calculated with the "functcomp" function in the R package "FD" (Laliberté et al., 2015). A Detrended Correspondence Analysis (DCA) was constructed with the R package "vegan" (Oksanen et al., 2017) because it is a more robust method for community ordination and corrects drawbacks from data sets with long ecological gradients (Oksanen, 2015). A matrix including aggregated abundance per species data across both study years was used for the DCA. The CWMs as well as field and landscape parameters were fitted onto the DCA using the function "envfit" in "vegan". This function calculates the correlation and associated p-values between the ordination of species assemblage per vineyard and the explanatory variables by random permutations ($n = 999$; Oksanen, 2015).

Additionally, we formulated conditional Random Forests (RF) to assess further the importance of the field and landscape parameters for wild bee traits. This recursive partitioning method and the calculation of the conditional variable importance (Strobl et al., 2009) was done with the R package "party" (Hothorn et al., 2006; Strobl et al., 2008, 2007). For each response (i.e. abundance of above-ground nesting, ground-nesting, solitary, eusocial and polylectic wild bee species, CWM of ITD) a RF with 500 trees was grown. The number of randomly chosen predictors at each tree's node was set to the square root of total predictors ($n_{\text{randompred}} = 4$; cf. Puech et al., 2014). Due to the low abundance of parasitic and oligolectic species those traits were not included in this analysis. To determine the importance of field and landscape parameters on single species we selected four species that represented different traits. The second criterion in choosing these species was their high abundance. *Andrena ovatula* represented a ground-nesting and solitary species, *Bombus lapidarius* an above-ground nesting eusocial species and *Lasioglossum marginatum* a ground-nesting eusocial species. The abundance of the two *Systropha* species (*S. curvicornis*, *S. planidens*), both ground-nesting and solitary, was pooled to represent strictly oligolectic species. The abundance of each selected species was used as a response variable in the same RF analysis settings as described above.

3. Results

In total, 84 wild bee species and 493 individuals were recorded during both years (Table A.3). Among those species, 31 were represented by a single individual only. *Lasioglossum marginatum* was the most abundant species, comprising 19% of the sampled individuals. One species, *Lasioglossum laterale*, a mediterranean "sweat bee" species was documented for the first time in Austria (Ebmer et al., 2016). We found no difference in wild bee species richness ($W = 41.5$, $P = 0.63$) nor in abundance ($W = 27.5$, $P = 0.44$) between the two viticultural areas (Carnuntum and Neusiedlersee-Hügelland).

Model averaging revealed effects of both field and landscape parameters on wild bee species and abundance (Fig. 2). At the field scale, forage availability had the strongest positive effect on wild bee species richness and abundance. Although the entomophilous flowering plant species richness (species numbers per observation, see plant list: Table A.4) was not included in the best fitting models, the dependency of forage availability on entomophilous plant diversity is indicated by the strong correlation ($cor = 0.66$, $P < 0.001$) of these parameters. Overall (mean ± SD), only a small number of entomophilous plants flowered in the inter-rows per observation (3.85 ± 2.29). Additionally, at the field scale, untilled inter-rows displayed a slightly negative effect on wild bee diversity and abundance compared to vineyards with alternating tilled inter-rows (Fig. 2). Alternating tilled inter-rows possessed slightly higher forage availability (Fig. A.1) and flowering entomophilous plant species richness (Fig. A.2) compared to untilled inter-rows.

At the landscape scale, the percentage of artificial entities, like villages and the distance to SNE (over 60% thereof fallows), affected both response variables positively. These effects were stronger for wild bee species richness than for abundance. Further, the percentage of artificial areas was a more important predictor for wild bee species richness than the distance to SNE (Fig. 2a), whereas this was reversed for wild bee abundance (Fig. 2b). Compared to forage availability, the percentage of woods was an equally important predictor for abundance (Fig. 2b) but had only a very small positive effect.

The CMW calculation revealed that the majority of individuals in vineyards were ground-nesting (72%) and polylectic (88%; Table A.5). Thus, neither nesting type nor lecty were significantly related to tillage regime or landscape parameters (Fig. 3). The RFs also revealed that forage availability was the most important predictor for the abundance of the different nesting types, sociality and polylectic wild bees (Fig. A.3 a–e).

Oligolectic wild bees only occurred in vineyards with high forage availability of the host plants. For example, *Eucera* species specialised on Fabaceae pollen were observed in high abundance in vineyards with seeded inter-rows containing *Trifolium* spp., *Medicago sativa* or *Onobrychis viciifolia*. *Systropha curvicornis* (22 individuals) and/or *S. planidens* (4 individuals) occurred in almost every vineyard, because their host plant *Convolvulus arvensis* was found in every vineyard. The RF indicated that the most important predictor for both *Systropha* species was the number of solitary trees and the SHDI (Fig. 4a), while forage availability and entomophilous plant species richness in the vineyards were not that important. Overall, 57% of all individuals were eusocial, 40% solitary and only 3% parasitic species. This ratio was reversed considering species richness, because 29% of all species were eusocial, 56% solitary and 12% parasitic (sociality of the remaining 3% is unknown). Sociality was significantly related to inter-row tillage (Random permutation test; $P = 0.001$). Eusocial species were related to untilled vineyards and significantly increased with a higher proportion of woods (Random permutation test; $P = 0.007$). This parameter was, apart from forage availability, the most important landscape predictor for eusocial as well as ground-nesting wild bees (RF results; Fig. A.3 a, d). For *Lasioglossum marginatum* (99 individuals in total; eusocial and ground-nesting) the proportion of entomophilous crops and landscape diversity (SHDI) were the most important predictors (Fig. 4b). For *Bombus lapidarius* (40 individuals in total) which is also eusocial but nests above-ground, the proportion of entomophilous crops on the landscape scale and the entomophilous plant species richness in the vineyards were the most critical parameters (Fig. 4c). For all above-ground nesting wild bee individuals together, landscape diversity (SHDI) and the proportion of artificial entities were important landscape parameters (Fig. A.3 e). Solitary species were closely associated with alternating tillage and significantly increased with higher numbers of solitary trees (Random permutation test; $P = 0.04$). Further, RF revealed the proportion of entomophilous crops to be an important landscape predictor for solitary wild bees (Fig. A.3 b). On contrary to these result, for the solitary and ground-nesting *Andrena ovatula* (28 individuals in total) the proportion of wood, SNE, non-entomophilous crops and vineyards were found to be the most important landscape parameters by the RF (Fig. 4d). Due to the low abundance of parasitic species, they were not represented by the CWMs (Table A.5) and therefore not included in the DCA (Fig. 3) or RF. The mean (± SD) CWM of inter-tegular-distance was 2.13 (± 0.37) mm and was significantly associated with untilled vineyards (Random permutation test; $P = 0.016$). On the landscape scale, the ITD increased with the

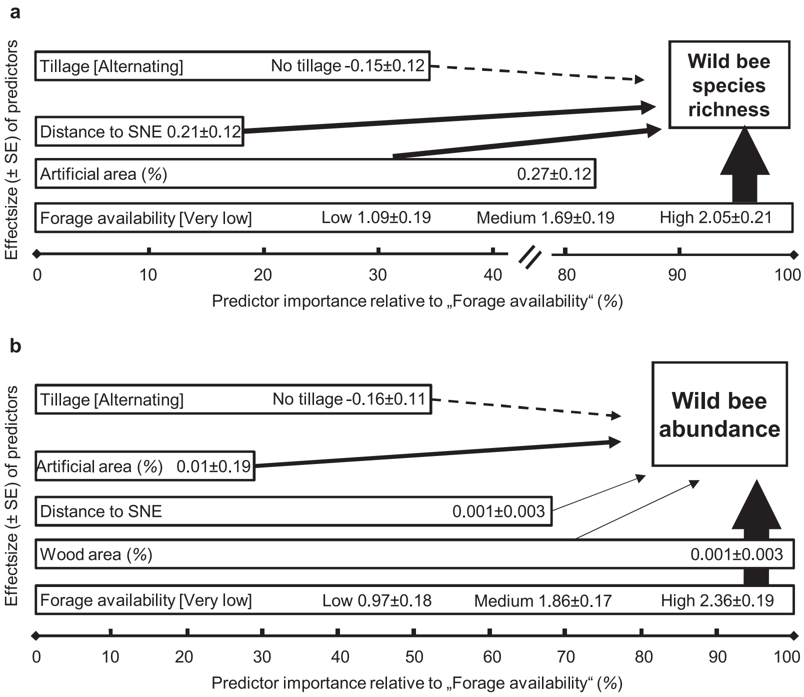

Fig. 2. Parameters affecting (a) wild bee species richness and (b) wild bee abundance in Austrian vineyards derived from model averaging including effect size (estimate values ± SE). *Bar length* = relative importance of a predictor in relation to the most important predictor (forage availability); *full line arrows* = positive effects; *dashed line arrows* = negative effects; *arrow line width* = effect size weighted by the averaged parameter estimate; *squared brackets* = base level for categorical parameter estimation.

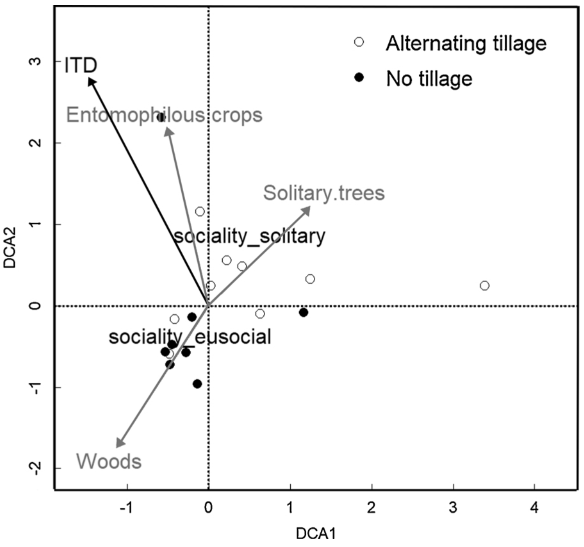

Fig. 3. DCA plot including significantly correlated CWM in black (community weighted means; ITD = inter-tegular-distance) and aggregated field and landscape parameters in grey (entomophilous crops and woods in %; solitary trees in total numbers) per vineyard. Significance level set at $P = 0.05$ based on permutation test (n = 999).

percentage of entomophilous crops (Random permutation test; $P = 0.005$) which were mainly sunflowers. The RF revealed different landscape parameters that represent landscape diversity (SHDI, proportion of SNE) to be important variables for explaining the ITD (Fig. A.3 f).

4. Discussion

We found that both field and landscape parameters affected wild bee species richness and abundance in central european viticultural landscapes. Overall, the quantity of floral resources was the most important factor. Eusocial wild bees benefit from untilled inter-rows, nevertheless, alternating tillage increased wild bee species diversity and abundance. In the surrounding landscape, wood, settlements or solitary trees provided additional habitats for nesting and foraging. In the studied vineyards, 12.3% of Austria's 690 wild bee species published in Gusenleitner et al. (2012) were represented.

4.1. Field scale

Forage availability, representing pollen and nectar resources, had the greatest effect on wild bee species richness and abundance. The method to estimate forage availability in this work has to be critically examined: Firstly, it is based on visual estimations which are more error prone (Morrison, 2016) than absolute counts of e.g. flower units. Inter-observer error was avoided as only the first author performed all cover estimations. Secondly, a flower coverage estimate does not fully assess nectar and pollen quantities and qualities which are known to be different for different plant species (e.g. Hicks et al., 2016). Measuring nectar and pollen quantity would certainly be one of the most accurate methods to assess forage availability. It was recommended by Szigeti et al. (2016) to combine methods that provide data with spatio-temporal resolution or high coverage. The approach in this study fulfils these requirements because forage availability was estimated on each sampling date (temporal resolution) and for each of the two neighbouring inter-rows, that comprised one transect, separately (spatial resolution). On a wider spatial scale, entomophilous crops were mapped and treated as independent predictor in data analysis. The results of the strong effect of forage availability are reliable because the RF revealed it to be the most important variable for the abundance of different traits. Further, this strong effect was documented in agroecosystems (Williams et al., 2015) as well as in other ecosystems like woodland remnants (Williams and Winfree, 2013), different types of fallows (Kuussaari et al., 2011) and urban sites (Hennig and Ghazoul, 2012). Mass flowering of single plant species are likely to increase the abundance of certain wild bee groups (Westphal et al., 2003; Zurbuchen and Müller, 2012). The high variable importance of entomophilous crops for *Bombus lapidarius* and *Lasioglossum marginatum* reported here indicates that even single wild bee species can be associated with the high availability of pollen and nectar resources from few plant species. Wild bee species richness is likewise strongly related to the diversity of plant species (Potts et al., 2003). Entomophilous plant species richness

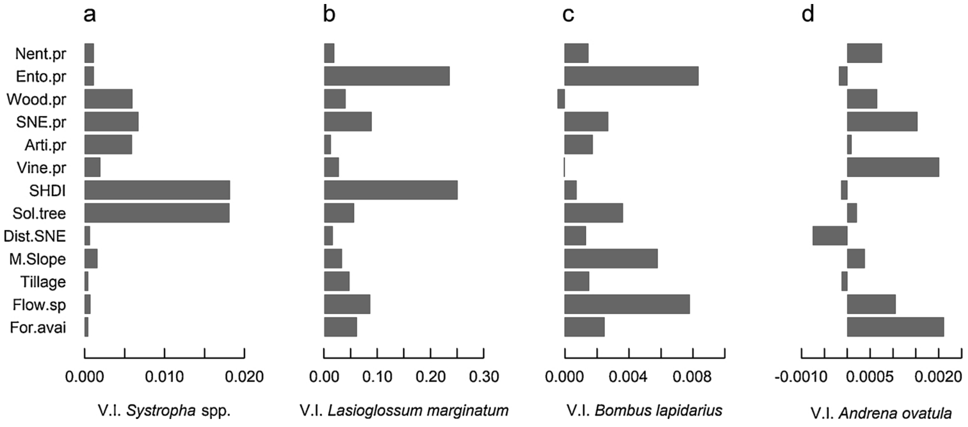

Fig. 4. Conditional variable importance (V.I.) of field (forage availability (For.avai), entomophilous plant species richness (Flow.sp), tillage regime (Tillage)) and landscape parameters (mean slope (M.slope), distance to SNE (Dist.SNE), number of solitary tree (Sol.tree), Shannon Landscape Diversity Index (SHDI), the proportions of vineyards (Vine.pr), artificial entities (Arti.pr), semi-natural elements (SNE.pr), woods (Wood.pr), entomophilous crops (Ento.pr), non-entomophilouse crops (Nent.pr)) for (a–d) the abundance of four wild bee species in vineyards each analysed separately by random forests.

did not improve the GLMMs with wild bee species richness or abundance as response. As more than half of the total wild bee species reported here were solitary, the importance of plant diversity for wild bee species richness is reflected in the RF result for solitary wild bee abundance. Similar results were reported from a wine-growing area in New Zealand, where butterfly species richness and abundance increased considerably in habitats with suitable nectar sources and larval host plants which were underrepresented in vineyards (Gillespie and Wratten, 2012).

Vineyard inter-rows can be considered as wildflower strips, for which it is known that they tend to get dominated by grasses over the years and should be renewed every 4 to 5 years to ensure floral resources (Schmid-Egger and Witt, 2014). In the studied vineyards, forage availability was similar at the two tillage regimes which could be explained by the general low tillage frequency. As only every second inter-row was tilled each year, temporally bare soil occurred from May to June and vegetation cover was restored during the rest of the year. However, the attraction of high floral resources in vineyard inter-rows could lead to increased pesticide exposure of wild bees and other flower visiting insects: Although, in the surveyed vineyards no insecticides were used for at least 5 years, in other conventional vineyards insecticides may be applied which are hazardous to bees (Brittain et al., 2010; e.g. Kwizda Agro, 2018a, 2018b, 2016). Further, in conventional viticulture high rates of herbicides and fungicides are applied, which could have negative effects on wild bees (Helmer et al., 2015; Sanchez-Bayo and Goka, 2014; Tesoriero et al., 2003). However, research on the effects of herbicides and fungicides focuses on honey bees or certain wild bee species (often bumblebees); therefore the effect on different wild bee species is uncertain.

We expected that ground-nesting wild bees would benefit from undisturbed soil of untilled inter-rows but the DCA did not reveal any relation of tillage regimes and nesting types. We found bare soil patches in vineyards of both tillage regimes and observed that ground-nesting species nested in both vineyard types. Alternating tillage did not negatively affect ground-nesting bees which could be explained by tillage depths ranging from 5 to 20 cm, whereas nests are located on average between 17 and 35 cm below the soil surface (Cane and Neff, 2011). The most abundant species, *Lasioglossum marginatum*, was probably not affected by tillage because they nest between 35 to 60 cm in the ground (Sakagami and Michener, 1962 cited in Cane and Neff, 2011 Appendix). This was also confirmed by the RFs because the tillage regime was a variable of minor importance to explain the total ground-nesting wild bee abundance as well as the abundance of *Andrena ovatula*, *Lasioglossum marginatum* and the two *Systropha* species. As only every second inter-row was tilled each year, enough undisturbed soil exists for ground-nesting species to complete juvenile stage and emerge as adult insect in the next season.

Our study shows that eusocial species benefitted from undisturbed soil conditions in untilled vineyards. This result is supported by findings from a meta-analysis where soil tillage negatively affected eusocial species in different agro-ecosystems (Williams et al., 2010). Eusocial species are more vulnerable to disturbances than solitary bee species, because they have a longer activity period. A single fertile female is responsible for breeding and a colony might be more difficult to restore after a disturbance than a single nest. Further, almost all eusocial species in our study were ground-nesting. Bumble bees were classified as above-ground nesting because they colonize pre-existing cavities above or below ground, therefore tillage could have negative effects on bumble bees. *Bombus lapidarius* prefers to nest above-ground (Scheuchl and Willner, 2016) which explains the low variable importance of tillage frequency. Due to their large body size and high activity range (Zurbuchen and Müller, 2012), this species is able to forage in vineyards while nesting in more distant habitats (e.g. wood edges). Solitary species probably colonize structures close to the vineyards and are attracted by the floral resources of infrequently tilled inter-rows.

4.2. Landscape scale

Our finding that the percentage of artificial areas in the surrounding landscape positively affected wild bee species richness and abundance suggests that urban areas provide important habitats for wild bees (reviewed in Hernandez et al., 2009). Indeed, private gardens enhance wild bee diversity and abundance and consequently increase pollination services because they offer higher floral resources throughout the vegetation period compared to surrounding agricultural areas (Samnegård et al., 2011). The amount of artificial areas in the studied viticultural landscape ranged between 1.4 and 40%, comprising a high proportion of villages, which conforms with results from a french study where wild bee diversity was highest in landscapes with 50% of impervious surface (Fortel et al., 2014). However, these authors did not find a positive effect of urban areas on wild bee abundance. In our study, the effect of artificial areas on wild bee abundance in comparison to species richness was also smaller. As it was reported by Cane et al. (2006), wild bee abundance responded heterogeneously to the degree of urbanization and was better explained by ecological traits: Above-ground nesting species increased within the vicinity of settlements because vertical structures (e.g. unplastered walls or garden sheds) provide pre-existing cavities in higher density on the contrary ground-nesting species were associated with less densely populated areas (Cane, 2005; Cane et al., 2006). The RFs for these two nesting types revealed a similar pattern. The percentage of artificial entities was among the most important landscape predictors for above-ground nesting wild bees.

In contrast to other studies (Kennedy et al., 2013; Kleijn and van Langevelde, 2006; Le Féon et al., 2010), we did not find a positive effect of the proportion of SNE on wild bee diversity or abundance. This could be related to our definition of SNE, which only included “open land” landscape features and excluded woods (Rollin et al., 2013 call it "herbaceous SN habitat"). The percentage of woods had a small positive effect on wild bee abundance in vineyards and was significantly related to eusocial species. This effect was also reported by Rollin et al. (2013) who explained this through the diversified floral resources and undisturbed nesting habitats of herbaceous margins, which especially favour eusocial wild bees (Nicholson et al., 2017). One third of the observed 22 eusocial species also use woods and their verges as habitats and another third are ubiquitous regarding their habitat requirements (Scheuchl and Willner, 2016; Westrich, 1989b). This conforms to other studies investigating the effects of landscape parameters on eusocial wild bees. For example, bumble bee species composition in fallows is clearly positively associated with wood cover in the surrounding landscape (Toivonen et al., 2016). The positive effect of woods on wild bees in this study is further explained by the semi-natural structure of the oak and oak hornbeam forests of the north-eastern Leithagebirge, which are part of the Natura 2000 network and are therefore protected under the European Habitats Directive and Birds Directive (Burgenländisch Burgenländisch Landesregierung, 2018). The high habitat value of oak woodlands and the negative effect of their conversion to vineyards on the diversity of plant and animal species was reported by Merenlender (2000). However, the vineyard area in our study region decreased from 2009 to 2015 by 16.6% (Österreich Wein, 2018, 2015) as forest cover increased throughout Austria (BFW, 2011). It has been shown that the conservation of woods within viticultural landscapes is interlinked to a range of ecosystem services, like carbon sequestration (Williams et al., 2011). Further, bird diversity was higher in highly structured viticulture landscapes that consist of small-scale vineyards within a landscape matrix with woods, shrubs and open habitats (Steel et al., 2017). However, woods and urban land have also been reported to be habitats for vine pathogen vectors (Baumgartner et al., 2006).

Solitary species increased with the number of solitary trees, which offer cavities or dead wood elements for above-ground nesting wild bees but also undisturbed soil around them as nesting habitat for ground-nesting wild bee species. The latter was reflected by the high importance of solitary trees for the two *Systropha* species. The moderate importance of solitary trees for *Bombus lapidarius* is explained by the high amount of cherry trees that are characteristically planted in the study region (Burgenländisch Burgenländisch Landesregierung, 2018). These trees flower in early spring when young bumble bee queens start to establish new colonies and thus require high quantities of pollen and nectar resources.

The increasing distance to the next SNE (not including woody areas) had a small positive effect on wild bee species richness and abundance. More than half (63%) of the closest SNE were fallows and 25% were grass strips. Two competing explanations arise here: nearby fallows and grass strips either represented poor habitat quality for wild bees, or quite on the contrary, the good habitat quality resulted in a pull-effect. According to field observations, the forage availability of fallows was low, supporting the first explanation. This should be interpreted with caution because the effect was weak and the variable was not considerably important for any trait group or species analysed with RFs. Depending on the age, management and type of seed mixtures, fallows and grass strips show a high variation in floral resources (Haaland et al., 2011; Kuussaari et al., 2011; Toivonen et al., 2015). Thus, local factors, such as fallow type and vegetation characteristics can affect the species and trait composition of flower-visiting insects even stronger than landscape structure (Toivonen et al., 2016). Therefore, further research on wild bees in agricultural landscapes should include additional sampling locations in non-crop habitats.

Decreasing landscape heterogeneity reduces pollinator species richness (Andersson et al., 2013; Connelly et al., 2015) and increases the number of larger species in simplified landscapes (De Palma et al., 2015). A similar effect was found on wild bees in viticultural areas; the ITD of wild bees increased with the percentage of entomophilous crops (mainly *Helianthus annuus* and partly *Brassica napus*), which ranged between 12 and 27% in the respective landscape circles. Apart from honey bees, short-tongued bumble bee species (e.g. *B. terrestris* and *B. lucorum*) are visitors of sunflowers (Rollin et al., 2013) and can benefit from this mass flowering entomophilous crop during summer to increase sexual reproductive success. The workers of the smaller *Lasioglossum marginatum* (mean ITD = 1.78 mm) are active between March and May (Scheuchl and Willner, 2016), which coincides with the florescence of *Brassica napus* in the study region. *L. marginatum* is known to forage on *Brassica napus* (Westrich, 1989b) which explains the variable importance of entomophilous crops for this species. Further, the variable importance of entomophilous crops for *B. lapidarius* and *L. marginatum* indicates their importance for crop pollination. However, these crops represent temporal limited pollen and nectar resources, thus a high diversity of entomophilous plants is crucial for wild bee species richness (Potts et al., 2003).

5. Conclusion

We conclude that both field and landscape parameters are important to increase wild bee diversity in viticultural landscapes. Increased wild bee diversity and abundance leads to greater pollination services provided to crops (e.g. Blaauw and Isaacs, 2014; Holzschuh et al., 2012; Klein et al., 2003) and wild plants. Similar to wildflower strips in arable fields, vegetated vineyard inter-rows have the potential to provide extra floral resources for wild bees. Forage availability in vineyards could be increased by less intensive mulching or the use of diverse cover crop mixtures. Additionally, variations in tillage frequency (no tillage vs. alternating tillage) could help to provide diverse habitats, which benefit both eusocial and solitary bees. Habitat types like woods, solitary trees and villages with gardens in the surrounding landscape increase wild bee abundance and trait diversity in vineyards. Despite increasing mechanisation, the conservation of solitary trees should be targeted as a measure to enhance habitat quality for wild bees in viticultural landscapes. The contribution of SNEs to pollinator enhancement depends on the actual provision of floral resources, which needs to be investigated in future research projects.

Author contribution

SK, BP, SW, JGZ conceived and planned the experiment; SK conducted the field work in both years; SK and BP identified wild bee species; SK, MS and MG did landscape mapping in the field, digitalization and GIS work; SK, SW and DP analysed the data; all other authors were involved in significant parts of the study, wrote and/or reviewed the manuscript.

Competing financial interests

The authors declare no competing financial interests.

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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.agee.2018.07.018.

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4.2. Wild bees in vineyards across Europe

In total, 113 wild bee species and 719 individuals were sampled in vineyards across Europe in 2016. Consistent with the results from Austria increased floral resource availability affected the total wild bee species richness and abundance strongly positively. For the total wild bee abundance and the species richness and abundance of solitary wild bees the positive effect of extensive inter-row vegetation management was enhanced by increasing floral resource availability. Landscape diversity had a minor positive affect on the total wild bee species richness, but compensated low floral resource availability in inter-rows for the eusocial wild bee abundance in vineyards.

Across Europe distinct wild bee communities and functional traits were present in vineyard inter-rows. Eusocial wild bees were characteristic for Austrian and French vineyards while solitary wild bee species were more abundant in Spanish and Romanian inter-rows. The highest abundance of bumble bees was reported from the Austrian vineyards, which resulted in the significant relation of body size (CWM of ITD) to the Austrian wild bee assemblage.

The effect of vegetation management intensity on wild bees and other pollinators in vineyards was not assessed by the meta-analysis, because only two publications were selected for data extraction. However, significant positive effects of extensive vegetation management on the overall biodiversity as well as on provisioning (e.g. grape yield), regulating (e.g. erosion protection, pollination, pest control or soil water balance) and supporting (e.g. soil fertility) ES were reported.

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Vineyard on a hill side in Romania with high floral resource availability in the inter-rows (Tânarve viticultural region; May, 2015; © D. Popescu)

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ORIGINAL RESEARCH

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Response of wild bee diversity, abundance, and functional traits to vineyard inter-row management intensity and landscape diversity across Europe

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Abstract

Agricultural intensification is a major driver of wild bee decline. Vineyards may be inhabited by plant and animal species, especially when the inter-row space is vegetated with spontaneous vegetation or cover crops. Wild bees depend on floral resources and suitable nesting sites which may be found in vineyard inter-rows or in viticultural landscapes. Inter-row vegetation is managed by mulching, tillage, and/or herbicide application and results in habitat degradation when applied intensively. Here, we hypothesize that lower vegetation management intensities, higher floral resources, and landscape diversity affect wild bee diversity and abundance dependent on their functional traits. We sampled wild bees semi-quantitatively in 63 vineyards representing different vegetation management intensities across Europe in 2016. A proxy for floral resource availability was based on visual flower cover estimations. Management intensity was assessed by vegetation cover (%) twice a year per vineyard. The Shannon Landscape Diversity Index was used as a proxy for landscape diversity within a 750 m radius around each vineyard center point. Wild bee

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communities were clustered by country. At the country level, between 20 and 64 wild bee species were identified. Increased floral resource availability and extensive vegetation management both affected wild bee diversity and abundance in vineyards strongly positively. Increased landscape diversity had a small positive effect on wild bee diversity but compensated for the negative effect of low floral resource availability by increasing eusocial bee abundance. We conclude that wild bee diversity and abundance in vineyards is efficiently promoted by increasing floral resources and reducing vegetation management frequency. High landscape diversity further compensates for low floral resources in vineyards and increases pollinating insect abundance in viticulture landscapes.

KEYWORDS

Apiformes, ecosystem services, floral resource availability, functional traits, GLMM, Shannon Landscape Diversity Index, vegetation management, viticulture landscapes

1 | INTRODUCTION

Wild bees and honey bees are important pollinators of crops (Brittain, Williams, Kremen, & Klein, 2013; Klein et al., 2007) and wild plants (Fontaine, Dajoz, Meriguet, & Loreau, 2006). Pollination efficiency of different crops is strongly related to wild bee species diversity (Földesi et al., 2015; Winfree et al., 2018) as well as functional diversity (Fontaine et al., 2006; Garibaldi et al., 2015). Research demonstrated that wild bees are threatened by intensive agricultural practices (Kremen, Williams, & Thorp, 2002) such as high pesticide application (Woodcock et al., 2017), and/or frequent soil tillage (Williams et al., 2010), which result in reduction of floral resource availability (Williams et al., 2015) and contribute to landscape simplification (Senapathi, Goddard, Kunin, & Baldock, 2017).

Wild bee diversity, abundance, and pollination are strongly positively affected by the enhanced quantity and quality of floral resources (Williams et al., 2015), increased landscape heterogeneity (Andersson, Birkhofer, Rundlöf, & Smith, 2013), and the proportion of (semi-) natural areas in agricultural landscapes (Nicholson, Koh, Richardson, Beauchemin, & Ricketts, 2017). However, wild bee species composition is differently affected by environmental disturbances and landscape configuration (Carrié et al., 2017; Hopfenmüller, Steffan-Dewenter, & Holzschuh, 2014) because functional traits are closely related to habitat requirements (Williams et al., 2010).

Vineyards cover about 7.6 million hectares worldwide (OIV, 2018). The commercial grape vine (*Vitis vinifera* L.) is self-pollinated and wind pollinated, thus pollination by insects only plays a minor role for grape yield (Cabello Saenz, Luis Villota, & Tortosa Tortola, 1994). Bees were rarely observed foraging on grapevine flowers (Vorwohl, 1977), but vineyards can provide habitats for wild bees to increase pollination for insect-pollinated crops, fruit trees, cover crops, and wild plants. Maintaining wild bee diversity is essential for the resilience of pollination services (Bartomeus et al., 2013; Brittain, Kremen, & Klein, 2013) and also enhances diversity of associated plants pollinated by wild bees (Biesmeijer et al., 2006). Improving habitats for pollinators simultaneously enhances ecosystem services like biological pest control, soil and water quality protection, or landscape aesthetics (Wratten, Gillespie, Decourtye, Mader, & Desneux, 2012). Establishing and maintaining noncrop flowering areas within the farmland matrix promotes the native plant community, provides habitats for a range of insects, bird and mammals, and thus contributes to biodiversity conservation (Wratten et al., 2012). Further, a spill-over effect of flower visitation rates in insect-pollinated crops from field margins was observed for wild bees, which increased crop yields in closer proximity to field margins (Woodcock et al., 2016). As winegrowers experience an increased consumer demand for eco-friendly produced wine (Schütte & Bergmann, 2019), establishing flower-rich habitats for wild bees in vineyards can be used for marketing.

Depending on the vegetation management intensity, vineyard inter-rows are comparable with field margins or wildflower strips in agricultural landscapes, which increase wild bee diversity (Haaland, Naisbit, & Bersier, 2011). Winegrowers manage inter-row vegetation by tillage, mulching, or herbicide application to mitigate potential water and/or nutrient competition between the vines and the inter-row vegetation (Pardini, Faiello, Longhi, Mancuso, & Snowball, 2002). The intensity of this disturbance varies among wine-growing areas across Europe according to local pedological and climatic conditions.

Wild bees in vineyards have been shown to benefit from biodiversity-friendly management practices and from mosaics of semi-natural elements within the viticultural landscape (Kehinde & Samways, 2014a, 2014b; Kratschmer et al., 2018). Further, species characterized by certain traits may respond similarly to a certain vegetation management measure or landscape configuration in wine-growing areas. For example, ground-nesting species could benefit from undisturbed soil conditions for nesting in permanently vegetated inter-rows. Further, larger species may compensate low landscape diversity with their increased activity range and forage in more fragmented landscapes (Zurbuchen et al., 2010). A meta-analysis

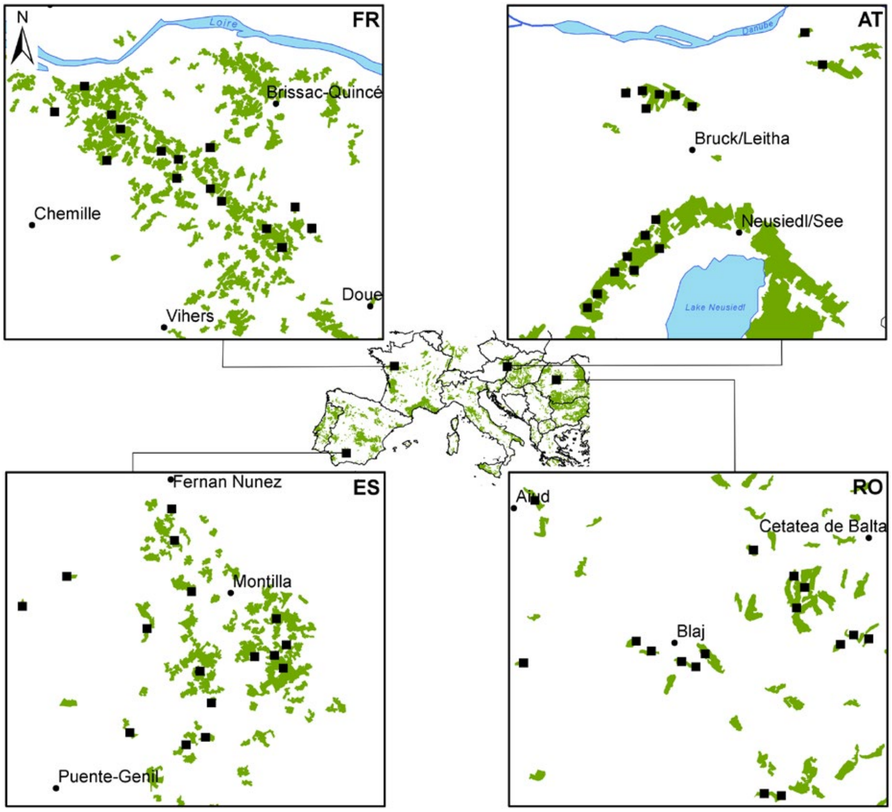

FIGURE 1 Maps of studied wine-growing areas across Europe. FR: Loire Valley, AT: Carnuntum and Neusiedler See-Hügelland, RO: Târnave and ES: Montilla Moriles. Green shading: Viticulture areas according to CORINE land cover (EEA, 2017). Squares: Location of studied vineyards and wine-growing areas

included only two studies about the effects of vineyard vegetation management on pollinators and concludes that knowledge about the effects of inter-row vegetation management on wild bee diversity is scarce (Winter et al., 2018). Further until now, studies about wild bee diversity and functional traits in response to vineyard management and in relation to landscape diversity in different climatic regions (i.e., different European countries) have not yet been carried out.

We hypothesized that vegetation management intensity, floral resource availability, and the surrounding landscape diversity affect wild bee diversity, abundance, and functional traits in vineyard inter-rows across Europe. We expected that inter-row vegetation management effects on bees would be less pronounced in vineyard with higher floral resource availability and in heterogeneous than in simpler landscapes.

2 | MATERIALS AND METHODS

2.1 | Study sites

This study was conducted in four viticultural areas across Europe (Spain, France, Austria, and Romania) in 2016. The locations of the viticultural areas (Figure 1) cover three European climate zones: warm Mediterranean climate in southern Spain (Montilla Moriles in Andalusia; 37°35′N, 4°38′W), temperate oceanic climate in North-Western France (Coteaux-du-Layon in Loire Valley; 47°23′N, 0°42′E), and temperate continental climate in Eastern Austria (Carnuntum; 48°6′N, 16°51′E and Neusiedler See-Hügelland; 47°52′N, 16°37′E Lower Austria and Burgenland) and Central Romania (Târnave in Transylvania; 46°13′N, 24°06′E).

In total, 63 vineyards were investigated that ranged in age from 5 to 61 years. The distance between the vines (in-row) ranged from 0.75 to 1.9 m, and the inter-row width varied between 1.5 and 3 m. Three different intensities of inter-row vegetation management were studied (Table 1): (a) permanent vegetation cover without any disturbance for at least 5 years (Austria, France, and Romania), (b) temporary vegetation cover in every second inter-row (Austria and Romania) or in every inter-row during the winter season (Spain) by tillage, and (c) bare soil management through frequent soil tillage (Spain and Romania) and/or application of herbicides (Spain, France) in all inter-rows. Tillage depths ranged between 5 and 40 cm across the countries. In each inter-row, the vegetation coverage (%) was estimated twice a year (at the beginning of the vegetation period and 2 months later) in four 1 × 1 m subplots. The averaged vegetation cover per inter-row differed significantly (Kruskal–Wallis test: $\chi^2 = 38.50$; $df = 2$; $p \leq 0.001$) among the management intensities. The Spanish inter-rows with temporary vegetation cover were managed more intensively compared to the temporary vegetated inter-rows in Austria and Romania which resulted in a comparatively lower vegetation cover (Table 1). Mulching was done 1–5 times in permanently and temporary vegetated inter-rows. All studied vineyards—with the exception of seven Spanish vineyards with deficit drip irrigation—were rainfed.

Floral resource availability was visually estimated at every sampling date and along every inter-row by the flower

TABLE 1 Mean ± *SD* vegetation coverage (%) per vegetation management intensity, method of vegetation management, and number of management events per year in the studied countries

Country	Vegetation coverage (%) and no. of vineyards			Vegetation management		Landscape circles	SHDI
	Permanently vegetation	Temporary vegetation	Bare soil	Method	Events per year		
AT	82.73 ± 11.5 *n* = 7	82.93 ± 14.5 *n* = 9	*n* = 0	Tillage	1–3	16	1.56 ± 0.3
ES	*n* = 0	56.08 ± 23.8 *n* = 8	19.95 ± 19.6 *n* = 8	Tillage and/or Herbicides	1–4	16	1.26 ± 0.2
FR	96.37 ± 2.9 *n* = 8	*n* = 0	21.08 ± 19.6 *n* = 7	Herbicides	1–4	15	1.54 ± 0.2
RO	63.56 ± 13.7 *n* = 4	63.45 ± 15.6 *n* = 7	35.06 ± 12.1 *n* = 5	Tillage	2–5	16	1.39 ± 0.3
All countries	84.44 ± 15.5 *n* = 19	68.30 ± 21.3 *n* = 24	22.90 ± 18.5 *n* = 20		1–5	63	1.43 ± 0.3

Note. Number of landscape circles mapped corresponds to the number of vineyards sampled per country. Mean ± *SD* Shannon Landscape Diversity Index (SHDI) per country.

coverage of all entomophilous plants in five categories (<1% = very low; 1%–5% = low; 5%–25% = medium; 25%–50% = high; and 50%–100% = very high) following an adapted DAFOUR scale (Gardener, 2012).

2.2 | Wild bee sampling and functional traits

Wild bees were sampled by a semiquantitative transect method in the vineyard inter-rows. The transects length ranged between 67 and 133 m in order to adjust to the different width of the inter-rows (1.5–3 m). To consider temporary vegetation cover management, each transect included two neighboring inter-rows. Each vineyard was sampled five times in 2016 for 15 min per sampling event. Sampling dates among the countries were synchronized to grapevine phenology (first budburst, first flower buds, full florescence, pea-sized berries, and beginning of maturation) to adapt to the different climatic zones (Bauer, Regner, & Schildberger, 2013). During the sampling process, each transect was walked slowly and wild bees were collected with an aerial net and later identified in the laboratory.

Functional traits of wild bees (Table 2) were selected according to the possible response to management, floral resource availability, and/or landscape diversity. Information on functional traits was gathered from the literature (Scheuchl & Willner, 2016) or expert's evaluation. As a proxy for the activity range and body size, we measured the intertegular distance (ITD in mm) with a digital microscope (Keyence VHX-5000) of 1–5 specimens from each species and averaged per species. This shortest linear distance between the bee's wings at the dorsal side of the thorax corresponds to the size of wing muscles and to the activity range of a species (Greenleaf, Williams, Winfree, & Kremen, 2007).

2.3 | Landscape survey

A 750 m radius around each sampled vineyard center was chosen for the landscape survey to get a minimum distance of 1,500 m between the study sites which covers the foraging distance of many wild bee species (Zurbuchen et al., 2010; Zurbuchen & Müller, 2012). In each landscape circle, the landscape structures following the EUNIS habitat classification (European Environment Agency (EEA), 2016) were mapped in the field during July 2015 (Austria) and between April and October 2016 (Spain, France, Romania). If available, country-specific data sets were used as baselines (Austria: BMLFUW, 2012; Spain: Consejería de Agricultura Pesca y Desarrollo Rural, 2011; France: IGN Institut Géographique National, 2012). Digitalization and conversions to raster data were done in ArcGIS 10.2 (ESRI, 2013). The SHDI (Shannon Landscape Diversity Index) of each landscape circle was calculated in FRAGSTATS v4.2 (McGarigal, Cushman, & Ene, 2012).

2.4 | Data analysis

Honey bee (*Apis mellifera*) counts were excluded from the main analysis, because their abundance to a great extent depends on

TABLE 2 Wild bee functional traits used as response variables in this study

Trait	Variable type	Definition	Rationale for selection
Nesting type	Ground nesting	Majority of wild bee species in Europe excavate nest in the ground	Interlinked with habitat requirements (e.g., bare compact ground or pre-existing cavities) which alter bee diversity and abundance
	Above-ground nesting	Nesting in pre-existing cavities, plant stems, dead wood (incl. *Bombus* spp.)	
	Parasitic	♀ lay their eggs in nests of specific host species	Less efficient pollinators (Garibaldi et al., 2015) but indicates vital host populations (Hudson, Dobson, & Lafferty, 2006)
Sociality	Solitary	Nest establishment and resource collection by each ♀ alone	Type of sociality could result in shorter (solitary) or longer seasonal activity (eusocial) and may affect duration in which a species is pollinating. Affected by vegetation management due to nesting type.
	Eusocial	Division of tasks: egg-laying ♀ and ♀ that collect resources (e.g., bumble bees, some Halictidae species)	
	Parasitic	See above	See above
Body size	ITD (mm)	The shortest linear distance measured between a wing tegulae across the dorsal thorax (Cane, 1987)	Strongly related to the flying distance of a species (i.e., the distance a female can fly to collect pollen and nectar; and affected by landscape features (Gathmann & Tscharntke, 2002; Greenleaf et al., 2007; Zurbuchen et al., 2010)
Lecty	Polylectic	Pollen generalists: Pollen is collected on different plant taxa but species can show a certain degree of flower constancy	A greater variety of plants is visited to collect pollen and nectar
	Oligolectic	Pollen specialists: Pollen is collected from closely related or single plant taxa	Morphological adaption to respective flower structure; occurrence of host plant is relevant

Note. Sociality was defined as by Michener (2007).

the location of nearby beekeepers' hives (cf. Carrié et al., 2017). However, considering the pollination services honey bees provide, their abundance was compared between the different management intensities. All statistical analyses were computed in R 3.4.3 (R Core Development Team, 2018). Collinearity among predictors was assessed by scatterplots and by testing significant correlations with Spearman correlation tests (significance level = $\alpha \le 0.05$).

The response variables species richness and abundance were aggregated across all sampling dates per vineyard. The predictor variables vegetation cover (proxy for vegetation management intensity) and floral resource availability were averaged per vineyard. Floral resource availability was represented by three classes ("very low," "low," and "medium") after averaging, due to missing observations of the levels "high" and "very high." The SHDI was used as index for landscape diversity because it was least collinear with the other predictors and therefore the best option to model its interactions with management intensity and floral resource availability.

Wild bee traits were summarized by community weighted means (CWM; R package "FD" Laliberté, Legendre, & Shipley, 2015). To evaluate significantly associated wild bee traits in vineyards, a PCA was constructed, including a Hellinger transformation to correct for the "arch effect" (Zuur, Ieno, & Smith, 2007). Further, the CWMs were fitted onto the PCA by vector fitting (with the "envfit" function of the "vegan" package; Oksanen et al., 2017). This function calculates the correlation and associated *p*-values ($\alpha \le 0.05$) between the ordination of species assemblage per plot and the explanatory variables by random permutations ($n = 999$; Oksanen, 2015). Finally, generalized linear models (GLMs) were used to analyze the effects of the three predictors on these significant associated traits (i.e., sociality and body size). As response variables, we used the CWMs of the body size and for sociality the number of eusocial and solitary species and their abundances.

Model selection was based on an information theoretic approach (Burnham & Anderson, 2002), and a candidate model set of 10 GLMs was formulated with different combinations of vegetation cover, floral resource availability, and SHDI and their interactions (Table 3). The country was used as predictor in every model to encompass country-specific effects. Species richness and abundance models were formulated as GLMs with Poisson and ITD as GLMs with Gaussian error distribution. Models were ranked by the second-order Akaike's information criterion (AICc; R package "AICcmodavg" Mazerolle, 2016). The cutoff rate to decide whether a model was the most parsimonious compared to the others was set at ΔAICc ≥ 2 (Motulsky & Christopoulos, 2003). Plots of relevant effects of the most parsimonious models were computed with the R package "effects" (Fox, 2003).

Model quality was assessed by diagnostic plots, dispersion values, and explained deviance (R^2_{GLM}). The model quality of eusocial wild bee GLMs appeared to be distorted because only one eusocial species (three individuals) was observed in Spain. Therefore, the Spanish vineyards were excluded from models with eusocial response variables. The most parsimonious model did not change noteworthy, but model quality improved.

TABLE 3 Candidate models and background hypothesis according to research questions

Background hypothesis	Candidate models
Intercept-only model	$x \sim 1$
Exclusive effect of countries	$x \sim$ Country
Effect of single predictors and countries	$x \sim$ Floral resource availability +Country
	$x \sim$ Vegetation coverage +Country
	$x \sim$ SHDI +Country
Effect of single predictors and interaction with country	$x \sim$ Floral resources availability: Country
	$x \sim$ Vegetation coverage: Country
	$x \sim$ SHDI: Country
Extensive soil management compensates low floral resource availability in vineyards	$x \sim$ Floral resource availability: Vegetation coverage +Country
Combined effects of floral resource availability, vegetation management and landscape diversity	$x \sim$ Floral resources availability +Vegetation coverage +SHDI + Country
Increased landscape diversity compensates low floral resource availability or intensive management	$x \sim$ Floral resources availability * SHDI +Country
	$x \sim$ Vegetation coverage * SHDI +Country

Note. SHDI: Shannon Diversity Landscape Index; x: Response variables (wild bee species richness: total, eusocial, solitary; wild bee abundance: total, eusocial, solitary; community weighted mean (CWM) of body size.

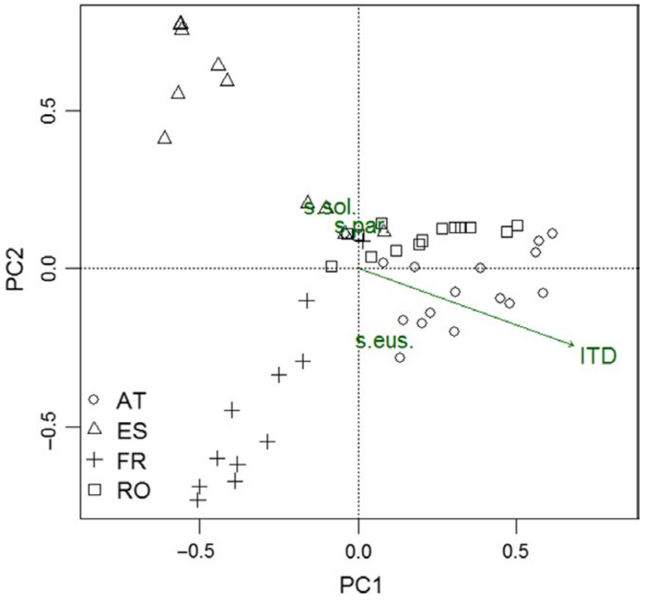

FIGURE 2 PCA for wild bee species assemblage in vineyards across Europe including wild bee traits based on significantly ($p \leq 0.05$) correlated CWM (community weighted means) values derived by vector fitting with permutation tests ($n = 999$). ITD = Intertegular distance; s.sol = solitary wild bee species; s.par = parasitic wild bee species; s.eus = eusocial wild bee species

3 | RESULTS

In total, 113 species and 719 individuals were sampled in vineyards across Europe (species list: Supporting Information Appendix S1: Table S1) and 217 honey bee individuals were counted. Austrian vineyards represented the highest wild bee diversity (64 species) followed by Romania (38 species), France (35 species), and Spain (20 species). Accordingly, the highest wild bee abundance was found in Austrian vineyards (329 individuals), followed by France (181 individuals), Spain (134 individuals), and Romania (77 individuals). Honey bees were most abundant in Austria (128 individuals), followed by Romania (59 individuals), France (23 individuals), and Spain (7 individuals). Honey bee abundance was significantly influenced by management intensity (Kruskal–Wallis test: $\chi^2 = 9.61$; $df = 2$; $p = 0.01$) being highest in temporary vegetated inter-rows (on average 4.92 ± 6.95 individuals ± *SD*) and lowest in bare soil vineyards (1.25 ± 2.73 individuals). Regarding wild bees, *Lasioglossum marginatum* (most abundant species in Austria) and *L. malachurum* (most abundant species in France) represented together 23.4% of all sampled wild bee individuals. In Spain, *Andrena tenuistriata* was most abundant (49.2%), and in Romania, *Halictus simplex* encompassed 14.3% of the individuals. In total, 46 species were represented by only one individual. On average, the highest species numbers were sampled

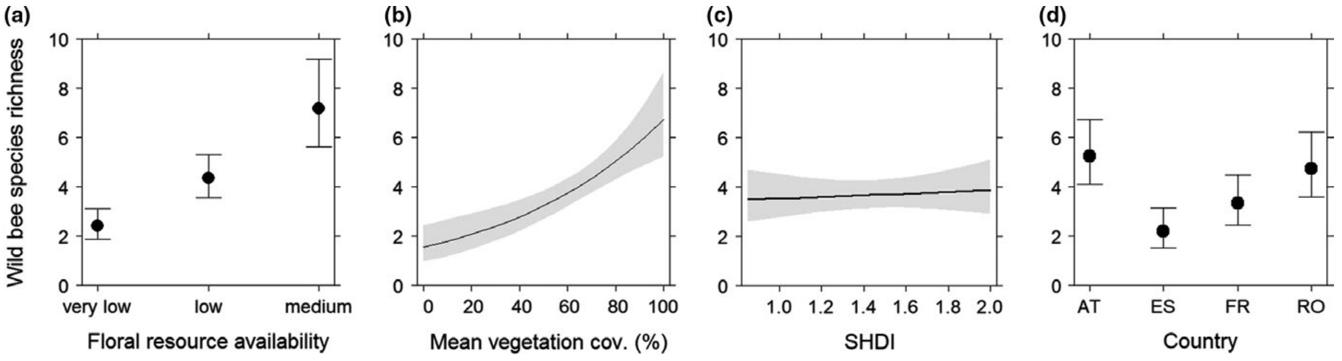

FIGURE 3 Wild bee species richness in vineyard inter-rows in four different countries in response to (a) floral resource availability, (b) vegetation cover (%), (c) landscape diversity (SHDI: Shannon Landscape Diversity Index), and (d) countries. Error bars/gray shading: 0.95 confidence intervals

TABLE 4 Model selection according to AICc for each response variable

	Wild bee species richness			Wild bee abundance			CWM
Models	Total	Eusocial	Solitary	Total	Eusocial	Solitary	ITD
x ~ 1	471.24	239.09	306.40	1,052.9	661.58	622.47	**82.61**
x ~ Country	370.02	210.33	277.83	868.83	520.67	555.91	**82.38**
x ~ Floral resource av. + Country	303.50	170.62	248.34	607.33	309.74	485.27	85.87
x ~ Vegetation cov. + Country	316.79	183.68	253.21	679.20	412.68	478.09	84.50
x ~ SHDI +Country	371.02	212.61	277.70	866.10	522.17	551.13	**83.85**
x ~ Floral resource av.:Country	308.29	178.13	255.19	604.51	308.88	488.84	95.64
x ~ Vegetation cov.:Country	317.27	182.65	253.53	676.80	408.05	484.16	85.42
x ~ SHDI:Country	371.19	212.6	278.08	867.89	527.86	546.78	**82.88**
x ~ Floral resource av.:Vegetation cov. + Country	290.12	**169.45**	**243.39**	**535.55**	299.74	**434.27**	88.83
x ~ Floral resource av. + Vegetation cov. + SHDI +Country	**287.01**	166.35	**241.37**	548.32	299.15	443.55	89.73
x ~ Floral resource av. * SHDI +Country	310.12	176.61	255.50	613.74	**293.28**	477.73	92.27
x ~ Vegetation cov. * SHDI +Country	321.37	187.89	256.60	679.35	412.66	473.60	88.66

Note. AICc of the most parsimonious models for each response in bold.
CWM: Community weighted mean; ITD: Intertegular distance; *x*: Response variable; SHDI: Shannon Diversity Landscape Index

during the period when the first flower buds appeared (1.49 ± 1.94; Supporting Information Appendix S1: Figure S1a) and during full florescence (1.46 ± 1.94; Supporting Information Appendix S1: Figure S1a) of the vines. The highest mean (± *SD*) abundances of wild bees (2.84 ± 4.61; Supporting Information Appendix S1: Figure S1b) were also sampled when the first flower buds appeared on the vines. The lowest mean species richness and abundance were sampled at the last sampling date when the grapes started to mature (Supporting Information Appendix S1: Figure S1).

Overall, 65% of all wild bee species were ground nesting and 25% were above-ground nesting. The majority (76%) of wild bee species in vineyards were polylectic and only 14% were oligolectic.

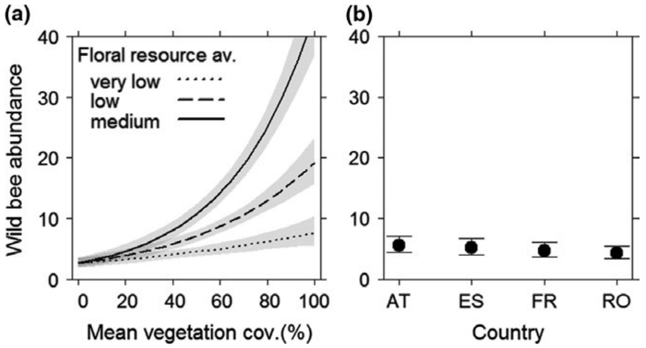

FIGURE 4 Wild bee abundance in vineyard inter-rows in response to (a) the interaction of vegetation cover (%) and floral resource availability, and (b) countries. Error bars/gray shading: 0.95 confidence intervals

Further, wild bee fauna of vineyards consisted of 26% eusocial species, 60% solitary species, and 4% species with insufficient information on sociality. Parasitic wild bees were dominant in three vineyards (two temporary and one permanently vegetated) and represented 10% of all species. The CWM of body size ranged from 0.9 to 3.0 mm ITD and was significantly related to the Austrian wild bee assemblages. Indeed, the mean (±*SD*) CWM of ITD was highest in Austria (2.10 ± 0.47 mm), followed by Romania (1.84 ± 0.44) and France (1.83 ± 0.52), and was lowest in Spanish vineyards (1.61 ± 0.53 mm). The fitted CWM revealed that sociality ($p = 0.001$) and body size ($p = 0.01$) were significantly parameters of the PCA (Figure 2).

The PCA revealed that the wild bee communities were clustered by country. Vineyards in Austria and Romania represented more similar species assemblages compared to Spain and France with more divergent wild bee communities. Further, eusocial wild bee species were characteristic for Austrian and French vineyards based on the high abundance of *Lasioglossum marginatum* in Austria and *Lasioglossum malachurum* in France.

In general, wild bee diversity, abundance and the functional traits that were significantly associated with the PCA's ordination in vineyards, were best explained by models including both floral resource availability and vegetation cover and their interaction (Table 4, Supporting Information Appendix S1: Table S2: GLM results). The average floral resource availability was generally low, but highest in Austrian and Spanish inter-rows and lowest in Romanian inter-rows (Supporting Information Appendix S1: Figure S2).

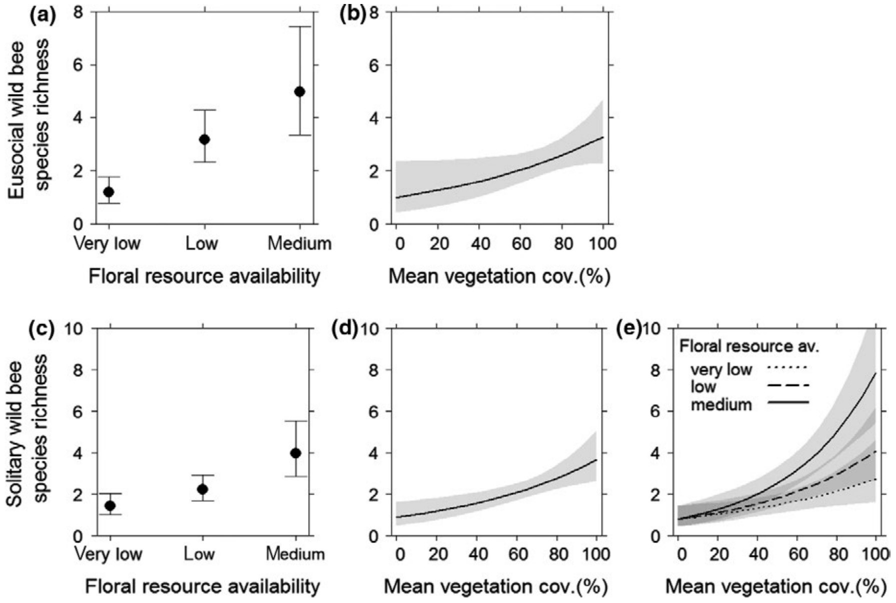

FIGURE 5 Eusocial wild bee species richness in response to (a) floral resource availability and (b) vegetation cover and solitary wild bee species richness in response to (c) floral resource availability, (d) vegetation cover, and (e) the interaction between floral resource and vegetation cover. Error bars/gray shading: 0.95 confidence intervals

The total wild bee species richness in vineyards increased with higher floral resource availability (Figure 3a) and vegetation cover (Figure 3b), whereas landscape diversity had only a minor positive effect (Figure 3c). The significant effect of the countries on wild bee species richness in the inter-rows (Figure 3d) is reflected in the species numbers reported from each county.

Total wild bee abundance increased by significant interactions of higher floral resource availability and mean vegetation cover. Thus, extensive vegetation management increased wild bee abundance even if floral resources were low or very low. Maximum values could be observed when floral resource availability was medium and vegetation cover greater than 60% (Figure 4a). The country effect improved the model fit but had a negligible effect on wild bee abundance (Figure 4b).

Eusocial as well as solitary wild bee species richness was significantly higher by increasing floral resource availability (Figure 5a,c) and mean vegetation cover (Figure 5b,d). Eusocial wild bee abundance also increased with higher floral resources (Figure 6a). Further, high landscape diversity compensated for low floral resource availability in vineyard inter-rows and led to increased eusocial wild bee abundance. Medium floral resources in vineyard inter-rows enhanced eusocial wild bee abundance even in simple landscapes (Figure 6b). Extensive vegetation management strategies increased solitary wild bee diversity (Figure 5e) and abundance (Figure 6c) even if low or very low floral resources were available in the inter-rows, while higher floral resources partly compensated for the negative effect of intensive vegetation management.

Except for the significant interaction between landscape diversity and floral resource availability on eusocial wild bee abundance, landscape diversity played a secondary role for eusocial and solitary wild bee species richness and abundance (Supporting Information Appendix S1: Table S2).

Wild bee body size was equally well explained by models that included the country, the landscape diversity, or the interaction of both. However, the intercept-only model was ranked within the most parsimonious models (Table 4) and the explained deviance of the mentioned models was low (R^2_{GLM} = 12%–16%; Supporting Information Appendix S1: Table S2) which implies the low explanatory value of the chosen predictors for wild bee body size in vineyards.

4 | DISCUSSION

Wild bee species richness, abundance, and functional traits in vineyard inter-rows strongly increased with higher floral resource availability and extensive inter-row vegetation management. Further, the total wild bee abundance as well as the diversity and abundance of solitary wild bees were significantly positively affected by the interaction of higher floral resources in extensively managed vineyard inter-rows. The surrounding landscape had a limited influence on wild bee species richness, abundance, and most functional traits. However, it played an important role for eusocial wild bees in compensating for low floral resource availability. Most of the wild bee species and individuals were ground nesting, solitary, and generalists regarding the plants they forage on.

Across the studied vineyards, 5.7% of the almost 2000 European wild species (Nieto et al., 2015) were recorded. The recorded species numbers per country (between 20 and 64) corresponds to other vineyard studies. For example, 25–31 wild bee species were reported in 12 and 10 vineyards, respectively, in South Africa (Kehinde & Samways, 2012, 2014a, 2014b) and 17 species from 10 vineyards in California (Wilson et al., 2018). On average, the bee abundance (wild and honey bees) per vineyard in our study was lower compared to the South African vineyards (Europe: 15 individuals/vineyard vs. South Africa: 160 individuals/vineyard; Kehinde & Samways, 2012) as well as the Californian vineyards (96 individuals/vineyard; Wilson et al., 2018). However, different sampling methods could also be a reason for the different abundances

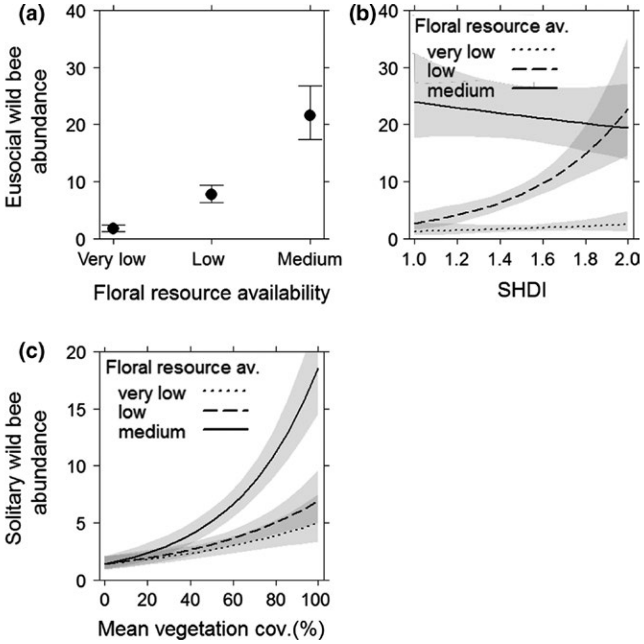

FIGURE 6 Eusocial wild bee abundance in response to (a) floral resource availability and (b) the interaction of landscape diversity and floral resource availability. Solitary wild bee abundance in response to (c) interacting effects of floral resource availability and vegetation cover. Error bars/gray shading: 0.95 confidence intervals

of the studies. The effect of the country on wild bee species richness (Figure 3d) was also reflected in the clustering of the wild bee communities in vineyards according to the countries (Figure 2, Supporting Information Appendix S1). The divergent climatic, geographic, and/or floral zones of the studied countries are possible reasons for the different species assemblages (Gusenleitner, Schwarz, & Mazzucco, 2012; Nieto et al., 2015; Ortiz-Sánchez, 2011; Polaszek & Mitroiu, 2013; Tomozei, 2010). It is notable that Spanish vineyards exhibited an unexpected low species richness even though the region in southern Spain is one of the diversity hot spots for wild bees in Europe (Nieto et al., 2015). The overall intensive inter-row management in vineyards and the low landscape diversity in our Spanish study region are the most likely reasons for the low bee diversity. The most abundant species in Spanish vineyards, *Andrena tenuistriata*, prefers Mediterranean-type shrublands as well as arable land as habitat (Roberts, 2014). The majority of those individuals (64.6%) were present in vineyards with temporary vegetation cover which demonstrates the benefit of less intensive disturbance for this ground-nesting species. Austrian vineyards comprised the highest wild bee diversity which conforms with the generally high wild bee diversity in eastern Austria (Nieto et al., 2015). Further, the landscape diversity was highest in the Austrian wine-growing region and inter-row vegetation treatments included the two least intensive managements.

The strong positive effect of increased floral resources on wild bees found in this study was already documented in other agroecosystems (Scheper et al., 2015; Westphal, Steffan-Dewenter, & Tscharntke, 2009), vineyards in South Africa (Kehinde & Samways, 2014a, 2014b) and California (Wilson et al., 2018), and natural or seminatural habitats (Haaland et al., 2011; Rollin et al., 2013). Furthermore, other pollinators like butterflies also respond positively to suitable nectar resources and larval host plants in wine-growing areas (Gillespie & Wratten, 2012).

Vineyard inter-rows are linear landscape elements and are comparable with flowering strips or field margins which can improve pollinator diversity, abundance, and pollination services for insect-pollinated crops (Haaland et al., 2011; Williams et al., 2015). The positive effect of increased floral resource availability in vineyards has to be examined critically because the attraction of wild bees could lead to increased pesticide exposure of these pollinating insects. However, the effect of pesticides and their active ingredients, which are used in viticulture, on wild bee diversity, abundance, and traits, was not studied and should be addressed in future research.

The strong positive effect of extensive vegetation management agrees with other studies reporting the benefits of extensive agricultural management practices for wild bees in different crop systems (Nicholson et al., 2017; Shuler, Roulston, & Farris, 2005), as well as vineyards (Kehinde & Samways, 2012, 2014a, 2014b). Moreover, a recent meta-analysis confirmed that positive affect of extensive management on overall biodiversity and ecosystem services (Winter et al., 2018). Ground-nesting bees benefit from undisturbed soil conditions and can utilize vineyard inter-rows as nesting habitat. Indeed, during field work, nesting activity of *Lasioglossum marginatum* and *L. lineare* was occasionally observed. In total, most eusocial (70%) and solitary (70%) species were ground nesting, but nesting types were not significantly associated with the PCA and not analyzed further with GLMs. In general, the high proportion of ground-nesting wild bees is characteristic for agroecosystems because nesting habitats are widely available (e.g., unsealed roads, field verges, bare ground below vine rows). Whereas structures for above-ground nesting wild bees (e.g., old plant material, deadwood elements) are often less abundant (Zurbuchen & Müller, 2012).

Further, floral resources are destroyed by frequent soil tillage or herbicide use in bare soil vineyards which amplifies the negative effect of intensive vegetation management. The combined positive effect of higher floral resource availability and vegetation cover on the total wild bee abundance is associated with the high abundance (79%) of ground-nesting eusocial wild bees. The remaining 21% eusocial (above-ground nesting) individuals were represented by bumblebees. These species colonize pre-existing cavities below, on or above, the ground for nesting and are much likely to be negatively affected by frequent soil disturbance. The same combined positive effects on solitary wild bees are explained by the high abundance (86%) and species richness (72%) of ground-nesting solitary wild bee species.

Even though we found a positive effect of landscape diversity on wild bee species richness, it was low, which could be explained by the superior effect of floral resource availability in the inter-rows. These results disagree with other studies which revealed the essential importance of landscape structures on wild bee communities (Kennedy et al., 2013; Nicholson et al., 2017). Conversely, it demonstrates the necessity for increasing floral resource availability on the landscape scale to increase and maintain wild bee species richness and thus adequate pollination services for insect-pollinated wild plants and crops (Winfree et al., 2018).

Eusocial wild bees were significantly associated with countries (Austria and Romania) where extensive inter-row vegetation management was realized because eusocial species are more susceptible to disturbances than solitary species (Williams et al., 2010). Only eusocial wild bee abundance was affected by the interaction of SHDI and floral resource availability which could be explained by their higher vulnerability to habitat fragmentation (Williams et al., 2010). Continuous floral resource availability during the vegetation period plays a crucial role for the sexual reproduction of eusocial wild bees because a lack of pollen and nectar can lead to a colony collapse in the reproduction phase during summer (Westphal et al., 2009). Landscape structures like fallows (Toivonen, Herzon, & Kuussaari, 2016), hedges (Morandin & Kremen, 2013), solitary trees, or edges of woods (Nicholson et al., 2017; Rollin et al., 2013) provide different foraging sites for wild bees. Furthermore, these structures may compensate for negative effects of low to very low floral resource availability on eusocial wild bees that nest in the inter-row space of vineyards (Kratschmer et al., 2018). Spanish vineyards possessed similar average floral resource availabilities as Austrian vineyards, which, according to our results, should benefit eusocial species. However, only one eusocial species was documented in Spanish vineyards. The more intensive vegetation management and low landscape diversity limited eusocial wild bee occurrence. This might decrease pollination provision at the landscape scale because pollination performance mainly depends on wild bee species richness (Winfree et al., 2018) and abundance (Winfree, Fox, Williams, Reilly, & Cariveau, 2015). Even though vines and olives, representing the dominant crops in the Spanish study region, do not rely on insect-pollination, but other insect-pollinated wild plants require pollination to guarantee long-term survival. This was reported from central Europe, by Biesmeijer et al. (2006) who showed a parallel decline of wild plants and their pollinators due to insufficient pollination.

We expected that increasing average body size of bee assemblages is related to decreasing landscape diversity, because larger species can forage at greater distances (Greenleaf et al., 2007). Further, if pollen availability is low it leads to a change in maternal resource allocation to offspring, resulting in smaller adults (Renauld, Hutchinson, Loeb, Poveda, & Connelly, 2016). These effects were not observed since body size was not noteworthy affected by SHDI or by any other predictor. This is likely due to an overlapping effect by the distinct species assemblage in each country: The body size of wild bees was related to the Austrian wild bee assemblages. We explain this by the high abundance and species richness of bumble bees in Austrian vineyards compared to France, Romania, and Spain. On the other hand, a high proportion of the individuals in Spain was represented by two small wild bee species (*Andrena tenuistriata*, average 1.29 mm ITD and *Panurginus albopilosus*, average 0.89 mm ITD).

In conclusion, the total wild bee diversity and abundance as well as solitary wild bee diversity and abundance benefitted from the combination of increased floral resource availability and extensive vegetation management intensity in vineyard inter-rows. Consequently, vineyard inter-rows can be important habitats for wild bees in viticultural landscapes. High landscape diversity played an important role in compensating for low floral resources for eusocial wild bees. Therefore, we recommend less intensive vegetation management such as infrequent vegetation disturbance to be implemented in vineyard inter-rows in order to achieve resilient pollination provision for insect-pollinated crops and wild plants in viticultural landscapes. Beside enhancing wild bee diversity and abundance through these measures also honey bees will benefit which is especially important for the pollination of mass flowering crops (Brittain, Williams, et al., 2013). The implementation of pollinator-friendly management ultimately benefits other ecosystem services like for example soil erosion mitigation, surface water runoff reduction, or biological pest control as well as biodiversity conservation (Wratten et al., 2012). Many of those ecosystem services are relevant for winegrowers and positively affected by extensive inter-row management intensities in vineyards (Winter et al., 2018). For example, extensive vegetation management significantly improves soil loss mitigation (Winter et al., 2018), which is highly relevant in vineyards that are situated on hilly terrain. Extensive management contributes to sustainable farming contributing to the UN sustainable development goals responsible consumption and production as well as life on land (UN, 2015). Further, biodiversity-friendly vineyard management practices (e.g., organic farming) are increasingly demanded by consumers (Schütte & Bergmann, 2019).

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CONFLICT OF INTERESTS

The authors declare no competing financial interests.

AUTHOR CONTRIBUTION

SK, BP, SW, JGZ, AN, FB, and MG conceived and planned the experiment; SK, DP, AF, and LM conducted the field work; SK and BP identified wild bee species; SK, MS, JAE, AF, AH, and MG did landscape mapping in the field, digitalization and GIS work; SK, SW, and DP analyzed the data; all other authors were involved in significant parts of the study, wrote and/or reviewed the manuscript.

DATA ACCESSIBILITY

Data available via Zenodo under: https://doi.org/10.5281/zenodo.2567423.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Viticultural landscape and permanently vegetated vineyard inter-rows in France (Loire Valley viticultural region, 2016; © M. Guernion)

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REVIEW

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Effects of vegetation management intensity on biodiversity and ecosystem services in vineyards: A meta-analysis

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Abstract

1. At the global scale, vineyards are usually managed intensively to optimize wine production without considering possible negative impacts on biodiversity and ecosystem services (ES) such as high soil erosion rates, degradation of soil fertility or contamination of groundwater. Winegrowers regulate competition for water and nutrients between the vines and inter-row vegetation by tilling, mulching and/or herbicide application. Strategies for more sustainable viticulture recommend maintaining vegetation cover in inter-rows, however, there is a lack of knowledge as to what extent this less intensive inter-row management affects biodiversity and associated ES.
2. We performed a hierarchical meta-analysis to quantify the effects of extensive vineyard inter-row vegetation management in comparison to more intensive management (like soil tillage or herbicide use) on biodiversity and ES from 74 studies covering four continents and 13 wine-producing countries.
3. Overall, extensive vegetation management increased above- and below-ground biodiversity and ecosystem service provision by 20% in comparison to intensive management. Organic management together with management without herbicides showed a stronger positive effect on ES and biodiversity provision than inter-row soil tillage.
4. Soil loss parameters showed the largest positive response to inter-row vegetation cover. The second highest positive response was observed for biodiversity variables, followed by carbon sequestration, pest control and soil fertility. We found no trade-off between grape yield and quality vs. biodiversity or other ES.
5. *Synthesis and applications*. Our meta-analysis concludes that vegetation cover in inter-rows contributes to biodiversity conservation and provides multiple

ecosystem services. However, in drier climates grape yield might decrease without irrigation and careful vegetation management. Agri-environmental policies should therefore focus on granting subsidies for the establishment of locally adapted diverse vegetation cover in vineyard inter-rows. Future studies should focus on analysing the combined effects of local vineyard management and landscape composition and advance research in wine-growing regions in Asia and in the southern hemisphere.

KEYWORDS
biodiversity, carbon sequestration, ecosystem services, meta-analysis, pest control, soil erosion, tillage intensity, vineyard

1 | INTRODUCTION

Over the centuries, human land use has shaped and altered the majority of our planet's landscapes (Foley et al., 2005). As these human-shaped ecosystems harbour one of the largest parts of terrestrial biodiversity world-wide, biodiversity conservation efforts should also focus on the identification and conservation of sustainable land use practices (Tscharntke et al., 2012). Across the globe, intensive land use focusing solely on production is a major driver of global change resulting in the decline of biodiversity, ecosystem functioning and multiple ecosystem services (ES) in agricultural ecosystems (Allan et al., 2015; Foley et al., 2005). Therefore, current and future land use practices should be evaluated concerning trade-offs between food production and the provision of biodiversity and other ES.

The concept of ES was originally developed to illustrate the benefits that natural ecosystems generate for society and to raise awareness for biodiversity and ecosystem conservation (Westman, 1977). The Millennium Ecosystem Assessment (2005) explicitly considered supporting ES as ecosystem functions underlying other ES like provisioning services (products obtained from ecosystems, for example, food, fibre, water), regulating services (benefits obtained from regulation of ecosystem processes, for example, climate regulation, flood regulation, erosion mitigation) and cultural services (non-material benefits people obtain from ecosystems, for example, recreational, aesthetic and spiritual gains). Despite the increasing research interest in elucidating the relationships between land use, biodiversity and ES, there are few studies actually measuring multiple ES and their responses to different agricultural management intensities (e.g. Björklund, Limburg, & Rydberg, 1999). In addition, only few studies cover different ES and their multifunctionality in vineyard systems (Winkler, Viers, & Nicholas, 2017).

Viticulture is among the oldest and most profitable forms of agriculture, covering about 7.5 million hectares world-wide (OIV, 2017). Vineyards cover a very broad range of latitudes and edaphoclimatic conditions, from 4° to 51° in the Northern Hemisphere and from 6° until 45° latitude in New Zealand in the Southern Hemisphere. Vineyards could theoretically offer rather attractive and stable habitats for a range of species, especially in inter-rows covered by diverse plant species, which are favourable for pollinators (Kehinde & Samways, 2014a) and invertebrates that provide pest control services (Shields, Tompkins, Saville, Meurk, & Wratten, 2016). Therefore, vineyards may benefit from and contribute to conservation and ES provision, especially as wine consumers increasingly appreciate environmentally friendly farming practices (Viers et al., 2013). However, vineyards are also among the most intensively managed agroecosystems, typically involving numerous pesticide applications, soil tillage operations and high landscape simplification (Nicholls, Altieri, & Ponti, 2008). The most important groups of pesticides sprayed in vineyards are fungicides, herbicides and to a lesser extent also insecticides. The intensive use of herbicides in vineyards is a global problem for the environment and humans as residues have been found in surface water, groundwater (Louchart, Voltz, Andrieux, & Moussa, 2001), grape juice and wines (Ying & Williams, 1999).

Vineyard management is influenced by climate, irrigation, soil type, grapevine variety, agri-environmental policies and most importantly winegrowers' decisions and attitudes. In general, inter-row vegetation is assumed to be beneficial for erosion prevention and biodiversity provision in vineyards. Nevertheless, inter-row vegetation is often removed due to perceived competition between it and vines for water and nutrients (Pardini, Faiello, Longhi, Mancuso, & Snowball, 2002). However, not all studies show the expected decline in grape yields (e.g. Ruiz-Colmenero, Bienes, & Marqués, 2011; Tesic, Keller, & Hutton, 2007), but similar or even higher yields in vineyards with vegetation cover in the inter-rows (Mercenaro, Nieddu, Pulina, & Porqueddu, 2014; Sweet & Schreiner, 2010). These contrasting results might be explained by climatic differences, the use of irrigation, vegetation type and management, which depicts the necessity of a quantitative review.

Most winegrowers control ground vegetation by means of tilling, mulching or herbicide applications. Intensive tillage has been shown to decrease plant and animal species diversity for some taxa (Kazakou et al., 2016; Paoletti et al., 1998). However, others revealed no significant effects or variable and conflicting responses to herbicide treatments (Caprio, Nervo, Isaia, Allegro, & Rolando, 2015).

Besides direct effects on species, vineyard management also affects the provision of certain ES such as grape production, pest control or the prevention of soil erosion (Winkler et al., 2017). Intensive soil tillage and herbicide application trigger soil erosion, which is a threat to biodiversity (Montanarella, 2005) and ES provision (Novara, Gristina, Guaitoli, Santoro, & Cerdà, 2013). Experimental results indicate a severe reduction in erosion rates, when winegrowers use cover crops instead of bare soil management (e.g. Ruiz-Colmenero et al., 2011). In addition, positive effects of the use of cover crops in vineyard inter-rows on pest control have been reported (Berndt, Wratten, & Scarratt, 2006; Sanguankeo & León, 2011). However, certain plant species may also increase potential pest species by acting as a host plant (Begum, Gurr, Wratten, Hedberg, & Nicol, 2006), by providing resources or shelter (Danne, Thomson, Sharley, Penfold, & Hoffmann, 2010), or by increasing food web complexity and intraguild predation (Finke & Denno, 2004).

The main objective of this study was to perform a meta-analysis to identify, whether extensive vineyard vegetation management practices have consequences on biodiversity and associated ES across viticultural regions world-wide. The supposed trade-off between provisioning services of wine yield and quality with other ES and biodiversity is of central interest for this study. Therefore, we addressed the following research questions: (1) Does extensive vineyard vegetation management increase biodiversity and ES provision in comparison to conventional practices? (2) Which ES categories or biodiversity parameters respond positively and which respond negatively to extensive vineyard vegetation management? (3) Which environmental parameters alter the response to vineyard management? The outcomes of this study will help to formulate agricultural policy recommendations in order to benefit service-providing biodiversity and associated ES.

2 | MATERIALS AND METHODS

2.1 | Literature search

We conducted a systematic literature search in two major databases, SCOPUS and Web of Science (WoS) Core Collection Database (SCI-EXPANDED index), for studies that compared ES or biodiversity with different vegetation management (initial database query 25 January 2016; detailed search terms in Appendix S1). This resulted in a total number of 1,429 publications.

After screening those papers by title 489 articles remained and after reading the abstracts for their relevance, 157 articles remained for full-text screening. Abstract screening was performed by two persons in parallel to cover different fields of expertise and to discuss which articles to include (for the detailed selection process see the PRISMA flow diagram in Figure S1). In the next step articles were screened based on a predefined set of inclusion and exclusion criteria. Only empirical datasets were included that compared at least two different soil or vegetation management treatments. Studies that included (1) less than three spatially independent replicates per treatment level, (2) vineyards under plastic or in greenhouses, and (3) treatments not directly manipulating soil or vegetation management in the vineyards (e.g. application of synthetic or external mulches or the use of different fungicide or insecticide treatments) were excluded. In addition, only studies, which reported means and any dispersion measure of the dependent variable (e.g. *SD* or *SEM*), were used. We contacted the authors of recently published papers with missing data of variance or additional information like irrigation regime of the treatments. Thereof, authors of 11 articles sent adequate datasets for the inclusion in this meta-analysis. We also screened the reference list of review articles and updated the search on the Web of Science and SCOPUS database on the 20 April 2017, thereby 11 additional articles could be included. In addition, two colleagues provided three datasets from unpublished reports and databases.

2.2 | Data extraction

In full-text screening and the follow-up data extraction the co-authors participated according to their expertise in viticulture (DPo), pest control (DPa), biodiversity (SK, SW, JZ), microbiology (BL) and hydrology/soil sciences (TB, PS, GG, JG). Each expert needed to document why an article was excluded (most frequently due to missing measures of variation or insufficient spatial replication); and if inclusion criteria were met, data and covariates were collected in a common database. If studies reported the outcome of several different treatments, which differed in species diversity, we only included the treatment with the largest contrast to the control, for example, bare soil vs. cover crop mixtures with highest number of plant species. As an exclusion of those datasets (n = 11 studies) did not change overall effect size considerably, this approach did not bias results. In general, we only took the data from the latest year or date if articles presented measurements across multiple time periods or consecutive years, because we expected the largest effect at the end of the study period. If that decision could not be met, we combined these separate effect sizes in one composite effect size measure considering non-independence of multiple comparisons within a study (Borenstein, Hedges, Higgins, & Rothstein, 2009, formulas 24.1 and 24.2 for two or 24.4 and 24.5 for several outcomes). This process was also used to calculate the combined effect of different localities, taxonomic subgroups within an order or soil layers. The extracted data were double-checked by the first author for correctness and consistency of terminology. Different measures of variation were converted to standard deviation to enable effect size calculation.

The extracted data were categorized in biodiversity, ES categories (provisioning, regulating and supporting ES) and ES types (Millennium Ecosystem Assessment, 2005, see Table 1 and Table S1). Soil fauna abundance, soil fauna feeding activity, mycorrhiza abundance, microbial biomass and respiration were assigned to the ES nutrient cycling, because these organisms play a key role in litter decomposition and organic matter mineralization in the soil (Wardle et al., 2016). If higher values of effect sizes would mean negative impacts on ES (e.g. abundance of pest species or soil loss), that is, ecosystem disservices, the sign of the effect size was reversed.

2.3 | Effect size calculation and statistical analyses

We calculated the log-response ratio (lnR) as the estimate of the effect size because effect sizes are not affected by different variances in the control and treatment groups and results are easily interpretable (Borenstein et al., 2009). Control was defined as high-intensity inter-row management (soil tillage or use of herbicides to remove vegetation, conventional or other types of intensive management), whereas treatment was defined as extensive inter-row vegetation management (vegetation cover, organic or other types of extensive vegetation management). The difference between treatment and control varies from the most extreme studies comparing bare soil with diverse cover crops or natural vegetation in the inter-rows to studies comparing vineyards using a single species as cover crop in comparison to diverse plant communities. The results are reported as the back-transformed values of the relative percentage of increase (positive values) or decrease (negative values) in comparison to the control treatment. We chose to analyse data with hierarchical mixed-effects meta-analysis models that allow incorporating fixed (moderators), true random effects as well as a nesting factor for effect sizes in the respective sources or articles. As several data points were extracted from a single article, we used the article ID as a nesting factor to avoid violating the assumption that effect sizes are independent from each other. We used the rma.mv function of the metafor package (Viechtbauer, 2010) for R (R Development Core Team, 2017) to fit mixed-effects models to incorporate the true variation in the effect size variation across studies and the fixed effects by adding moderators (Borenstein et al., 2009). The effects of treatment are significant, if the confidence interval (CI) did not overlap with zero (Borenstein et al., 2009).

We used the following explanatory variables as moderators for the effects of management: (1) irrigation (irrigated or rainfed vineyards); (2) climate according to Köppen–Geiger's classification (Kottek, Grieser, Beck, Rudolf, & Rubel, 2006; Mediterranean, oceanic, steppe and continental climates); (3) study design (single vineyard [block/one vineyard] or several vineyards each with randomized block design [block/several vineyards], or multiple vineyards as replicates); (4) treatment-control types (bare soil [as a result of tillage, herbicides or both] vs. vegetation cover, conventional vs. organic management or other types of extensive vs. intensive inter-row vegetation management); (5) vegetation management types (no herbicides vs. herbicide use, no tillage vs. tillage and other types of vegetation management like a combination of herbicides and/or tillage vs. vegetation cover or mulching vs. mowing); (6) ecosystem service category and types according to the Millennium Ecosystem Assessment (2005).

Plots for mean effect sizes and 95% CIs were produced with the R package plotrix (Lemon, 2006). Mixed-effects models with restricted maximum likelihood estimations for estimating the random effects were selected based on significant *Q*-statistics for residual heterogeneity of moderators and a model difference in Akaike's Information Criteria for small sample size (AIC_c) of at least 2 ($\Delta AIC_c > 2$; cf. Motulsky & Christopoulos, 2003). Models including irrigation had a lower sample size as irrigation data were not available from every study. Therefore, we needed to perform separate mixed-effects models to compare the respective AIC_c values (see Table S2). Multiple comparisons between different moderator levels of mixed-effects models were performed with the general linear hypotheses (glht) function of the multcomp package (Hothorn, Bretz, & Westfall, 2008).

2.4 | Publication bias and sensitivity analysis

As studies reporting a significant effect have a higher likelihood of being published than studies with null results, we explored the possibility of publication bias graphically (funnel plot) and statistically (regression test with sample size as predictor; Rothstein, Sutton, & Borenstein, 2005). In addition, we calculated Rosenthal's fail-safe number (Rosenthal, 1979) to estimate the number of unpublished studies, which would erase the significant effect measured by the meta-analysis. Furthermore, we calculated hat values as a measure of potential outliers in the space of predictors and standardized residuals to identify influential outliers (Viechtbauer & Cheung, 2010). Effect sizes, which were two times larger than the average hat value and standardized residual values which exceeded 3.0 were considered outliers (Habeck & Schultz, 2015) .

3 | RESULTS

In total, we extracted 181 datasets from 74 articles covering major wine producing regions world-wide except Asian countries, New Zealand and Argentina (Figure 1, Table S1). The publication dates span from 1992 to 2017. Therefrom, 60 articles originated from the initial search and 14 additional sources from unpublished datasets provided by research colleagues and additional articles from an updated search (see previous chapter and Figure S1).

The different categories of ES were well represented in the datasets with a focus on regulating ES (Figure 1). About 40% of all datasets originated from irrigated vineyards, 50% were rainfed vineyards and the other studies did not provide information on the use of irrigation (Table S1). Most datasets came from vineyards under Mediterranean climates ($n = 100$), oceanic climates ($n = 56$), and steppe or continental climates ($n = 22$; three studies included vineyards from different climates). Most studies implemented randomized block designs within one experimental vineyard ($n = 113$), only few studies implemented block designs in several vineyards ($n = 12$), whereas 56 datasets used individual vineyards as replicate. The majority of studies investigated the effects of bare soil management (mostly due to tillage, sometimes by use of herbicides or both) compared to cover crops or natural vegetation ($n = 137$ datasets). We investigated the effects of conventional vs. organic management in

27 studies and 17 datasets originated from other types of intensive vs. extensive vegetation management like the contrast of single to diverse cover crop species in inter-rows or mulching vs. mowing of vegetation.

Overall, there was a 19·8% increase in biodiversity and ecosystem service provision due to extensive vegetation management in comparison to the control treatment (Figure 2). With respect to climate, the effect of extensive vegetation management was significantly positive in studies conducted under Mediterranean and oceanic climate, but not in steppe or continental climates. The mixed-effects model showed a significant effect of study design on ES and biodiversity (Table S2, Figure 2). The difference between effect sizes of studies using between vineyard replication vs. using within and between vineyard replication (block/several vineyards) was significant, only the latter did not show a positive response to extensive vegetation management (n = 12). Studies comparing vegetation cover vs. bare soil (M = 17.1%) and organic vs. conventional management (M = 39.7%) showed significant positive effects to extensive vegetation management, whereas other studies with less pronounced differences between treatment and control did not. Studies comparing vegetated inter-rows to herbicide application in inter-rows resulted in the highest positive effect, followed by the majority of studies investigating tillage vs. vegetation cover. Other forms of vegetation management like the combined use of herbicides

TABLE 1 Summary of the ecosystem services (ES) (according to the Millennium Ecosystem Assessment, 2005) and biodiversity datasets extracted from 74 included studies

ES category/biodiversity	ES type/biodiversity	Subset (number of datasets included)	Variable
Biodiversity	Biodiversity	Flora (6)	Plant species richness
		Fauna (18)	Earthworm species richness
			Spider species richness and abundance
			Beetle species richness and abundance
			Grasshopper species richness
			Insect pollinator species richness and abundance (bees, butterflies)
			Bird species richness
Provisioning	Grape quality and quantity	Grape quantity (23)	Grape yield
		Grape quality (22)	Must quality (sugar content, titratable acidity, yeast assimilable nitrogen)
Regulating	Erosion protection	Soil loss (9)	Soil loss
		Erosion-related soil parameters (8)	Water retention
			Topsoil penetration resistance
			Aggregate stability
			Saturated hydraulic conductivity
	Carbon sequestration	Soil carbon (19)	Soil carbon content
	Pollination	Pollination (2)	Flower visitations
			Seeds per plant
	Pest control	Natural enemy-related parameters (21)	Abundance of potential natural enemies
			Percentage of parasitism and predation
		Pest-related parameters (13)	Pest abundance
			Damage per vine and plot
	Soil water balance	Soil water balance (6)	Water stress integral, water loss, volumetric soil water content
Supporting	Soil fertility	Soil biota (17)	Soil fauna abundance (nematodes, earthworms, springtails, Oribatida, invertebrates) and biological quality indicator
			Arbuscular mycorrhiza abundance (fungal spores and colonisation)
		Nutrient cycling processes (17)	Soil fauna feeding activity
			Soil microbial biomass
			Soil microbial respiration and activity
			Soil macronutrient content and availability

and tillage or mulching as control in comparison to more extensive types of vegetation management did not result in an overall significant positive effect.

The largest mean effect size (*M* = 53.2%) was observed for biodiversity which was also significantly higher than the other ecosystem service categories. However, all ES were significantly positively affected by extensive vegetation management and the inclusion of that moderator significantly improved the model AIC$_c$ values (Table S2). The integration of the moderator ecosystem service type improved model fit (alias ΔAIC$_c$) more effectively than ES categories (Table S2, Figure 3).

Considering the type of ES in the model, biodiversity benefitted most from extensive vegetation management with a significant difference to all other ecosystem service types. Furthermore, carbon sequestration, pest control and soil fertility showed significant positive responses to extensive vegetation management in the mixed-effect model with the moderator ES type. If soil erosion was split up into two subsets of parameters measuring soil loss and in general erosion-related soil parameters, there was a strong positive effect of extensive vegetation management on soil loss mitigation (*M* = 161.9%). This means that soil loss was strongly reduced by using cover crops instead of bare soil management. Pest-related parameters (positive values show mean lower values of pest species in the treatment), one of the two subsets of the ES-type pest control, also showed a significant positive response to extensive vegetation management in comparison to the non-significant effect on natural enemies.

Funnel plots, regressions tests ($z = 1.79$, $p = .07$), and a fail-safe number of 29,663 showed no sign of publication bias in the presented meta-analyses (details in Appendix S3).

4 | DISCUSSION

To our knowledge, this is the first meta-analysis summarizing the effects of vineyard management on biodiversity and associated ES across the globe. Across studies, extensive vegetation management resulted in a 20% increased biodiversity and ES provision. Irrigation, study design, treatment-control type, ES category/biodiversity and ES type consecutively improved the model fit. We detected the strongest increase of 50% in biodiversity due to extensive vegetation management. Additionally, carbon sequestration, pest control and soil fertility also showed significant positive responses to extensive vegetation management. A subset analysis of the ES type erosion protection resulted in the largest increase (160%) for studies investigating actual soil loss of vineyards with vegetation cover vs. bare soil management.

Interestingly, irrigation did not increase the positive effect of extensive vegetation management. In fact, rainfed vineyards showed a comparatively larger positive response. The decreased effect in irrigated vineyards might be due to decreasing pest control ES as several studies (Costello, 2008; Irvin, Bistline-East, & Hoddle, 2016) showed that irrigation may increase the incidence of certain leafhopper pest species as they prefer vigorously growing vines. Such side

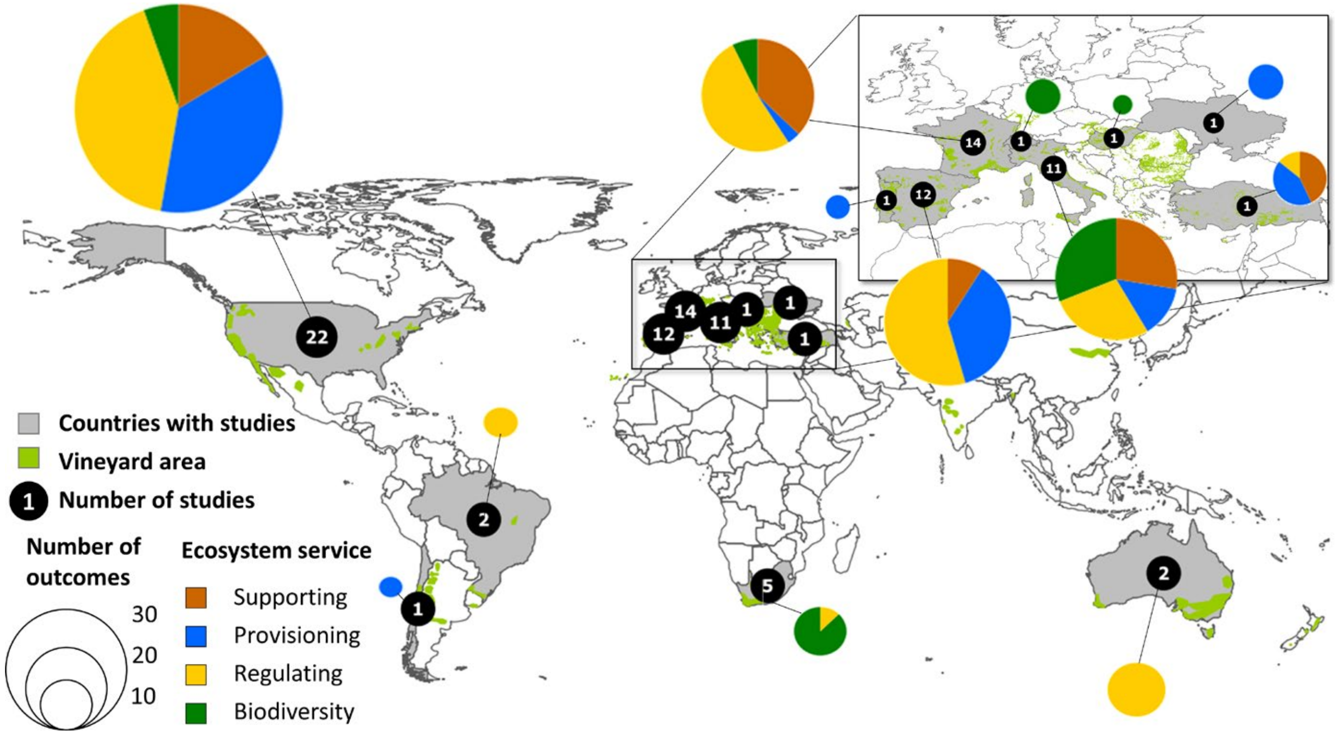

FIGURE 1 Political map of the world showing the number of involved studies per country and the wine-growing regions in green shading, number of outcomes symbolize the sample size per country (source: Corine Land Cover for European vineyard area; world-wide vineyard area based on national maps)

effects can occur under dry climate conditions, where irrigation is more common and natural enemies cannot control pests (Tscharntke et al., 2016). Climatic effects on the outcome of extensive vegetation management were smaller than expected. In contrast to continental and steppe climates, studies conducted in Mediterranean and oceanic climates showed significant positive responses. Differences were not related to the use of irrigation, as approximately half of all datasets originated from irrigated Mediterranean vineyards, whereas 83% of all datasets in continental or steppe climates descended from irrigated vineyards. Steppe or semi-arid climates are characterized by rainfall deficiency (Kottek et al., 2006), which increases the need for irrigation.

Previous narrative reviews also found overall positive effects of environmentally friendly management on biodiversity and ES provision of inter-row vegetation management in vineyards (Guerra & Steenwerth, 2012) and of cover crops in vineyards and olive groves (Pardini et al., 2002). However, some studies indicated trade-offs between production and other ES (e.g. Morlat & Jacquet, 2003). The review of Guerra and Steenwerth (2012) discussed the relationship of (potential) water stress created by cover crops and concluded that the combination of factors like water regime, cover crop species, management, duration of cover crop establishment, age of vines is very complex and therefore studies show conflicting results. Despite the potential reduction in wine yield and available soil water, water competition between vines and cover crops also creates benefits from some winegrowers (Guerra & Steenwerth, 2012). The reduced vine growth may decrease the costs associated with vineyard operations like fruit thinning and leaf pulling for producing high-quality wine (Guerra & Steenwerth, 2012). In this meta-analysis, we could not detect any overall negative effect of inter-row vegetation cover on grape quantity or quality; nevertheless, in vineyards of dry climates without irrigation grape yields could decrease if vegetation is not carefully managed.

We found a significant difference in effect size dependent on the study design of the considered studies. The non-significant response of datasets from randomized block designs in several vineyards is most likely the result of the low number of studies, which mainly cover soil loss and grape yield. The type of treatment-control slightly altered the effects of extensive vegetation management. However, it should be remarked that also sample sizes differed considerably with

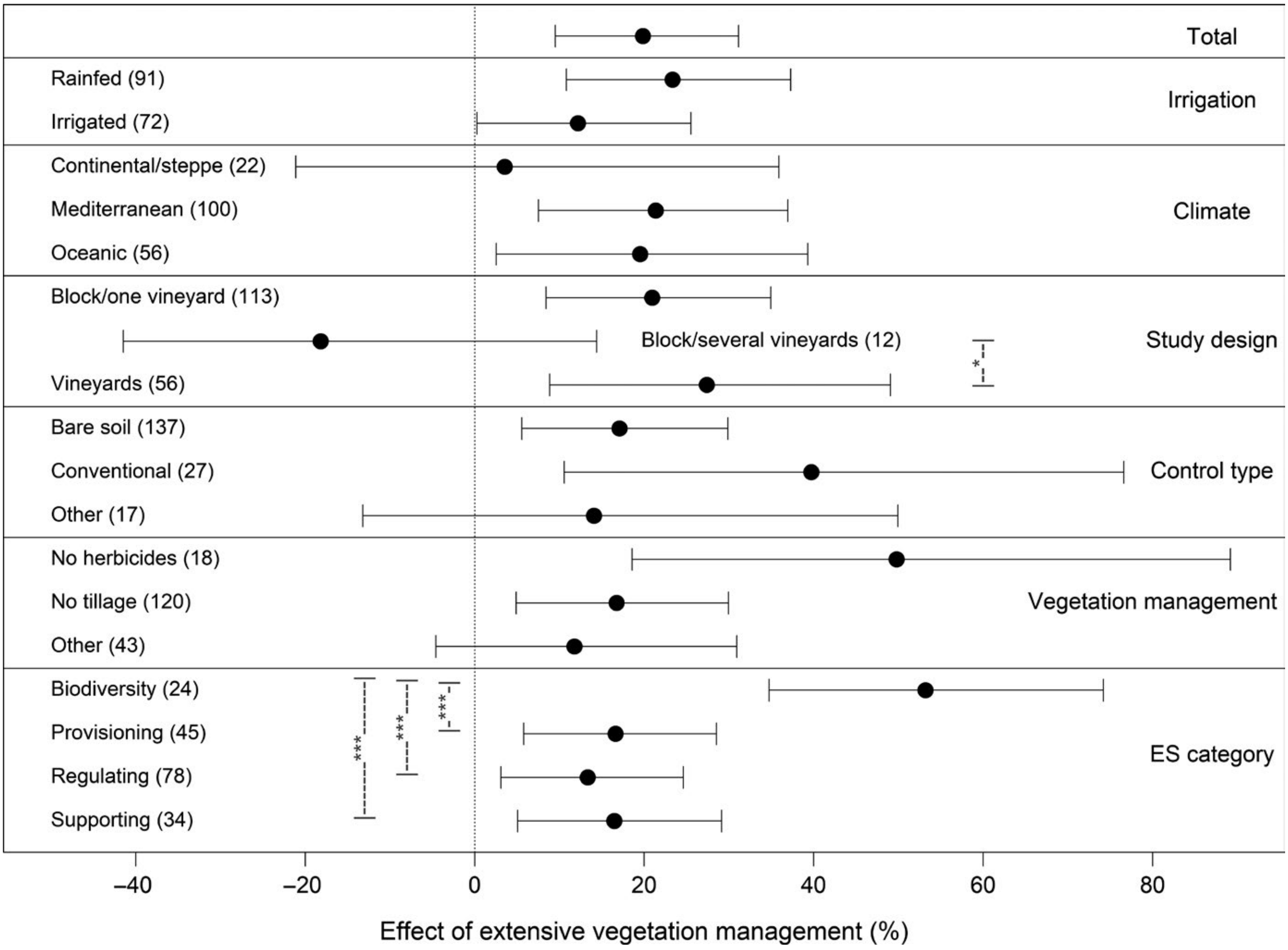

FIGURE 2 Effects of extensive vegetation management in vineyard inter-rows on overall effect size. Significant differences between moderator levels are indicated by whiskers with the associated level of significance (*$p < .05$, ***$p < .001$). Numbers in brackets show the sample size of the datasets

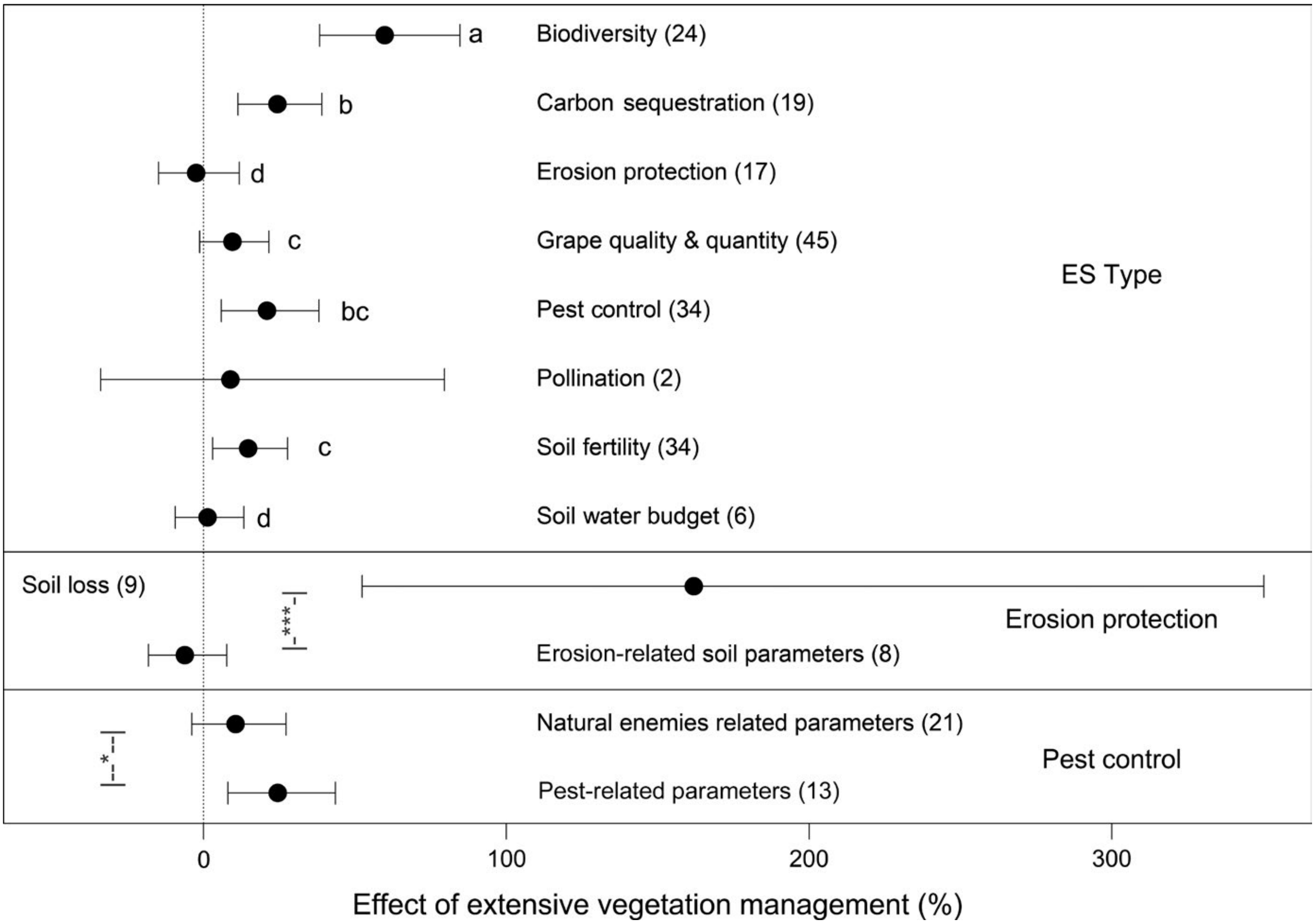

FIGURE 3 Mean and 95% confidence intervals of the effects of extensive vegetation management in vineyards on biodiversity and ecosystem services (ES) types. Significant pairwise differences between groups are indicated by different letter combinations or by whiskers with the associated level of significance (*$p < .05$, ***$p < .001$) for the subsets. Due to the small sample size, pollination was excluded from the pairwise comparisons. Erosion protection and pest control were further split up because subsets (see Table 1) differed significantly from each other in their overall effect sizes. Numbers in brackets show the sample size

56% of all datasets from studies comparing organic vs. conventional management investigated biodiversity. These differences might have increased the associated effect size as biodiversity variables responded strongly positive to extensive vegetation management. Regulations for organic winegrowing do not obligate winegrowers to use cover crops, but in our dataset all organic vineyards used vegetated inter-rows in the vineyard (only three studies did not include information on inter-row management). In general, organic management has been shown to increase biodiversity by 30% (Tuck et al., 2014). Inter-row vegetation management without herbicides was especially beneficial for ES and biodiversity provision. Herbicide application also resulted in the largest negative effect on nematode abundance and soil food web structure compared to tilled or vegetated olive orchards (Sánchez-Moreno et al., 2015).

Ecosystem services categories and types significantly improved mixed-effect models and provided insights into possible trade-offs between biodiversity and ES provision. Overall, extensive vegetation management had an especially large positive effect on biodiversity. This result is very promising, as biodiversity was shown to have positive effects on most ES (Balvanera et al., 2006). Species richness is just one measure of diversity, although the most commonly used and also well acknowledged by the public and policy makers (Batáry, Dicks, Kleijn, & Sutherland, 2015). Hence, further dedicated studies should consider the effects of management intensity on species of conservation concern. Furthermore, increased biodiversity and species abundance might also play a role in sustaining plant–pollinator networks (Kehinde & Samways, 2014a), on which future studies could focus. The few existing literature shows that insect pollinator diversity and abundance is enhanced by organic management (Kehinde & Samways, 2014b) or by reintroducing native plants within and outside vineyards (James, Seymour, Lauby, & Buckley, 2015). This effect is mainly related to a greater number of plant species in vineyard inter-rows (James et al., 2015; Kehinde & Samways, 2014a) or the availability of more nesting sites for ground nesting species. In addition to local management, the proportion of high-quality habitats for pollinators at the landscape scale can have strong effects on pollinator diversity and associated ES (e.g. Kennedy et al., 2013). However, this aspect could be not considered in the current study due to a lack of sufficient studies.

Besides biodiversity, all other ES categories showed significant positive responses to extensive vegetation management. However, we could not confirm the supposed trade-off between provisioning services wine yield/quality vs. biodiversity, regulating or supporting ES. The effect sizes were positive for all ES types but not significant for soil parameters like aggregate stability or saturated hydraulic conductivity, which are assumed to be correlated with a decrease in soil erosion. Obviously, soil loss is a parameter directly addressing erosion, therefore it is most suitable to be used as an indicator for erosion protection despite being highly variable and depending on seasonal conditions (Biddoccu, Ferraris, Opsi, & Cavallo, 2016). In contrast, erosion-related parameters (aggregate stability, hydraulic conductivity, penetration resistance, porosity, wettability) contain a rather heterogeneous set of indicators that are only indirect measures of soil erosion (Castillo & Gómez, 2016). Positive relationships between aggregate stability and soil water repellency have been reported in a meta-analysis (Zheng, Morris, Lehmann, & Rillig, 2016). However, as many different aggregate stability indices have been proposed as proxy for soil loss (e.g. Ramos, Nacci, & Pla, 2003), careful consideration is required at indicator selection. The decrease in soil erosion of vegetated inter-rows is mostly due to the mechanical protection by vegetation and their residues, whereas its impact on other soil physical properties is less intense than the impact on soil erosion, more variable across experiments and so more difficult to detect. Finally, improved soil properties can also enhance carbon sequestration and water filtration (Parras-Alcántara, Lozano-García, Keesstra, Cerdà, & Brevik, 2016).

Extensive vegetation management also positively affected soil fertility, which can be attributed to stimulatory effects on soil biota such as earthworms (Briones & Schmidt, 2017). However, we should note that most studies investigating tillage effects on soil biota were conducted in arable crops, but tillage in perennial vineyards is not always detrimental to earthworms (Faber, Wachter, & Zaller, 2017; Vršic, 2011). Besides earthworms, springtails have been studied in vineyard soils. Herbicide-treated inter-rows decreased springtail abundance and diversity, whereas tillage reduced only their abundance but not their diversity (Renaud, Poinsot-Balaguer, Cortet, & Le Petit, 2004). Overall, tillage is known to be an important factor in affecting mycorrhizal communities in soils because it directly affects the integrity of the mycelial network (Verbruggen & Kiers, 2010). Studies on the effects of tillage on mycorrhiza in vineyards are scarce. For example, Trouvelot et al. (2015) found that vegetated inter-rows favour arbuscular mycorrhizal fungi in the soil and roots of grapevines. Thus, effects of tillage on soil biota will consequently also support ES-like nutrient cycling and soil formation (Brussaard, de Ruiter, & Brown, 2007). Reduced soil management was also shown to significantly increase carbon sequestration (Zehetner et al., 2015), which links to a wide range of other ES like the contribution to atmospheric CO_2 regulation (Montanaro, Xiloyannis, Nuzzo, & Dichio, 2017).

Extensive vegetation management also had a significant positive effect on pest control. Taking a closer look, there was a difference between the overall effect size from pest-related parameters, which showed a significant positive response to extensive vegetation management, whereas natural enemy-related effect size did not differ significantly from zero. This phenomenon was also detected in other crops such as peach, olive or citrus (Paredes, Cayuela, Gurr, & Campos, 2015). Vegetation cover can increase the diversity and abundance of certain natural enemies that may promote intraguild predation (Finke & Denno, 2004), which in turn can reduce the effectiveness of ground cover for pest control. In addition, some plant species promoted in ground cover can increase, rather than decrease, pest abundance (Danne et al., 2010; Landis, Wratten, & Gurr, 2000). Further research on this ES should be pointed to the analyses of landscape, ground cover composition and trophic relationships between the biodiversity actors.

Most of the studies analysed in this meta-analysis had an experimental setting in a single vineyard, so it is not possible to analyse the combined effects of local vineyard management and landscape composition. It is crucial to identify the key ecological actors in biological control and their relationships among each other to promote management measures designed for different landscape situations (Straub, Finke, & Snyder, 2008; Tscharntke et al., 2016). It has to be noted, however, that the majority of studies used for the current meta-analysis were conducted in the USA and Europe, whereas other important wine producing regions such as South America, Australia and New Zealand, or Asia are under-represented.

Taken together, this meta-analysis demonstrated that extensive inter-row vegetation management significantly contributed to the provision of multiple ES and biodiversity conservation in vineyards. As most vineyard vine rows are kept free of vegetation, and vegetation cover is often not maintained year-round or in every inter-row, most vineyards contain patches of bare ground. This mosaic of heterogeneous vegetation patches provides beneficial conditions for taxa, which benefit from bare ground like ground-foraging bird species (Schaub et al., 2010) or wild bees (Potts et al., 2005). Results showed that intensive herbicide use and frequent tillage decreased ES and biodiversity provision. Policy instruments like agri-environment schemes provide powerful tools, which may change management decisions, as the majority of farmers usually do not consider the effects of management on ES and other externalities. European agri-environmental policies subsidize farmers to adopt vegetation cover in the vineyard inter-rows in order to prevent soil erosion. Some schemes encourage farmers not to use herbicides, which were shown to be especially beneficial for ES and biodiversity provision. Despite the overall positive effects of extensive vegetation management, grape quantity and quality may decrease in rainfall-deficient climates without irrigation (Marques, García-Muñoz, Muñoz-Organero, & Bienes, 2010; Ruiz-Colmenero et al., 2011). Therefore, cover crop management, like the frequency and timing of mulching or tillage and the choice of plant species has to be adapted to the local climate and weather conditions to balance trade-offs between wine production, biodiversity and ES provision (Guerra & Steenwerth, 2012). Reduced vegetation management intensity will also benefit winegrowers in the long run as a multitude of ES, such as soil erosion mitigation, soil fertility and pest control, improved.

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AUTHORS' CONTRIBUTIONS

S.W. and P.B. designed the study; all authors helped with data extraction from publications; S.W. collected and prepared data; S.W. and P.B. analysed data; all authors contributed to the writing of the manuscript. All authors gave final approval for publication.

DATA ACCESSIBILITY

Data available via Zenodo https://doi.org/10.5281/zenodo.1162154 (Winter et al., 2018).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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4.3. Pollen resources

So far, only pollen samples from April (n = 13) and June (n = 31) were analysed, which allows to assess the importance of fruit trees and grapevine, additionally to the plants in the inter-rows as pollen resources for wild bees in vineyards. In total, pollen loads from 20 different wild bee species were analysed and 27 pollen types, which accounted at least 1 % of the total counted grains in a single sample, were identified (Table A2 in Appendix). On average, 2.82 (±1.47 SD) different pollen types were collected per sampled bee individual. Wild bees in vineyard inter-rows collected mainly pollen of the *Crepis*-type, *Stellaria graminea*-group and *Sorbus*-group during April (Figure 6a).

During the full florescence of grapevine in June (Figure 6b), predominantly pollen of two *Trifolium*-types (*T. repens*-type, *T. pratense*-type) and of the *Vicia*-type were collected in vineyard inter-rows. Further, two *Lasioglossum lineare* and one *Osmia caerulescence* individual, which were sampled in the inter-row transect, had collected high proportions (61-88 %) of grapevine pollen in June.

In total, 15 individuals belonging to 7 species (*Andrena dorsata*, *Apis mellifera*, *Bombus terrestris*, *Lasioglossum laticeps*, *L. lineare*, *L. malachurum*, *L. pygmaeum*) were sampled from flowering grapevine; pollen samples of 6 individuals (4 species: *A. dorsata*, *Apis mellifera*, *L. laticeps*, *L. lineare*) were analysed and comprised high proportions of grapevine pollen (Figure 6c). In particular, five individuals carried almost only grapevine pollen (93-100 %), while the pollen load of one *L. lineare* individual consisted almost equally of *Phacelia tanacetifolia* pollen (57 %) and *Vitis vinifera* pollen (43 %).

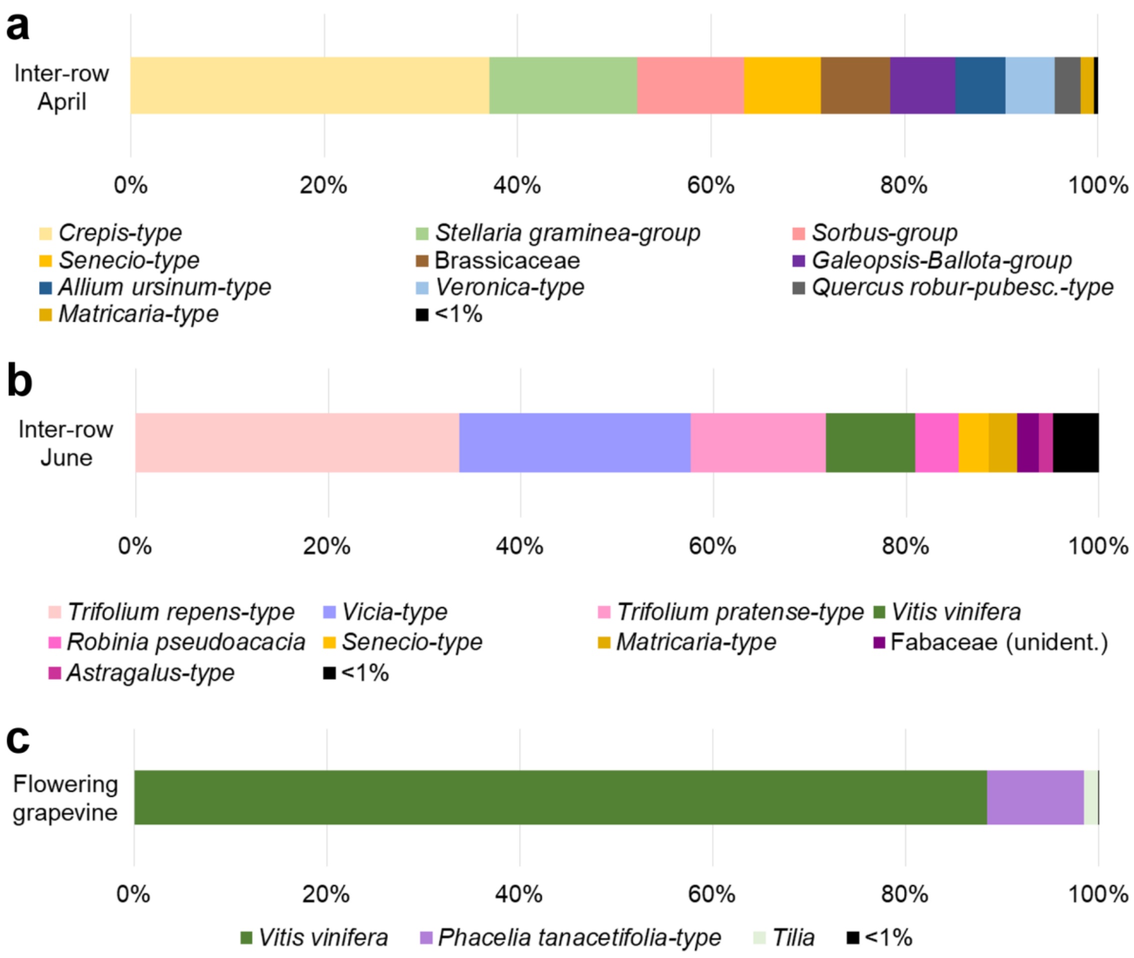

Fig. 6 Pollen types collected by wild bees in vineyard inter-rows in a) April (n=13) and b) June (n=31) as well as c) pollen collected by wild bees sampled on flowering grapevine in June (n=6). Pollen types that represented <1% in the respective month were summarized.

The pollen samples from *Osmia cornuta* trap nests, a species that was not sampled in the vineyard inter-rows, showed that the females collected predominantly pollen from the *Sorbus*-group and *Quercus* in viticultural landscapes (IV). On average (± SD), the pollen richness per trap nest was highest in the viticultural region (4.75 ± 0.96) compared to the other land use regions (urban region: 3.75 ± 1.71; village-structured region: 3.25 ± 1.50; agricultural region: 1 ± 2). Similarly, the average (± SD) number of brood cells per trap nest was highest in the viticultural region (136.35 ± 57.45) and followed by the village-structured region (74.5 ± 18.65) and the urban region (64 ± 78.84). The lowest mean number of brood cells was found in *O. cornuta* trap nests in the agricultural region (20.25 ± 40.5).

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*Authors contributed equally

Osmia cornuta couple; the two horns in the female’s face are acknowledged in the species’ common name – “Horned mason bee”

Pollen availability for the Horned Mason Bee (*Osmia cornuta*) in regions of different land use and landscape structures

Running title: Pollen availability for the Horned Mason Bee

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Abstract

1. *Osmia cornuta* is a generalist regarding its habitat requirements and is used for pollination in orchards. The species collects pollen from different plant taxa, but pollen richness and pollen quantity in a nest may be affected by land use and landscape structures.

2. We studied the availability of pollen resources for *Osmia cornuta* across different land use types (one urban-, village-structured-, agricultural and viticultural region each) by pollen analysis in the context of landscape structures.

3. In total, 16 pollen types were identified in 1180 brood cells collected by *O. cornuta*. On average (±SD), the highest pollen richness per region (n=4) was found in the viticultural region (4.75±0.96) and the lowest in the agricultural region (1±2). *Osmia cornuta* collected predominantly pollen from the *Sorbus*-pollen group, which includes *Prunus* species. *Salix* was primarily collected in the village-structured and the agricultural region, and *Quercus* was frequently found in samples from the viticulture region. The highest mean (±SD) number of brood cells per region (n=4) was found in the viticulture region (136.35±57.45) and the lowest in the agricultural region (20.25±40.5). Increasing proportions of green areas in urban and village-structured regions affected the pollen richness positively, whereas agricultural areas had a negative impact on pollen richness and the number of brood cells.

4. We concluded that the polylectic *O. cornuta* uses a wide range of flowering plants dependent on their availability. The maintenance of fruit trees as well as

willow- and oak trees enhances floral resources qualitatively and quantitatively for *O. cornuta* specifically in intensively farmed agricultural areas.

Keywords: Apiformes, pollen analysis, *Osmia cornuta*, pollen type richness, metabarcoding

Introduction

Wild bees are important pollinators for crops and wild plants (Klein et al., 2007; Ollerton et al., 2011), and are dependent on structurally diverse landscapes for floral resources and nesting habitats (Morandin & Kremen, 2013). The fragmentation of natural habitats through agricultural intensification has resulted in the loss of nesting sites and floral resources for wild bees (Le Féon et al., 2013). The availability of pollen was reported as a limiting factor for the reproduction success of different wild bee species. For example, the lower number of brood cells, due to decreased pollen availability by increased competition between conspecifics, resulted in a lower number of adult *Megachile rodundata* bees in the following year (Pitts-Singer & Bosch, 2010). Further, *Osmia cornuta* females may adapt to decreasing pollen availability by reproducing smaller and more male than female offspring, because males need less food for development (Bosch, 2008). Studies have demonstrated that regions with diverse types of land use, e.g. grasslands in residential areas, urban park meadows and uncultivated land, have a positive impact on wild bee species richness and abundance (Fischer et al., 2016; Mandelik et al., 2012). Further, wild bee species richness and abundance positively affects pollination efficiency, leading to higher yields and better fruit quality (Klein et al., 2007; Holzschuh et al., 2012; Földesi et al., 2015; Winfree et al., 2018). In the agricultural landscape, the conservation of natural habitats, grasslands and semi-natural habitats e.g. hedges (Morandin & Kremen 2013), fallows (Toivonen et al., 2015), woods (Rollin et al., 2013), unsealed roads or road margins (Kleijn & van Langevelde, 2006), enhances wild bee species richness and abundance (Kennedy et al. 2013). Urban areas provide important nesting and foraging habitats, as well as favourable microclimatic conditions for thermophilic wild bees (Hernandez et al., 2009). Especially private gardens and allotments in urban areas offer important pollen- and nectar resources for wild bees throughout the year (Fischer et al., 2016; Baldock et al., 2019). Further, it has been reported that urban areas are of primary benefit to generalistic (polylectic) and cavity nesting wild bee species (Eremeeva & Sushchev, 2005).

Osmia cornuta (Latreille 1805) is a wild bee species common to Europe and a generalist regarding its habitat requirements (Bosch, 1994; Westrich, 2018). It is a solitary species occurring mainly in villages and urban areas, but also colonizing forest edges, where the females establish their nests in almost every available pre-existing cavity (e.g. holes and cracks in house walls, loess- and clay walls, dead wood elements) (Scheuchl & Willner 2016). One nest consists of 10-20 brood cells built mainly in linear order. Each brood cell consists of an egg and a provisioned food reserve of pollen and nectar for the larvae. The entrance of each finished nest is plugged with moist soil or mortar. In central Europe, *O. cornuta* occurs in spring with an active flight period between March and the beginning of May (Westrich 2018).

Osmia cornuta is a pollen generalist (Westrich 2018) and commonly used for pollination in orchards, especially in pome and stone fruit plantations (Bosch, 1994). It has a greater pollination efficiency than *Apis millifera* in orchards (Vicens & Bosch, 2000a; Ladurner et al., 2002) because of higher stigma contact rates, more flower visits per minute (Monzón et al., 2004) and a higher tolerance to unstable weather conditions (Vicens & Bosch, 2000b). Further, the generalistic foraging behavior of *O. cornuta* leads to the pollination of different entomophilous plant species (Bosch, 1994). The preferred floral resources are pollen from Rosaceae species (Bosch, 1994) but *Salix*, *Corydalis* and *Acer* (Haider et al., 2014; Westrich, 2018) are also foraged. Moreover, *Osmia* species collect *Trifolium repens* pollen and pollen from wind-pollinated trees like *Quercus* and *Betula* (MacIvor et al., 2014). Schindler and Peters (2011) studied the foraging behavior of *O. cornuta* in orchards in relation to the surrounding landscape. They found that pollen diversity was higher in trap nests situated in heterogeneous landscapes compared to more simplified landscapes with less diverse floral resources. There are only a few studies about the impact of land use and landscape structures on the foraging behavior of *O. cornuta*, but foraging behavior of other *Osmia* species was already studied in a landscape context (Williams & Kremen, 2007; Persson et al., 2018).

The aim of this study is to evaluate available pollen resources for *O. cornuta* in regions of differing land use types (agriculture, viticulture, urban and village-structured) in Eastern Austria. The research questions are: Which plants are important pollen resources for *O. cornuta* in regions of different land use? Do the pollen resources foraged by *O. cornuta* differ across these regions? How do land use regions and landscape structures affect the number of provisioned brood cells and pollen richness in *O. cornuta* trap nests?

Materials and Methods

Study area

This study was conducted in four regions of differing land use (i.e. urban, village-structured, agriculture, viticulture) in eastern Austria (Fig. 1). The urban study sites in Vienna, (48°12'30N 16°22'19E) represented those with the highest ground sealing and building density (Appendix Table 1). The distance between trap nest sites (Appendix Table 2) ranged from 1.5 to 10.3 km. The study sites in the village-structured region in and around Lanzenkirchen (Lower Austria, 47°73'N 16°23'E) comprised a mixture of allotment gardens and agricultural and industrial land and distances between trap nest sites ranged from 0.2 to 10.7 km (Appendix Table 2).

The agricultural land use in the Marchfeld region (Lower Austria, 48°13'5.842''N 16°36'16.667''E) was characterized by low proportions of semi-natural elements (SNE) and urban areas. The distance between trap nest sites ranged from 0.3 to 5.1 km (Appendix Table 2). The viticultural region Neusiedlersee-Hügelland (47°53'40''N 16° 38' 47''E) was represented by a high coverage of vineyards with wood-covered hills and the lowest proportion of urban areas. The distance between trap nest sites ranged from 1.7 to 4.4 km (Appendix Table 2). Ambient temperatures during April 2016 were similar across the regions. The average temperatures in April ranged between 10.5°C in the village-structured region and 11.7°C in the viticultural region (data derived from near weather stations; ZAMG, 2016).

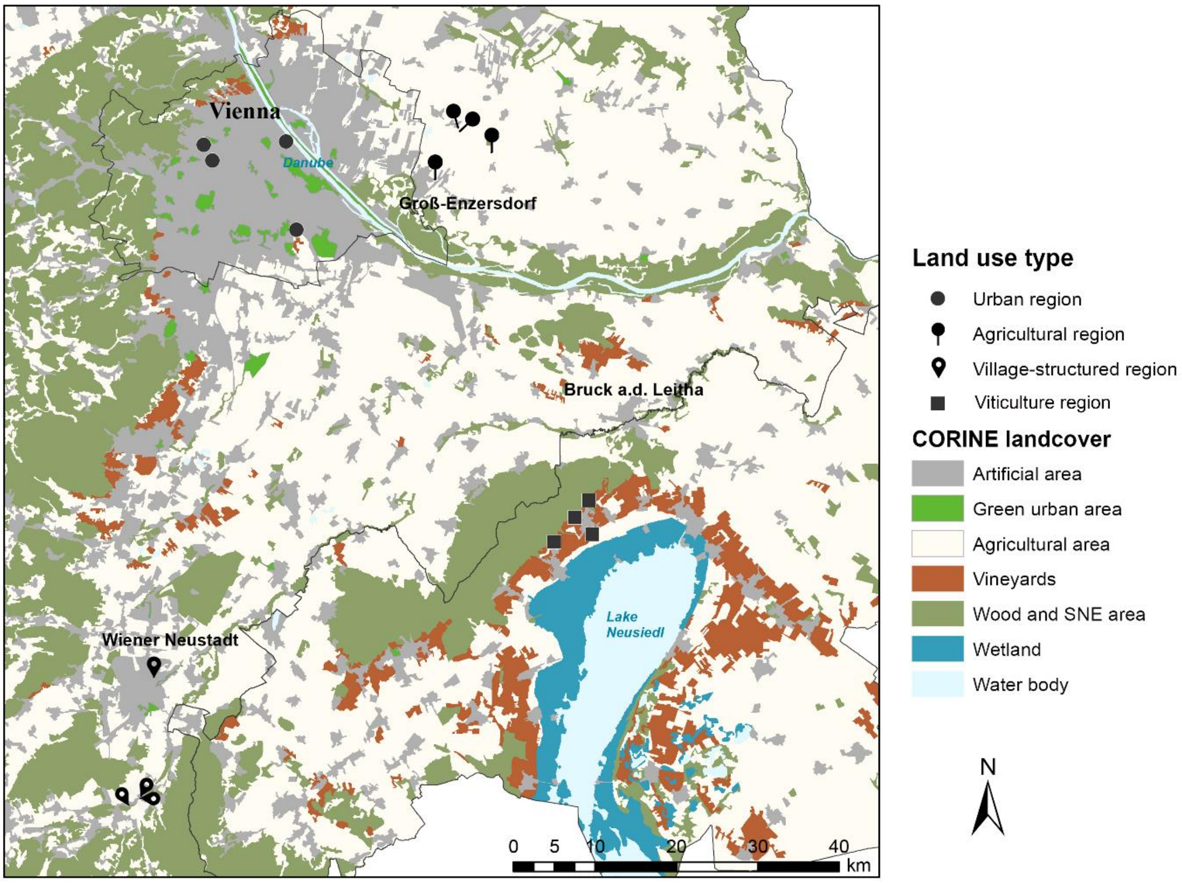

Fig. 1 Overview map with the study regions of different land use and the four locations of trap nests per region. Landscape structures according to CORINE land cover (Umweltbundesamt GmbH, 2012).

Pollen sampling and analysis

In each region, four study sites were chosen (Fig. 1) and one trap nest per site was set up in early April 2016 to collect pollen foraged by *O. cornuta* females. Each trap nest was composed of two stacked wooden plates (16.0×16.0×1.6 cm) with ten half-round channels (15.0×0.8 ×0.8 cm) per plate (Fig. 2a) placed in wooden shelters for weather protection 45.0 cm above the ground (Fig. 2b). They were situated on balconies in the urban region, which ranged in height between 4 and 9 m above the ground level. Therefore, the 45 cm height of the trap nest applies to the ground of the balcony. The trap nests were situated in gardens in the village-structured region, near hedges or shrubs in the agricultural region and near vineyards in the viticultural region. These locations were chosen because they were, based on our expertise, found to be representative structures in the respective region. To ensure the colonization by *O. cornuta* eight cocoons (equal number of male and female cocoons, distinguishable by their different sizes) were placed in a small paper box with an exit hole next to the trap nests. The trap nests were considered to be colonized by the starter population, because *O. cornuta* is unselective regarding its nesting habitat, frequently colonizes artificial nests and searches in close proximity to its hatching place for a nesting site (Westrich, 2011, 2018). The cocoons for the starter populations were collected from trap nests colonized in eastern Austria in the spring of 2015. The traps were collected after three weeks in the field (end of April), which can be considered the end of the climax of breeding activity of *O. cornuta* (Westrich, 2018). All paper boxes were intact when we collected the trap nests and all cocoons were opened. We therefore, were sure that none of the cocoons got lost prior to hatching and that all cocoons hatched. Further, at this point most of the brood had developed to the egg or young larval stage and therefore most of the pollen remained in the brood cells and was available as sample. The number of brood cells per nest was counted as a proxy for nesting success. We did not use the amount of holes used in a trap nest (as proxy for the number of nesting females) or the number of cells per hole (as proxy for reproduction per nesting female), because one female could also construct more than one nest (Persson et al., 2018) and we did not frequently monitor the nests (Williams & Kremen, 2007; Persson et al., 2018). The pollen of each nest was harvested and stored together in a 50 ml tube per nest at 20°C.

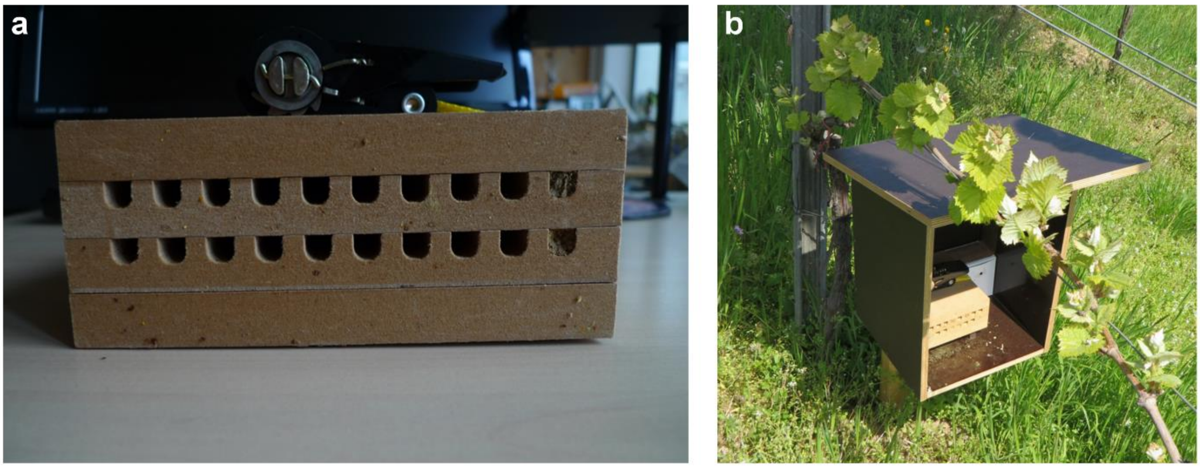

Fig. 2 Design of (a) the trap nest consisting of two stacked wooden plates (16×16×1.6cm) with ten U-shaped holes (15×0.8×0.8cm) and (b) set-up of a trap nest in the field –right to the trap nest the box including the starter population was placed.

To determine pollen richness six subsamples per trap nest tube were selected based on various pollen colours by considering the estimated proportion of different colours in each trap nest. Each pollen subsample was homogenised in a 2 ml Eppendorf-Tube with 1.5 ml ethanol 96% and disposable pipettes were used to apply a sample of the pollen to a microscope slide. The pollen was embedded in fuchsine (Roth, Fuchsine basic (C.I. 42510)) dyed glycerine (Roth, Glycerin Rotipuran) to increase the contrast of structures on the pollen grains. Using a light microscope (magnification: 400x, 600x), the pollen types in each sample were identified based on literature (Beug, 2015) and pollen databases (AGES Abteilung für Bienenkunde und Bienenschutz, 2016; AutPal – Society for the Promotion of Palynological Research in Austria, 2016). In each subsample 300 pollen grains were counted. Using a light microscope, pollen of closely related plant taxa can be difficult to identify at a species level, therefore similar pollen grains were aggregated to pollen types or groups (Beug 2015; see Appendix Table 3).

In addition, and for a more detailed picture of the floral resources utilized by *O. cornuta*, the pollen identification was evaluated by molecular methods. This was performed by sequencing the pollen of two of the study sites: one from the viticulture region (N1) and the other from the urban region (W3). For each site, six subsamples were taken. Despite the same traps being used, these do not correspond to the subsamples used in the morphological pollen analysis. Each subsample in the molecular analysis corresponded to a different nest. The initial pollen amount used for DNA isolation per subsample varied between 5 and 50 mg. Each subsample was isolated and sequenced independently. For DNA isolation, pollen cell walls were disrupted mechanically by homogenizing the material with zirconium beads and lysis buffer in a RETSCH MM 200 (Retsch, Germany) mixer mill. The remainder of the DNA isolation was performed using the MagSi-DNA Vegetal kit (Steinbrenner, Germany) according to manufacture recommendations. Taxa were identified by part of the trnL-F region using the primers e and f from Taberlet et al. (1991). This marker was chosen because of its ability of producing recovering high variation, increasing the determination power, with relatively conserved primer binding sites, decreasing possible PCR biases (Kraaijeveld et al., 2015; Bell et al., 2016). DNA sequences were produced using the Illumina technology (Illumina, USA). To do so, amplicon sequencing libraries were constructed using the same protocol described in Lanner et al. (2018). The resulting libraries were pooled and sent for PE 250bp sequencing in an Illumina MiSeq at the Genomics Service Unit at Ludwig Maximillian Universität, Munich, Germany.

The resulting Illumina reads were quality controlled with cutadapt (Martin, 2011) by excluding adapter sequences and low-quality regions with average Phred scores below 20. Paired reads were merged using PEAR (Zhang et al., 2013) and amplification primers were trimmed using script 1 from Curto et al. (2019). The resulting reads were dereplicated and blasted against all Spermatophyta chloroplast sequences present in GenBank. Blast search was done using the scripts from

Hawkins et al. (2015). Only matches with a similarity above 90% were considered further. Additionally, only the best match per read was taken into consideration. The relative amount of pollen was accessed by read count per taxa.

Landscape analysis

The landscape structures (Table 1) were mapped in ArcGis 10.4 (ESRI, 2016) within a 500 m radius around each trap nest, as the foraging distance of *O. cornuta* ranges between 200 and 600 m (Gathmann & Tscharntke, 2002; Zurbuchen et al., 2010) and the species predominantly forages in radius of 200 to 300 m (Schindler & Peters, 2011). The landscape data for this study was taken from different sources. For the urban region, the categories on landscape structures were already specified, because the data was extracted from the geodataviewer of the city of Vienna (Stadt Wien, 2015). For the vineyard region, data from the BiodivERsA project VineDivers (www.vinedivers.eu) was used, in which the landscape categories were defined prior to field mapping (see Kratschmer et al., 2018 for detailed method). Therefore, it was possible to differentiate between “entomophilous crops” (i.e. insect pollinated crops) and “non-entomophilous crops” (i.e. wind- or self-pollinated crops) or “unsealed roads” (i.e. dirt roads) and “gravel roads”. The landscape structures of the village-structured and the agricultural regions were mapped based on orthophotos by basemap.at (Stadt Wien und Österreichische Länder bzw. Ämter der Landesregierung, 2016). Thereby the category “cropland” (Table 1) was used for all agricultural areas, because differentiating between “entomophilous crops” and “non-entomophilous crops” was impossible by orthophoto mapping. Similar was done by using the category “green areas” to summarize “parks”, “private gardens”, “green spaces along roads”, “green courtyards”, “community gardens” and “meadows” (i.e. green areas near buildings) in the data set from Vienna. Further, “storage sites” and “construction sites” were also summarized under “green areas” because e.g. sand pines vegetated with pioneer plants can be found there and may provide foraging resources. Due to the different precision of the data-sets, the landscape structures were summarized into 11 categories (Table 1) using the nomenclature of the European Nature Information Systems (EUNIS, Davies et al. 2004). The proportion of landscape structures within each circle was used for further statistical analyses.

Table 1: Landscape structure categories used for the landscape analysis following the EUNIS habitat classification (Davies et al. 2014). The “final category” was used to summarize the landscape data used in the BiodivERsA project VineDivers and urban structures according to the City of Vienna (Stadt Wien 2015) and for mapping of the agricultural and village-structured landscape based on orthofotos.

Final Category	Landscape structures (BiodivERsA)	Urban structures (City of Vienna)
Semi-Natural Elements	Fallows, grass strips, natural grasslands, pastures, sparsely wooded grasslands, unsealed paths and roads, orchards	
Agriculture	Entomophilous crops, non-entomophilous crops	Cropland
Green areas	Green areas	Meadows, other green spaces, green areas, storage sites, construction sites, cemeteries
Hedges and trees	Hedges, tree rows, isolated trees	
Vineyards	Vineyards of different management intensity	Vineyards
Buildings	Buildings	Monuments, fountains, roofs, buildings, glass buildings, kiosks, walls, porches, fences, other buildings, overbuildings
Wetland	Wetlands including accompanying herbaceous vegetation	
Wood area	Woodlots	Forests
Roads	Roads and gravel roads	Roads, crosswalks, traffic islands, telephone booths, street furniture, stairs, station equipment, various traffic areas, parking spaces, pavements, cycle paths, pedestrian areas, speed ramps, railway tracks, railway sectors
Water entities	Ponds and rivers	Natural water bodies
Artificial/constructed entities	Artificial elements	Paved areas, courtyards, swimming pools, sports fields

Data analysis

Pollen types or groups representing less than 1 % of the pollen grains counted in a subsample were combined (Appendix Table 3) and excluded from statistical analysis (c.f. Westrich, 1986; Beil et al., 2008), as they could represent contamination. Statistical analyses were computed in R 3.4.3 (R Core Development Team, 2018).

Prior to data analysis, Moran's I Tests were conducted to check for spatial autocorrelation due to the close proximity of some sites (Appendix Table 2) with the R package "ape" (Paradis et al., 2004). The two response variables (pollen richness and number of brood cells) were aggregated among each trap nest site and tested against the respective distances (m) between the sites (calculated with the Geographic Distance Matrix Generator V1.2.3 Ersts, 2016). Neither significant spatial autocorrelation among trap nest sites for pollen richness ($p = 0.28$) nor number of brood cells ($p = 0.11$) was detected.

To assess similarities of pollen types foraged by *O. cornuta* within a region, a principal components analysis (PCA) was constructed using the R Package „vegan" (Oksanen et al. 2018). The effect of regions and landscape structures (i.e. predictors) on the pollen richness and the number of brood cells (i.e. responses) was assessed in two steps: First, conditional Random Forests (RF) with 500 trees were computed to calculate the conditional variable importance (Strobl et al., 2009) of the predictors for each response variable by using the R Package "party" (Hothorn et al., 2006; Strobl et al., 2008). The number of randomly chosen predictors at each tree's node was set to the square root of total predictors ($n = 4$; cf. Puech et al. 2014). The variable importance of predictors that exceeded the first quarter of the variable importance scale was characterized as the most important predictor variable for the respective response. Further, the effect sizes and whether the effects of these predictors are positive or negative, is not shown by the RFs. This was assessed by formulating Generalized Linear Mixed Models (GLMMs) with Poisson error distribution using the R package "lme4" (Bates et al., 2015). To account for the nested pseudo-replication of the subsamples in a trap nest the trap nest IDs were used as random factors to model pollen richness. Further, the region was set as random factor to account for the similarities of pollen types within a region shown by the PCA. Additionally, one model including the region as a fixed factor and the trap nest ID as a random factor was formulated, to assess the effect of the regions in detail. For the analysis of the number of brood cells, the region was set as a random factor. The model with region as fixed factor was computed as Generalized Linear Model (GLM). The selection of the most parsimonious model for each response was carried out with the second order Akaike Information Criterion (AICc) using a cut-off at $\Delta\ AICc > 2$ (Motulsky & Christopoulos 2003; R package "AICcmodavg" Mazerolle 2016). The effects of these models were then plotted using the R package "effects" (Fox et al., 2016).

To account for the small sample size of trap nests per region, a power analysis was performed based on Green & Macleod (2016) with the R-package „simr". The effect size of predictors in the most parsimonious models was tested with a z-test based on 1000 simulations. Using the exact effect size from the models based on the data would give misleading results, because this would be a retrospective calculation (Hoenig & Heisey, 2001). Therefore, only a 50% value of the respective effect size (Green & Macleod, 2016) was used to assess the power, because power generally increases with effect size. Table 4 in appendix gives the results of the GLMMs and the power analysis.

Results

In total, we identified 16 pollen types (Appendix Table 3) and counted 1180 brood cells in the 16 *O. cornuta* trap nests. The highest average (±SD) pollen richness per trap nest was found in the viticultural region (4.75±0.96), followed by the urban (3.75±1.71) and village-structured regions (3.25±1.50). The lowest pollen richness was found in the agricultural region (1±2), where only one trap nest was colonized with brood cells. *O. cornuta* females collected pollen of the *Sorbus*-pollen group in all four regions, which included pollen mostly from Rosaceae species (Fig. 3). *Salix* was collected in high proportions in the village-structured and the agricultural regions (Fig.3). Further, in the viticulture region, *Quercus* was found in high proportions and pollen from *Fagus* and the *Allium ursinum*-type were exclusively documented here.

This pattern was also revealed by the PCA, due to similar pollen types being found in trap nests within the same region (Fig. 4). Three trap nests in the viticulture region and one urban site contained mainly *Quercus* pollen. The viticultural sites were embedded in landscapes with the highest mean proportions of wood areas (26.50±22.28%). The other three urban sites were similar to the fourth viticulture site and two village sites, where mostly Rosaceae pollen was collected. The only site with provisioned brood cells in the agricultural region was surrounded by a larger proportion of settlements with small gardens (23.1%) compared to the other agricultural sites (2.6±4.6%). It was therefore similar to two village-structured sites, which contained a larger proportion of agricultural areas (33±7.07%) compared to the other two village sites.

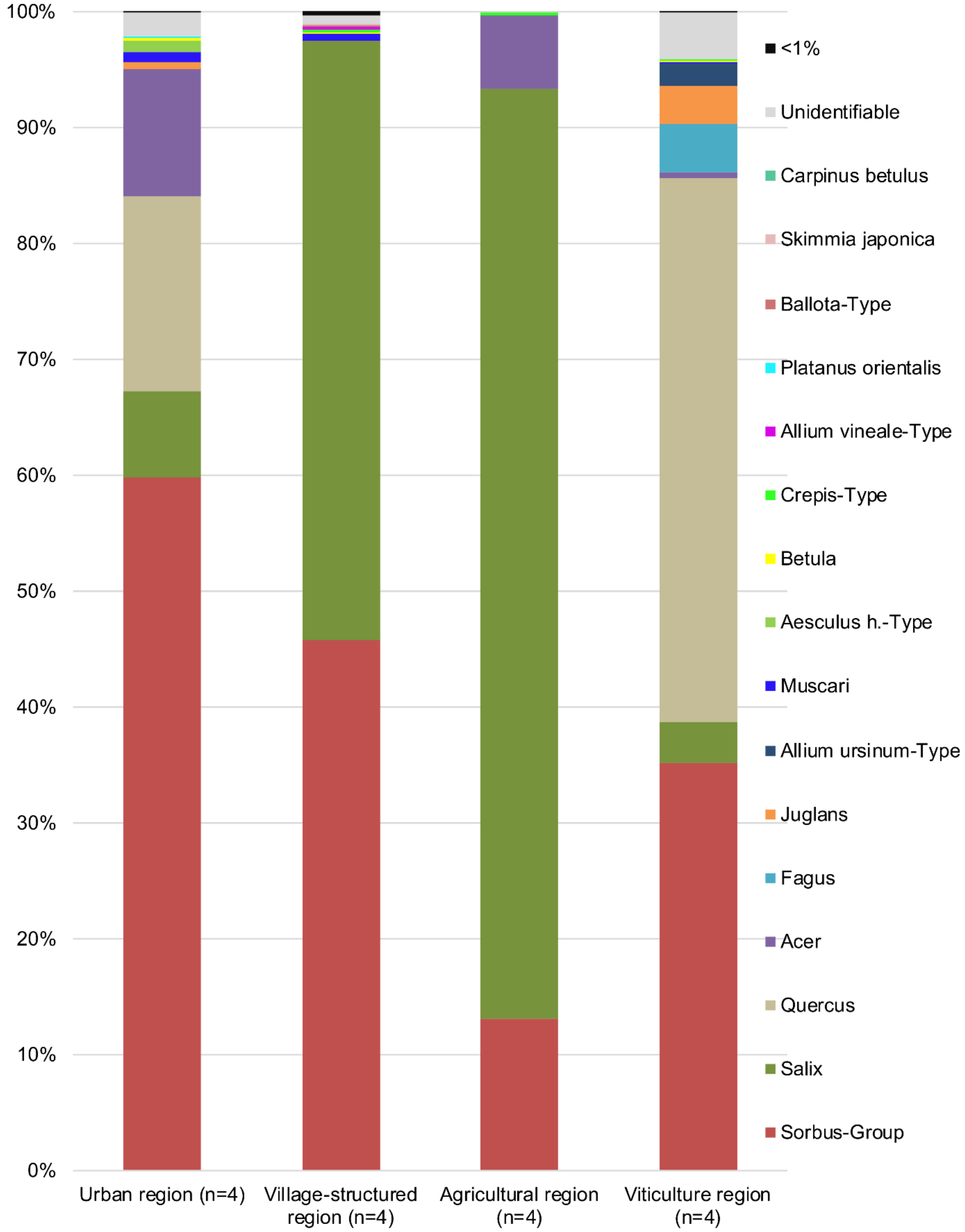

Fig. 3 Pollen types identified in *Osmia cornuta* trap nests in four regions of different land use. Pollen types that appeared <1% in a sample were summarized and included: *Cannabis*, *Primula*, *Viola tricolor*-type

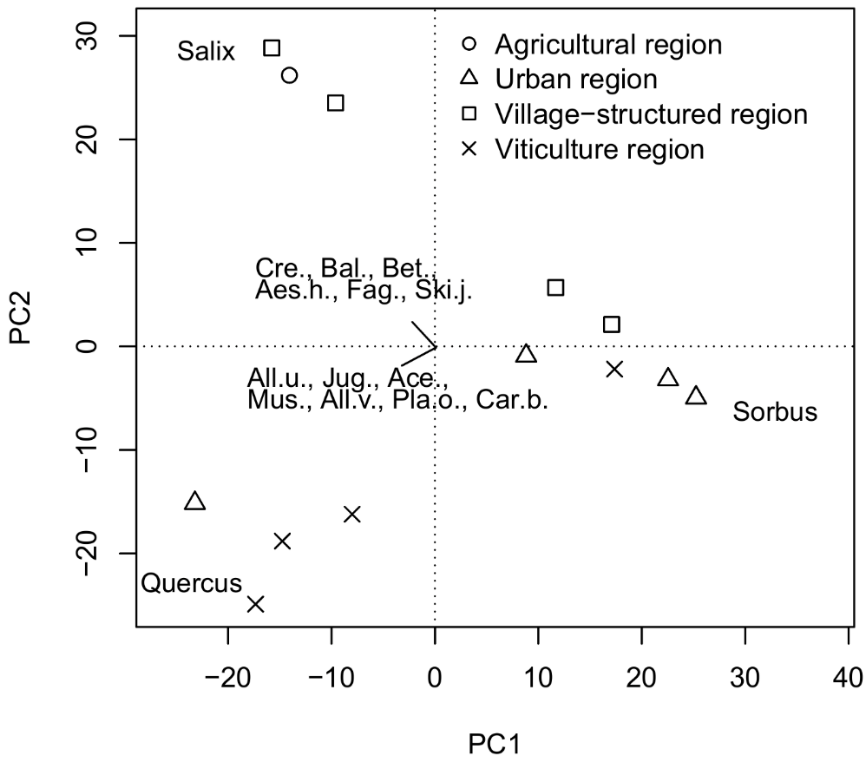

Fig. 4 PCA with similarities of pollen types within the regions. The most collected pollen types/groups were *Sorbus*, *Salix*, *Quercus* and clearly associated to the regions. Pollen types with lower amounts clustered in the centre: *Crepis* (Cre.), *Ballota* (Bal.), *Betula* (Bet.), *Aesculus hippocastanum* (Aes.h.), *Fagus* (Fag.), *Skimma japonica* (Ski.j.), *Allium ursinum* (All.u.), *Juglans* (Jug.), *Acer* (Ace.), *Muscari* (Mus.), *Allium vineale* (All.v.), *Platanus orientalis* (Pla.o.) and *Carpinus betulus* (Car.b.). To improve readability whiskers and abbreviations were added.

For molecular identification, a total of 665,557 reads were produced from which 280,876 passed the quality control step. These corresponded to 214,700 unique sequences, matching a total of 261 taxa, of which 17 taxa were represented by above 1%. Ten taxa were identified at the species level, six at the genus level and one at family level. Within one locality, we obtained between 15,025 and 31,898 good quality reads per subsample translating into 11,855 to 23,246 unique sequences matching between 4 to 13 taxa. This varied between four and eight for the viticulture site and between 11 and 13 for the urban site (Appendix Table 5). These results were congruent with morphological identification. All taxa identified morphologically were also found using molecular data (Table 2), although *Aesculus hippocastanum* and *Platanus orientalis* only matched at the genus level. Morphological identification showed that *Quercus* and *Sorbus*-group were the most frequent taxa in both regions analyzed (Viticulture and Urban regions, respectively). *Quercus* species were represented by 88,101 unique sequences where 3,675 had more than one read. With respect to *Prunus* sp., 83,459 unique sequences were detected but only 3,975 had more than one read. Some of these could be assigned to species, *Prunus avium*, *P. domestica*, *P. laurocerasus*, *P. undulata*, Hereby, *P. undulata* is not recorded from the region. The remaining taxa were also successfully identified per site, although there were some exceptions. For example, in the urban environment, *Quercus* species were the second most frequent pollen types assessed by morphological identification, while there was no sequence assignment to this taxon in this site for molecular data. Also, for some taxa there was some incongruence in the relative frequency of the pollen types based on molecular and morphological identification. The largest difference was found in the viticulture trap, where the most frequent pollen type for one of the subsamples analysed by the molecular approach was Allium ursinum instead of *Quercus* sp., which we found most frequently in the other subsamples assessed by morphological identification.

Table 2. Taxa identified based on trnL-F primers e and f. Information concerning the correspondent pollen type in the morphological identification and the site where it was found also added.

Taxa	Morphological identification	Site found
Docyniopsis tschonoskii	*Sorbus*-group	Urban
Malus sp.	*Sorbus*-group	Urban
Prunus avium	*Sorbus*-group	Urban and Viticulture
Prunus domestica	*Sorbus*-group	Urban
Prunus laurocerasus	*Sorbus*-group	Urban
Prunus sp.	*Sorbus*-group	Urban and Viticulture
Prunus undulata	*Sorbus*-group	Urban
Prunus virginiana	*Sorbus*-group	Urban
Pyrus sp.	*Sorbus*-group	Urban
Rosaceae sp.	*Sorbus*-group	Urban
Salix babylonica	*Salix*	Viticulture
Quercus sp.	*Quercus*	Viticulture
Acer maximowiczianum	*Acer*	Urban
Acer sp.	*Acer*	Urban and Viticulture
Acer pseudoplatanus	*Acer*	Urban
Fagus sp.	*Fagus*	Viticulture
Allium ursinum	*Allium ursinum*- type	Viticulture

The highest mean (±SD) number of brood cells per trap nest was found in the viticulture region (136.35±57.45) followed by the village-structured region (74.5±18.65) and the urban region (64±78.84). The lowest mean (±SD) number of brood cells was counted in the agricultural region (20.25±40.5).

According to the RFs, the most important predictors for pollen richness were the region and the proportion of agriculture and green areas (Fig. 5a). For the number of brood cells, the regions as well as the proportion of woodlots, agriculture and semi-natural elements were the most important predictors (Fig. 5b).

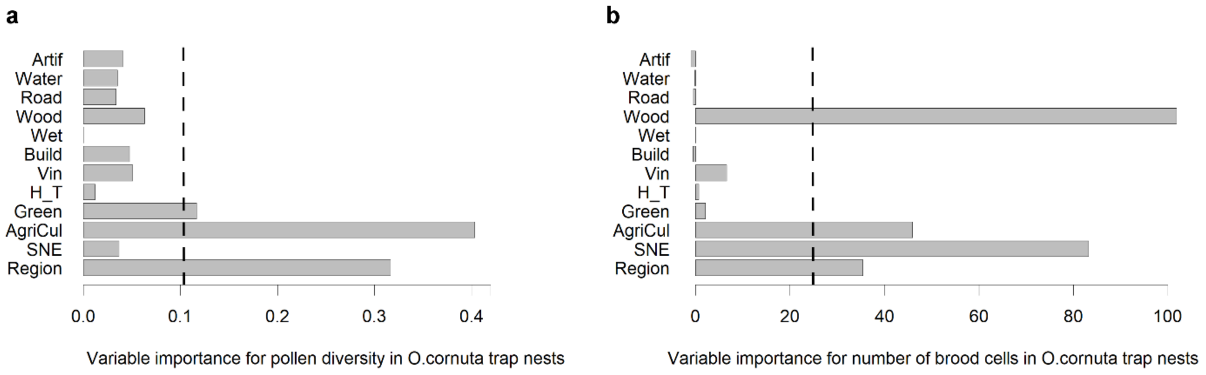

Fig. 5 Random forest conditional variable importance (V.I.) of land use regions and landscape structures (semi-natural-elements (SNE), agriculture (AgriCul), green areas in city or villages (Green), hedges and trees (H_T), vineyards (Vin), buildings (Build), wetlands (Wet), woodlots (Wood), roads and gravel roads (Road), ponds and rivers (Water), artificial areas (Artif) for (a) pollen richness and (b) number of brood cells in *Osmia cornuta* trap nests. Dashed line=Variables exceeding ¼ of the V.I. scale are considered in further modelling.

Three models were equally suited at explaining the variation of pollen richness in *O. cornuta* nests (Table 3). The agricultural region (Fig. 6a) and the increasing proportion of agricultural areas (Fig. 6b) affected the pollen richness negatively. Whereas the increasing proportion of green areas (Fig. 6c) and the other regions affected the pollen richness positively (detailed GLMM Results in Appendix Table 4). However, these results do not identify, which of the other regions was most beneficial in enhancing pollen richness in the trap nests. For the analysis of the number of brood cells, only one model was the most parsimonious. The number of brood cells decreased strongly by an increasing proportion of agricultural areas (Fig. 7).

Table 3. Model sets and model selection by AICc to analyse the effects of region and important landscape structures assessed by Random Forests on pollen richness and number of brood cells in *Osmia cornuta* trap nests; the effect of region on the number of brood cells was modelled as generalized linear model

Response variable	Predictors in GLMM/GLM	K	Δ *AICc*
Pollen richness	**~ Region + “Trap ID”**	**5**	**0.00**
	~ Green areas + “Region” + “Trap ID”	**4**	**0.67**
	~ Agriculture areas + “Region” + “Trap ID”	**4**	**0.94**
	~ 1 + “Region” + “Trap ID”	3	6.93
No. of brood cell	**~ Agriculture + “Region”**	**3**	**0.00**
	~ Region	4	48.96
	~ SNE + “Region”	3	55.79
	~ Woodlots + “Region”	3	61.45
	~ 1 + “Region”	2	68.84

“..”	random factors
K	number of estimated parameters
Δ *AICc*	Difference between the AICc to next parsimonious model; cut-off = Δ *AICc* ≥ 2
Bold	most parsimonious models

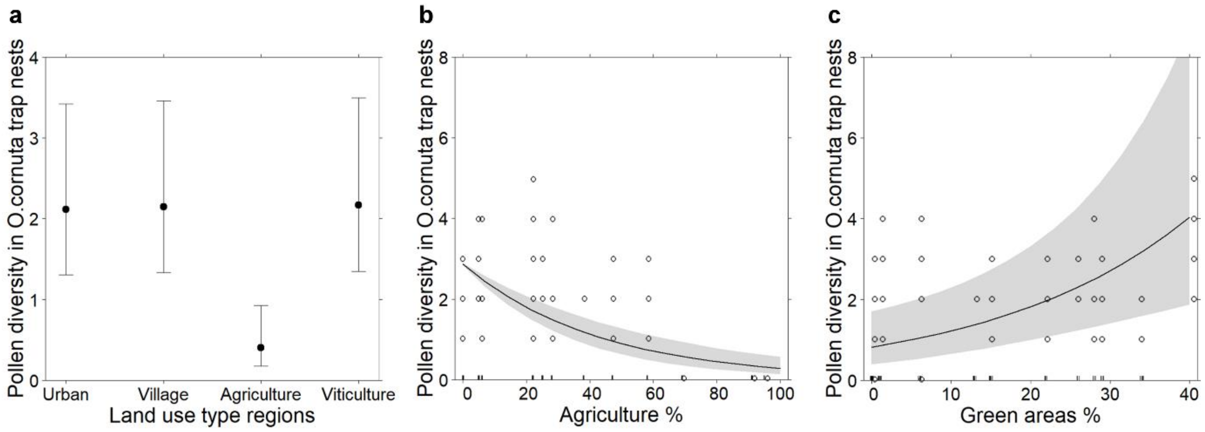

Fig. 6 Predicted values for pollen richness (per subsample) in *Osmia cornuta* trap nests in response to (a) land use regions and (b, c) landscape structures within a 500 m radius. Error bars/grey shading: 95% CI

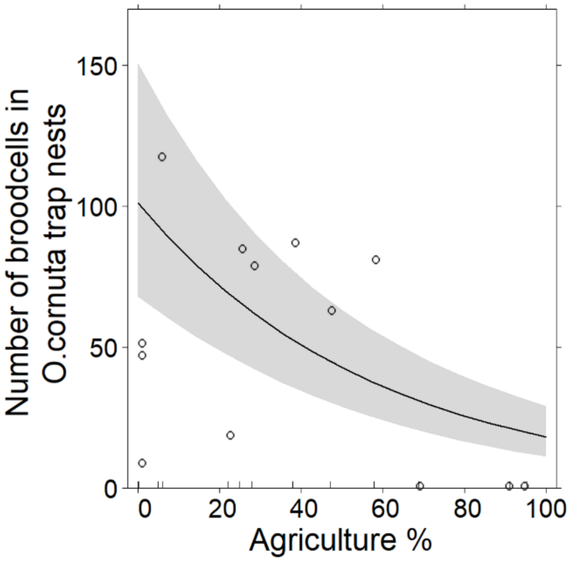

Fig. 7 Predicted values for the number of brood cells in Osmia cornuta trap nests in response to the proportion of agricultural areas within a 500 m radius. Grey shading: 95% CI

Discussion

Osmia cornuta collected 16 different pollen types with high percentages of Rosaceae, *Salix*, *Quercus* and *Acer*. The results are in accordance with other studies, which found *Prunus*, *Salix* and *Acer* as the primary pollen collected by *O. cornuta* (Haider et al., 2014; Westrich, 2018). Further, *O. cornuta* collects pollen from other plant families/genera such as Papaveraceae (Haider et al., 2014) or *Malus* (Márquez et al., 1994) and is a foraging generalist, as pollen from up to 6 different plant families was found in samples from single females (Eckhardt et al., 2014). Our result show that *O. cornuta* preferably collects pollen from trees, especially Rosaceae in the land use regions we studied here and confirm that it is suitable pollinator for orchards (Bosch, 1994; Monzón et al., 2004).

Molecular methods showed congruent results with the morphological identification, increasing the robustness of our conclusions. In some cases, it was possible to discriminate taxa at the genus or species level, where this was not possible by morphological identification. Also, multiple haplotypes were found, thus demonstrating the potential of this method to discriminate intraspecific variation in the foraged plants. Not all subsamples were composed by the same pollen-types. Each subsample corresponded to pollen from different nests, so they were likely collected by different individuals. Thus, indicating that not all individuals used the same pollen sources. There was some incongruence when compared with morphological identification, namely the relative frequency of some of the taxa. When using constructed species communities, Bell et al. (2018) found little correlation between pollen amount and read counts for both ITS and rbcl. For that reason, the authors recommended that metabarcoding data should rather be used as a qualitative result. Morphological inspection identified *Quercus* sp. pollen as the second most frequent type in the Viticulture region, which was completely missed using molecular data. This can be explained by the fact that only a small subset of the samples collected per site was used. Another explanation can be the fact that only one trap per site was used. Each trap represents a maximum radius of 600 m of foraging area. It is possible that the area surrounding the chosen traps had a different vegetation composition to the sum of all traps in the region. Moreover, there are limitations inherent to the metabarcoding approach. The main ones are: an incomplete reference database not allowing matches with high similarity (Meyer & Paulay, 2005), biases formed due to preferential amplification of some taxa (Taberlet et al., 2012), or taxonomic misidentification of names in the gene bank. All the missing taxa have trnL-F sequences in GeneBank, so a low-quality database is not the likely explanation. However, we cannot exclude the existence of PCR biases caused by preferential annealing of the primers in some taxa. This limitation could be overcome, using PCR free approaches such as genome skimming (Taberlet et al. 2012) or multiple marker sets with different affinities for the different taxa studied (Fazekas et al., 2008). Some of the species named due to a match in a molecular reference database are not recorded from Austria, e.g. the evergreen Asian species *Prunus undulata*. Another evergreen *Prunus* that is commonly cultivated in gardens and parks was also identified (*P. laurocerasus*).

In this work we decided to use the intergenic region trnl-f for molecular identification. This is not the most commonly used marker for pollen identification and the chloroplast region rbcl and the ribosomal DNA marker ITS are preferably used (e.g. Richardson et al., 2015; Bell et al., 2017; Suchan et al., 2019). rbcl is used for its universality since it is a more conserved region, which grants it less PCR biases, however, this same characteristic provides less discriminatory power in its identification (Bell et al., 2017b). ITS is more variable and it has potentially a better discriminatory power, which can also have its caveats. Bell et al., (2017b) showed that the ITS missed complete groups, which can be a consequence of mutation in the primer binding site. This is one of the main problems with DNA barcoding. More variable markers are more prone to primer biases while marker that are more universal usually amplify regions with lower variation (Bell et al., 2016). The trnL-F region can minimize this problem. The primers are designed in the tRNA regions which are very conserved, but they span an intergenic region that is highly variable and thus provides a higher discriminatory power. This region has shown to have a higher discriminatory power for pollen identification (Kraaijeveld et al., 2015) and diet assessment (Pinho et al., 2018). Nevertheless, the identification based on a single marker, especially at the species level, may be affected by incomplete lineage sorting and hybridization. To overcome this problems authors have suggested the use of a multiloci approach for pollen identification (Richardson et al., 2015a; Bell et al., 2016, 2017b). Moreover, since different primers will show biases towards different taxa many of the above-mentioned problems will be overcome.

We have shown that agricultural regions and an increasing proportion of agricultural areas surrounding the nests had a negative effect on pollen richness and the number of brood cells. This was possibly due to the general low availability of pollen foraging plants in the simple landscape of the agricultural region. A similar effect was reported from Californian agro-ecosystems, where increased isolation from (semi-)natural habitats decreased the offspring reproduction of *Osmia lignaria* significantly (Williams & Kremen, 2007). However, the conclusions from our results have to be treated with caution, because we only obtained pollen from one of the trap nests in the agricultural region. Therefore, the pollen richness may be only representative for foraging resources within the activity range (200-600m) of *O. cornuta* females but not necessarily for the whole agricultural region. Further, the power of some predictors in the GLMMs and model qualities assessed with diagnostic plots reveal that results and interpretations are difficult to generalize. The results of our study should be interpreted and discussed in the light of the small sample size. Further, they underline that the reduction of floral resources for wild bees in agricultural landscapes leads to the decrease of available pollen, which is necessary for the provision of brood cells (Le Féon et al., 2013; Schindler et al., 2013; Hass et al., 2018). Subsequently, female wild bees are unable to provide adequate quantities of food to their offspring, as intensively farmed agricultural landscapes frequently contain monocultures with short flowering periods and low plant diversity (Mandelik et al., 2012). The high proportion (98.9%) of tree pollen in the trap nest of the agricultural region and the absence of herbaceous flowering plants demonstrate that *O. cornuta* is dependent on woody plants like *Salix*, Rosaceae and *Acer* in these intensively managed regions.

Based on the results from morphological identification, the highest pollen richness was present in trap nests in the viticulture region. Here, a high proportion of *Quercus* pollen was collected despite trap nests being situated in vineyards near *Prunus* trees. Oak and oak-hornbeam forests of the northeastern Leithagebirge seem to provide more attractive pollen than cherry trees. Further, the highest number of brood cells was found in the viticultural region and the RF analysis revealed the importance of wood areas for the number of brood cells. However, the model including the proportion of wood was not amongst the most parsimonious models and therefore the positive effect revealed by this model was not presented in the result section. This could lead to an increased abundance of that species in the following year. This result has been underpinned by another wild bee study conducted in this viticultural region, where the increasing proportion of woods positively affected the total wild bee abundance present in vineyards (Kratschmer et al., 2018). It further corresponds to Leong et al. (2016) who studied bee phenology in urban, agricultural and natural landscapes. Their results showed that the highest bee abundance was present in semi-natural landscapes (i.e. oak woods, grasslands, meadows).

The positive effect of green areas on pollen richness can be explained by the range of plants on extensively managed meadows in urban areas and private gardens. The high proportion of Rosaceae pollen in the samples of urban and village-structured regions can be explained by the popularity of fruit trees in private gardens. Urban regions offer various flowering plants throughout the year that can be used by pollinators as food sources (Goddard et al., 2010). This was also underpinned by the molecular analysis of the pollen samples from the urban region, where different native and non-native *Prunus* species were found. Complex landscapes have a positive effect on wild bee diversity (Mandelik et al., 2012; Fischer et al., 2016) and provide, as we have evaluated, a higher variety of food in the form of different plants for individual wild bee species. Further, villages and urban areas provide a high variety of pre-existing cavities (e.g. wall chinks, plaster holes or even small drain pipes) that are welcome nesting habitats for *O. cornuta* (Westrich, 2018).

Conclusion

We report a significant negative impact of the intensive agricultural landscape surrounding the trap nest sites of this study, on the pollen richness and quantity for *O. cornuta* females that forage food for their offspring. Urban regions, village-structured regions and viticulture regions provide better pollen availability, when compared to areas with a high proportion of agricultural land. On the basis of these results, further planning should support the promotion of fruit trees as well as willow, oak and maple species particularly in intensively used agricultural areas. The promotion of extensively managed land, like grassland and semi-natural elements should also have a positive impact on food availability for *O. cornuta*. Small gardens and parks that provide important floral resources for polylectic wild bees in urban regions and villages should be considered in the planning of urban areas to increase the reproduction success of solitary wild bees such as *O. cornuta*.

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Authors Contribution: BPa and SK conceived and planned the experiment, SK and BPa conducted the field work in 2016, BPe conducted pollen preparation, pollen identification and pollen counting with the light microscope, SK and BPe did GIS work and analyzed the data. MC and HM designed molecular experiments and protocols, MC performed the lab work and sequence analysis; all authors wrote the paper and participated in its revision under the lead of SK. All authors read and approved the final manuscript.

Conflict of interest: The authors declare that they have no potential conflict of interest in relation to the study in this paper.

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4.4. Rare wild bee species

This section provides ecological information on rare wild bees found in vineyard inter-rows with a focus on the Austrian fauna. Abundance of the respective species is given along with the sampling date, location and vineyard inter-row management intensity. Unless otherwise indicated, identification of specimen was done by myself and reviewed (ref.) by Bärbel Pachinger. Individuals that were sampled in near-by vineyard inter-rows and not included in the species list in the core publications (I, II) are marked with asterisks.

Andrena polita **Smith, 1847**

1♂: 10 July 2015, Arbesthal (AT), permanently vegetated vineyard, leg. S. Kratschmer, ref. K. Mazzucco

This solitary ground-nesting species prefers open ground patches of sandy, clayey and loessy soils, where small nest aggregations may be found (Scheuchl and Willner, 2016). This corresponds well to the soil of this vineyard, which is described sandy with high porosity (BMF, 2016). The species colonizes dry-warm habitats for example extensive meadows, vineyard fallows, ruderal sites, forest edges or sand- and clay pits. It is oligolectic on Asteraceae and preferably collects pollen from Cichorioideae and is active between May and September in one generation (Scheuchl and Willner, 2016; Westrich, 2018)

Andrena varia **Pérez, 1895**

3♀, 3♂: 16 February 2016, Alcaudon, close to Santaella, Córdoba (ES); temporary vegetated vineyard, leg. D. Paredes, det. F. Gusenleitner

This species was recorded from northern Marocco and Algeria so far (Gusenleitner and Schwarz, 2002; Rasmont et al., 2013) and was now recorded for the first time in Europe. There is no knowledge about the ecology of that species available (written communication: F. Gusenleitner, April 2019). It can be said for sure, that *Andrena varia* is like all other *Andrena* species ground nesting (Michener, 2007).

Bombus haematurus **Kriechbaumer, 1870**

1♀: 14 June 2016, Purbach (AT), permanently vegetated vineyard, leg. S. Kratschmer

This eusocial species prefers woods, forest edges and clearings, where small colonies are established in pre-existing cavities in the ground (e.g. mouseholes) (Scheuchl and Willner, 2016). The species is polylectic and hibernated queens emerge in March, young queens and males can be observed by July. Since 1995, when it was recorded for the first time in Austria, the species recently spreads in South-eastern Austria (Bossert and Schneller, 2014)

Eucera pollinosa **Smith, 1854**

1♀: 21 May 2016, 1♂: 18 May 2015, Breitenbrunn (AT), permanently vegetated vineyard, leg. S. Kratschmer; 1♀: 29 May 2016, Crăciunelu de Jos (RO), leg. L. Macavei

Recent literature indicates the species as *Eucera pollinosa* Smith, 1854 instead of *Eucera chrysopyga* Pérez, 1879 (see also Gusenleitner et al. (2012)). The species is oligolectic on Fabaceae with a preference for *Vicia* spp. and *Astragalus* spp. The species prefers dry-warm, steppe-like habitats, where the females excavate nests in the ground on sparsely vegetated sandy patches (Scheuchl and Willner, 2016; Wiesbauer, 2017). These habitats are characteristic for the region around the Lake Neusiedl and the soil in this vineyard is classified as sandy loam and Tschernosem with loess (BMF, 2016). The species was only recorded in the eastern part of Austria until now (Burgenland, Lower Austria and Vienna) (Gusenleitner et al., 2012).

Halictus smaragdulus **Vachal, 1895**

1♀: 10 July 2016, Purbach (AT), permanently vegetated vineyard; *1♀: 11 July 2016, Prellenkirchen (AT), permanently vegetated vineyard, leg. S. Kratschmer, det. B. Pachinger, ref. K. Mazzucco; 1♀: 29 May 2016, Sânmiclăuş (RO), bare soil vineyard, leg. L. Macavei

Pauly et al. (2015) recognize six different species in the cryptic species complex of the furrow bee *Halictus smaragdulus*. According to their results, the specimens recorded in Austria and Romania belong to *Halictus submediterraneus* (Pauly, 2015). It is a polylectic, eusocial species that builds small colonies and prefers dry-warm habitats like nutrient-poor grasslands, inland dunes and rock steppes (Scheuchl and Willner, 2016; Westrich, 2018). These habitats are still found in the rural areas in eastern Austria, where the species was recorded in Burgenland, Lower Austria and Vienna (Gusenleitner et al., 2012) The soil in both vineyards (Purbach, Prellenkirchen) is described as sandy loam (BMF, 2016), which corresponds to the preference for sandy grounds for nest establishment of that species (Wiesbauer, 2017).

Hylaeus imparilis **Förster, 1871**

1♀: 12 August 2015, Hundsheim (AT), permanently vegetated vineyard, leg. S. Kratschmer, ref. K. Mazzucco

The determination of *H. imparilis* is difficult because it is one of four species in the *H. brevicornis*-group and was synonymous to *H. brevicornis* for a long time. However, it was recently declared a species, which was also confirmed by DNA barcoding and thorough morphological analysis (Schoder et al., 2018). Due to these taxonomic difficulties, little is known about the distribution as well as the biology and ecology of *H. imparilis*. It is certainly solitary and nests above-ground, either in small pre-existing cavities or it gnaws cavities in dry plant stems. It is active between July and August (Scheuchl and Willner, 2016). The polylecty was recently confirmed by pollen analysis and a preference for small-flowered plants like Apiaceae, Brassicaceae or Crassulaceae was reported (Schoder et al., 2018).

Hylaeus trinotatus **(Pérez, 1895)**

1♀: 13 June 2016, Purbach (AT), temporary vegetated vineyard, leg. S. Kratschmer, ref. K. Mazzucco

One of the first records of this species for Austria originated also from Purbach (Schwarz and Gusenleitner, 1997) and Zettel et al. (2011) reported two other sampling sites in eastern Austria (Gänserndorf and Neusiedl am See). The species is solitary, probably polylectic, active between June and September, and nests above-ground. So far, only nests in reed galls were observed and the preferred habitats are vegetated banks, wetlands or moors (Scheuchl and Willner, 2016; Westrich, 2018). This conforms to the location of the vineyard, which is in vicinity of the Neusiedlersee reed-belt.

Lasioglossum griseolum **(Morawitz 1872)**

1♂: 11 August 2015, Purbach (AT), temporary vegetated vineyard, 1♀: 13 April 2016, Arbesthal (AT), permanently vegetated vineyard, 1♀: 21 May 2016, Breitenbrunn (AT), permanently vegetated vineyard, leg. S. Kratschmer

This ground nesting species populates dry-warm locations such as nutrient-poor grasslands, fallows, ruderal sites and steppes and is solitary (Ebmer, verbal message 11 June 2019). In Austria, it was also only reported from Burgenland, Lower Austria and Vienna so far (Gusenleitner et al., 2012). There is no knowledge about preferred soil characteristics but the soil of and around the vineyards was documented as sandy loam or loamy silt with low coarse fractions (BMF, 2016). The species is polylectic, as the usage of Campanulacea and Lamiaceae was documented (Westrich, 2018; Zettel et al., 2005), but prefers Lamiaceae as pollen resource.

Lasioglossum laterale **(Brullé, 1832)**

1♀: 10 April 2016, Purbach (AT), temporary vegetated vineyard, leg. S. Kratschmer, det. A.W. Ebmer

This rare Mediterranean furrow bee was recorded in a vineyard in Burgenland for the first time in Austria. This ground-nesting, solitary species prefers warm and dry habitats in the vicinity of woods. Pollen analysis from the collected pollen of the individual in Austrian vineyards confirmed the polylectic foraging behaviour (V). For this ground nesting species no preferred soil characteristics are documented; the soil in and around the vineyard was described as sandy loam (BMF, 2016).

Lasioglossum mesosclerum (Pérez, 1903)

1♀: 12 May 2015, Göttlesbrunn (AT), temporary vegetated vineyard, 1♀: 22 May 2016, Donnerskirchen (AT), temporary vegetated vineyard, leg. S. Kratschmer, det. A.W. Ebmer

This rare Mediterranean-west-asian furrow bee colonizes dry-warm habitats with steppe characteristics and was so far recorded from sites in eastern Austria in Oberweiden (Lower Austria), Stammersdorf and Bisamberg (Vienna) as well as at the Danube Island and in the Danube park (Vienna) (summarized in Zettel et al., 2015, 2013). The females are active between April and August and the males emerge in August and September (Scheuchl and Willner, 2016). The females excavate nests in the ground but there is no knowledge about preferred soil conditions. The soils in and around the vineyards were characterised as loam and sandy loam with low coarse fractions as well as loamy silt (BMF, 2016). The polylectic foraging behaviour was confirmed (Ebmer, verbal message 11 June 2019).

Lasioglossum minutissimum (Kirby, 1802)

5♀: 10 June 2016, Breitenbrunn (AT), permanently vegetated vineyard, 1♀: 19 May 2016: Höflein (AT), temporary vegetated vineyard, *1♀: 10 June 2016, Winden (AT), temporary vegetated vineyard, leg. S. Kratschmer, ref. K. Mazzucco

This polylectic, solitary species is active between April and September (males emerge from July on). Nests are excavated in loamy walls or in horizontal, sparsely vegetated patches with sandy soils, which were also described in and around the vineyards (BMF, 2016). Preferred habitats are nutrient-poor or extensively managed grasslands, sand-, gravel- or loam pits, sand dunes, drifting sand sites or ruderal sites (Scheuchl and Willner, 2016; Westrich, 2018)

Osmia claviventris Thomson, 1872

*1♂: 12 June 2015, Göttlesbrunn (AT), permanently vegetated vineyard, 1♂: 17 June 2016, Göttlesbrunn (AT), permanently vegetated vineyard, leg. S. Kratschmer

The limiting factor for this polylectic species is its nesting habitat because the females gnaw tunnels in plant stems of raspberries, blackberries, thistles or mulleins. Wood edges, clearings, hedges, ruderal sites, gravel- and loam pits are characteristic habitats colonised by this species (Scheuchl and Willner, 2016; Westrich, 2018). The avoidance of dry-warm areas of the Pannonicum (Zettel et al., 2016) is questionable since the study region is influenced by the Pannonian climate. Further, the wild bee collection at the Institute for Integrative Nature Conservation Research includes another specimen from Breitenlee in Vienna which is also under the influence of the Pannonian climate.

Systropha planidens Giraud, 1861

*1♀: 17 June 2016, Prellenkirchen (AT), *1♀: 11 July 2016, Prellenkirchen (AT), both in permanently vegetated vineyard, 1♀: 11 June 2016, Prellenkirchen (AT), temporary vegetated vineyard, 1♂: 13 June 2015, Purbach (AT), *1♀: 08 July 2015, Purbach (AT), *1♂: 14 June 2016, Purbach (AT), 1♀: 11 July 2016, Purbach (AT), 1♀: 10 July 2016, Winden (AT), all in permanently vegetated vineyards, 1♀: 11 July 2016, Purbach (AT), temporary vegetated vineyard, leg. S. Kratschmer

The solitary species is strictly oligolectic on *Convolvulus* spp. and the most important pollen resource is *Convolvulus arvensis* in the Austrian study region. The nests are excavated in the soil on sparsely vegetated horizontal or steep patches like for example field paths, vineyard edges or slopes (Westrich, 2018). No preference for nesting substrate was reported as the species nests in sandy, loessy, loamy but also compact substrates. Dry-warm habitats such as vineyards, fallows or ruderal sites are important for the occurrence of this species which is active between June and August (Scheuchl and Willner, 2016; Westrich, 2018).

Publication V: Ebmer et al. (2016) Beiträge zur Entomofaunistik 17, 77-83

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Female *Lasioglossum laterale* on *Asphodelus fistulosus* in Greece (Crete; June 2002; © A.W.Ebmer)

Beiträge zur Entomofaunistik 17: 77–83 | Wien, November 2016

Lasioglossum (*Lasioglossum*) *laterale* (Brullé, 1832) (Hymenoptera: Apidae), eine seltene mediterrane Halictidae, neu für Österreich

P. Andreas W. Ebmer*, Sophie Kratschmer** & Bärbel Pachinger**

Abstract

***Lasioglossum* (*Lasioglossum*) *laterale* (Brullé, 1832) (Hymenoptera: Apidae), a rare mediterranean Halictidae, new for Austria.** – The rare mediterranean furrow bee *Lasioglossum laterale* (Brullé, 1832) is recorded from Burgenland, for the first time in Austria. Notes on its discovery, general distribution, and flower visits are presented. The habitats of this bee can be characterized as warm places in the vicinity of forests. An analysis of the pollen confirms a polylectic foraging behaviour.

Key words: *Lasioglossum laterale*, Apidae, new record, Austria, Burgenland, vineyard.

Zusammenfassung

Lasioglossum (*Lasioglossum*) *laterale* (Brullé, 1832) ist eine seltene Schmalbiene mit mediterraner Verbreitung, die nun im Burgenland erstmals für Österreich nachgewiesen werden konnte. Die Entdeckungsgeschichte, die Gesamtverbreitung und Angaben zum Blütenbesuch werden dargestellt. Die Lebensräume dieser Bienenart können als Wärmestellen in der Nähe von Wäldern charakterisiert werden. Eine Pollenanalyse bestätigt ein polylektisches Pollensammelverhalten der Art.

***Lasioglossum* (*Lasioglossum*) *laterale* (Brullé, 1832)** (Abb. 1)

Funddaten: Burgenland, Purbach, N47°55'02", E16°40'69", 10.IV.2016, 1 ♀, leg. S. Kratschmer.

Die Schmalbiene wurde in einer begrünten Fahrgasse eines Weingartens gefangen (siehe Abb. 2). Die Landschaft in der näheren Umgebung (Kartierung auf einer Fläche von 750 m Radius um die Fundstelle) setzt sich aus Weingärten (28 % Flächenanteil), naturnahen Landschaftselementen mit zahlreichen Brachflächen (28 %), Agrarflächen exkl. Weingärten (22 %), Wald (14 %) und Siedlungsgebiet (8 %) zusammen. Trotz des Fundortes im Pannonikum handelt es sich bei *L. laterale* um keine Steppenart. Wie von Fundorten im Mittelmeerraum bekannt, ist die Furchenbiene wald-affin, wenngleich sie nicht als strenge Waldrandart oder Waldlichtungsart bezeichnet werden kann. Der Fundort in Purbach mit dem besonderen Klima der umliegenden Waldstücke passt gut in dieses Bild.

In neueren Bestimmungswerken wird *L. laterale* in Ebmer (1970) und Amiet & al. (2001) angeführt, Taxonomie und Systematik werden ausführlich von Ebmer (1988) dargestellt.

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Abb. 1–2: (1) Weibchen von *Lasioglossum laterale*, Kreta, Levka Ori, Weg von Ammoudari zum Kastro, *Cupressus/Acer sempervirens*-Zone, 1100 m SH, N35°17'53", E24°10'01", 3. Juni 2002, an *Asphodelus fistulosus*. (2) Fundort von *Lasioglossum laterale* – Fahrgasse eines Weingartens in Purbach im Burgenland. / (1) *A female of Lasioglossum laterale, Kreta, Levka Ori, path from Ammoudari to Kastro, in Cupressus-Acer sempervirens zone, 1100 m a.s.l., N35°17'53", E24°10'01", June 3rd, 2002, on Asphodelus fistulosus. (2) Locality of Lasioglossum laterale, a vineyard inter-row in Purbach, Burgenland.* © 1: P. Andreas W. Ebmer; 2: S. Kratschmer.

Nahestehende Arten: *Lasioglossum laterale* steht in den taxonomischen Merkmalen dem in Mitteleuropa gut bekannten *L. sexnotatum* (Kirby, 1802) am nächsten, insbesondere im Grundbauplan der Genitalstrukturen der Männchen, für die eine sehr schmale und lange ventrale Gonostylusmembran charakteristisch ist. Hinsichtlich der Körpergröße und der rostbraunen Behaarung auf Kopf und Thorax sowie in den Merkmalen der Punktierung ist *L. laterale* von den in Mitteleuropa vorkommenden Arten dem *L. subfasciatum* (Imhoff, 1832) am ähnlichsten. Die Männchen dieser Art haben jedoch ein deutlich anderes Genital.

Noch näher als *L. sexnotatum* steht *L. equinum* Ebmer, 1978, das nach dem Weibchen aus dem Iran (Khorramabad) beschrieben und später im Osten der Türkei sowie im Norden Israels gefunden wurde. Das derzeit noch unbeschriebene Männchen, das L. Packer dem Erstautor aus den Bergen im Norden Israels, vom Hermon (1500 – 1600 m SH) und Merom (850 – 1050 m SH) mitgebracht hat, hat ebenfalls den Genitalgrundbauplan von *L. sexnotatum* und *L. laterale*, wenngleich die ventrale Gonostylusmembran am Ende löffelförmig verbreitert ist.

Entdeckungsgeschichte: Es ist wohl den wenigsten Apidologen bekannt, dass das mehrbändige Werk der Expedition nach „Morea“ (der damaligen Bezeichnung für die Peloponnes), in dem Brullé (1832) und viele andere Wissenschaftler publiziert haben, eng mit dem griechischen Freiheitskrieg zusammenhängt. Am 25. März 1821 nahm Bischof Germanos von Patras in der Klosterkirche Agia Lavra westlich Kalavryta den Klephtenführern den Eid ab, nicht zu ruhen, bis Hellas vom Joch der Osmanen befreit sei. Der 25. März ist daher heute der griechische Nationalfeiertag. In den folgenden Wirren landete im Februar 1825 im Südwesten der Peloponnes ein 17.000 Mann starkes Heer unter Ibrahim Pascha, dem Sohn des damaligen Vizekönigs von Ägypten, Muhammad Ali, um dem Sultan zu Hilfe zu kommen. Dieser hatte ihm für die militärische Intervention Kreta und die Peloponnes versprochen.

Die Wende zu Gunsten der Griechen brachte die Intervention der Großmächte, als ein britisch-französisch-russisches Geschwader die ägyptische Invasionsflotte am 20. Oktober 1827 in der Bucht von Navarino (heute Pylos) versenkte. Um das Heer aus Ägypten zu entwaffnen und den russischen Einfluss zurückzudämmen (der Zar des orthodoxen Russland sah sich als besonderer Beschützer der orthodoxen Griechen), landete im August 1828 ein 14.000 Mann starkes französisches Expeditionskorps unter General Nicolas-Joseph Maison (1770 – 1840) bei Koroni (südlich von Kalamata) und blieb auf der Peloponnes bis 1833 (Zelepos 2014). Unter diesem militärischen Schutz waren auch viele Wissenschaftler tätig: Ethnologen, Geographen, Geologen, Zoologen und Botaniker, die im Südwesten der Peloponnes und bis nach Sparta und Tripolis unterwegs waren.

Die Ausbeute der Hymenopteren erhielt damals der angesehene Entomologe Gaspard August Brullé (1809 – 1873) zur Bearbeitung. In vielen Bänden erschienen die Ergebnisse dieser Morea-Expedition, der 3. Band Zoologie, 1. Teil „Crustacés“, schon 1832. Entsprechend den damaligen drucktechnischen Möglichkeiten mit Bleiletternsatz und

Druckanlegmaschinen erfolgten diese Publikationen unglaublich rasch; Frankreich wollte sich als wissenschaftlich führende Nation in Europa auch mit der nun besser möglichen Erforschung Griechenlands positionieren.

Auf den Seiten 327–360 des 3. Bandes, 1. Teil, beschrieb Brullé (1832) die Bienen dieser Expeditionsausbeute: 42 Arten waren neu für die Wissenschaft und 26 bereits zuvor beschriebene Arten wurden faunistisch erwähnt. Es ist viel zu wenig bekannt, dass Brullé damit die erste systematisch-faunistische Darstellung der Bienen Griechenlands publiziert hat. Viele der darin neu beschriebenen Arten sind noch heute gültige Namen für gut abgesicherte Biospezies. Brullé konnte ja noch „aus dem Vollen schöpfen“. Von den Halictidae wurden sieben Arten als neu beschrieben, davon fünf heute noch gültige Namen und nur zwei Synonyme: *Pseudapis bispinosa* (unter *Nomia*), sowie *Lasioglossum laterale*, *L. pallens*, *L. marginatum*, *L. pauperatum* (unter *Halictus*); Synonyme sind *Halictus bifasciatus* (= *L. laterale*) und *H. semiaeneus* (= *L. aeratum*).

Kritisch gesichtete Gesamtverbreitung von *L. laterale*: Furchenbienen (Halictidae) gelten als schwer zu determinieren. Der Erstautor hat in den über 50 Jahren seiner Tätigkeit viele falsche Determinationen in Sammlungen vorgefunden. Verbreitungsangaben dürfen daher nicht unkritisch übernommen werden; oft hilft eine Prüfung nach Plausibiliät. In dieser Arbeit wurden nur gedruckte Arbeiten berücksichtigt, nicht aber im Internet kursierende Faunenlisten. Bei Verbreitungsdaten werden – soweit möglich – die Sammler angegeben; diese bürgen für die korrekten Funddaten.

Scheuchl & Willner (2016) haben ein ungemein akribisches Lexikon der Wildbienen Deutschlands, Österreichs und der Schweiz herausgegeben. Erwin Scheuchl hat für jede Art Verbreitungsangaben nach Ländern erstellt und dafür rund 9000 (!) Publikationen ausgewertet. Wegen der lexikalisch nötigen Verkürzung wird jedoch das Verbreitungsprofil vergröbert. Für *L. laterale* gibt es zum Beispiel aus Spanien nur einen historischen Fund. Für Polen geht die Angabe auf einen Botaniker namens Anasiewicz zurück. Diese ist aber vom klimatischen Anspruch her unglaubwürdig, weshalb *L. laterale* von Pesenko & al. (2000) von der Liste der Arten Polens gestrichen worden ist. Für ein Vorkommen im Kaukasus gibt es keinen gesicherten Anhaltspunkt, vermutlich liegt eine Verwechslung mit *L. subfasciatum* vor.

Lasioglossum laterale ist eine seltene bis sehr seltene mediterrane Art mit Verbreitungsschwerpunkt im südlichen Griechenland und auf Kreta. Sie kann als vorwiegend balkanisch-ostmediterrane Art bezeichnet werden, mit Ausstrahlungen nach Westen bis Katalonien und nach Osten nur bis ins westliche Kleinasien. In Griechenland ist *L. laterale* am häufigsten auf der Peloponnes und auf Kreta zu finden, selten in Mittel- und Nordgriechenland und auf der jonischen Insel Kefalonia. Eigentümlicherweise fehlt die Art auf den sehr gut durchforschten ostägäischen Inseln Lesbos, Chios und Samos.

Peloponnes: Tripolis, Mistra (loci typici; Brullé 1832). Olympia, 21.III.1964, 3 ♀♀, 24.III.1964, 1 ♀, 20.IV.1964, 2 ♀♀; Mistra, 12.IV.1996, 1 ♀, 16.IV.1969, 4 ♀♀; Agrinion, 7.IV.1963, 3 ♀♀; Korinth, 29.III.1966, 1 ♀; Xylokastron, 15.IV.1970, 1 ♀; Vytina, 29.IV.1970, 1 ♀, alle leg. Grünwaldt. Zachlorou, 28.V.1964, 1 ♂, leg. Schwarz. Megalopolis, 17.IV.1968, 1 ♀, Museum Leiden. Elis, Oros Minthi, 800 – 850 m SH, 19.V.1992, 1 ♀; Elis, Smerna, 650 – 700 m SH, 18.V.1992, 1 ♀, leg. Rausch.

Kalogria, 23.III.1995, 1 ♀, 27.IV.1995, 1 ♀; Ano Trikala, Killini, 1700 – 1900 m SH, 15.VII.1997, 1 ♀; Kotili im Likeo-Gebirge, 900 – 1100 m SH, 22.VI.1997, 1 ♂; Taygetos, von Toriza nach Proph. Elias, 1600 m SH, 16.VII.2006, 1 ♂; antikes Samikon, 24.III.2000, 1 ♀; Gortis, Ataiholos, 19.IV.1993, 1 ♀, alle leg. Arens. Lakonia, Skoutari, 20 – 75 m SH, 28.IV.2012, 1 ♀; Parnon, östlich Kosmas, 850 m SH, 1.V.2012, 1 ♀; N Sparta, SW Karyes, 750 m SH, 4.V.2012, 1 ♀; Elis, NE Lalas, 750 m SH, 7.V.2013, 9 ♀♀; SE Kalavryta, 870 m SH, 7.V.2014, 1 ♀, alle leg. Zettel. Chelmos NW, 1900 m SH, 28.VII.1981, 1 ♀; Lakonia, Oitylo N Areopoli, 20 m SH, *Olea*-Zone, 25.IV.2015; Taygetos, von Kryoneri zum Schutzhaus, 1100 – 1300 m SH, *Pinus/Abies*-Zone, 27.V.2008, 1 ♂, alle leg. Ebmer.

Mittel- und Nordgriechenland: Delphi 13.IV.1963, 1 ♀; Delphi-Itea, 1.IV.1966, 1 ♀, beide leg. Grünwaldt. Magnisia, südlich Volos, Platania, 5.IV.2000, 1 ♀, 19.IV.2000, 1 ♀, 21.IV.2000, 1 ♀, 27.IV.2000, 1 ♀, 28.IV.2000, 1 ♀, alle leg. K. Standfuss. Thesprotia, Morfio, 105 m SH, 24.IV.2002, 1 ♀, leg. Neumeyer. Thessalien, Mt. Ossa, NE Anatoli, 950 m SH, 6.V.2015, 1 ♀, leg. Zettel. Nomos Kavala, Pangaion W Eleftheroupolis, 1150 – 1200 m SH, 24.VII.1992, 1 ♂, leg. Ebmer. Berg Athos, Filothea, 400 m SH, 25.IV.1987, 1 ♀, leg. Blank. Litochoron, 3.VI.1989, 1 ♂, leg. Kudrna.

Kefalonia: Mt. Ainos, 1550 m SH, 16.IV.1992, 1 ♀, leg. Blank. Ainos, nordwestlich des Gipfels, 1100 – 1200 m SH, 4.VI.1990, 1 ♀, leg. Rausch.

Kreta: Ida Gebirge, W Skinakas, 1050 – 1100 m SH, Weide, 8.VI.1993, 4 ♀♀, leg. Rausch. NE Vrouchas, 300 m SH, *Olea*-Zone, 4.V.2001, 1 ♀; Meronas / Gerakari, Ag. Irini, 650 m SH, *Quercus*-Waldrand, 8.VI.2002, 1 ♀; Levka Ori, von Ammoudari nach Kastro, 1100 m SH, *Cupressus/Acer sempervirens*-Zone, 3.VI.2002, 6 ♀♀; Levka Ori, Akones, 950 – 1150 m SH, *Acer sempervirens*-Zone, 4.VI.2002, 3 ♀♀; Levka Ori, E Vigla, *Castanea*-Kultur, 700 m SH, 7.VI.2002, 1 ♀, alle leg. Ebmer.

Türkei: 10 km W Adapazari, 4.V.1976, 1 ♂, leg. Ressl & Holzschuh. Istanbul, Belgrat Orman, 8.V.1968, 1 ♀, The Natural History Museum London. Antalya, Beldibi, 23.IV.1988, 1 ♀, leg. Wolf. Südwesttürkei, Baffa-See, Kalk-Trockenrasen, 19.IV.1986, 1 ♀, leg. P. Hartmann. Westtürkei, Bucak, 100 – 300 m SH, 11.IV.1995, 1 ♀, leg. Kraus. Burdur, det. Warncke, Zoologische Staatssammlung München. Namrun / Icel, 1200 m SH, leg. Warncke.

Bulgarien: Arkutino S Burgas, 20.VI.1970, 1 ♂, leg. Wallis, coll. Burger.

Kroatien: 10 km NE Poreč, 25.VI.2005, 3 ♂♂, leg. Dathe. Insel Krk, 1 ♀ ohne Datum, leg. Mader.

Slowenien: Hrastovlje, Zanigrad, 29.III.2008, an *Prunus mahaleb*, 1 ♀, mit Foto, leg. A. Gogala. Dazu gibt Gogala (2009) auch an, die Kopula beobachtet zu haben: Damit wäre diese Art eine der ganz wenigen, bei denen die Männchen im Frühling fliegen. Nach Meinung des Erstautors ist dies im Einzelfall nicht ausgeschlossen. Die wenigen sicheren Daten, die von Männchen vorliegen, wie etwa das vom 4. Mai von Adapazari, zeigen eine solche Möglichkeit, doch die übrigen Daten von Ende Mai bis in den Juli hinein ergeben das für Halictidae in Südeuropa übliche Auftreten der Männchen.

Italien (Festland): Piemont, San Benedetto – Belbo, III.1980, 1 ♀, 24.V.1980, 1 ♀, leg. Pagliano. Triest, 1 ♀, Naturhistorisches Museum Wien. Lazio, Monte Cimino, 600 m SH, 18.IV.1949, 2 ♀♀; Lazio, Monte Giescone, 550 m SH, VII.1947, 1 ♂, leg. Comba. Apulien, Monte Gargano, 1 ♀, leg. Kraus. Basilicata, Laghi di Monticchio, 18.IV.1963, 1 ♀, leg. Pagliano. Kalabrien, Aspromonte (Blüthgen 1931); Kalabrien, Aspromonte, 1350 m SH, 1.VII.1973, 1 ♂, leg. Bytinski-Salz. Kalabrien, Monte Pollino, 6.VII.1987, 1 ♀, leg. Pagliano.

Sizilien: Ätna, Südhang, VI – VIII, 7 ♀♀, 2 ♂♂, leg. Hamann. Ätna, Massa Annunziata, 650 m SH, 30.IV.1965, 2 ♀♀, The Natural History Museum London. Ätna, 1 ♂, leg. Pschorn-Walcher. Ätna, 1500 m SH, 22.VI.1978, 1 ♂, leg. Hüttinger.

Frankreich: Der Erstautor sah keine Exemplare aus diesem Land; ihm liegen nur die Literaturdaten von Pérez (1890: 180) vor, die dieser unter dem Synonym „*H. bifasciatus* Brullé“ meldet und dabei als Synonym „*H. fallax* Mor.“ stellt, doch diese Art gehört zu einer ganz anderen Artengruppe. Es kann schon sein, dass Pérez *L. laterale* im Sinn des Lectotypus vorlag, die er als „RR“ = sehr selten von „Bordeaux, Toulouse, Pyr.“ meldet.

Spanien: „Barcelona ♀ 189., collect. A.Weis", „Halictus lombardicus Walk. [?]" (unpublizierter Sammlungsname), det. Friese 1900, Senckenbergmuseum Frankfurt. Obwohl Spanien sehr gut erforscht ist, der Erstautor vor allem aus dem Naturalis Biodiversity Center in Leiden (Niederlande) sehr große Aufsammlungen erhielt und er selbst vier Reisen unternahm, ist kein weiteres Exemplar bekannt geworden.

Regionalverbreitung in Mitteleuropa:

Schweiz, Tessin, „auf den Feldern zwischen Locarno und Losone zu beiden Seiten der Maggia" (Frey-Gessner 1903: p. 200) loci typici von *H. ticinensis*, von denen der Autor weder die Anzahl noch das Sammeldatum in seiner Beschreibung anführt. Letzter historischer Fund, den der Erstautor sah: Locarno, 28.IV.1903, 1 ♀, leg. Weis, Senckenbergmuseum Frankfurt. Die alte Notiz für „Zürich", die auf Schulthess zurückgehen soll und von Blüthgen (1921: 269) zitiert wird, ist von der heutigen Kenntnis der Gesamtverbreitung und der klimatischen Ansprüche endgültig zu löschen. Es kommt ja sehr schnell etwas in die Literatur und wird dann endlos abgeschrieben; und es ist sehr schwer, solche Meldungen wieder aus der Literatur zu entfernen.

Südtirol: Bozen, 21.IV.1904, 1 ♀, 5.V.1906, 1 ♀, ohne Sammler, Senckenbergmuseum Frankfurt. – Der Raum Bozen ist durch das Wachstum der Stadt und die Wandlung der Landwirtschaft zum intensiven Obstbau in ihrem Umland massiv verändert. Ohne nähere Angaben, wo im Raum Bozen gesammelt wurde, ist eine Nachsuche aussichtslos.

Ungarn: Budapest, 18.V.1922, 1 ♀, 28.V.1922, 1 ♀, ohne Sammler, Sammlung AGES (früher Bundesversuchsanstalt für Pflanzenbau) in Wien. NW Örtilos-Szentmihalyhegy, leider ohne nähere Daten, aber neuere Aufsammlungen (Józan 1995). Der Fundort liegt in Südwest-Ungarn, im Gebiet des Zusammenflusses von Drau und Mur an der kroatisch-ungarischen Grenze.

Slowakei: Kamenica nad Hronom bei Štúrovo, 8.V.1962, 1 ♀, leg. Z. Pádr, Biologiezentrum Linz. Dieser Fund aus dem Gebiet des Donauknies ist der nächste rezente zum neuen Fundort im Burgenland. Eine Einwanderung von Osten her entlang der Donau ist naheliegend.

Blütenbesuch: Es gibt nur wenige publizierte Angaben. Frey-Gessner (1903: 201) schreibt: „...wo ich die Art im Frühjahr (April und Mai) zur Zeit der Lewatblüthe auf dieser Pflanze nicht selten fand". Lewat ist der schweizerische Name für Raps und Kohlrübe, *Brassica napus*. In Slowenien beobachtete Gogala (2009) die Art an Steinweichsel, *Prunus mahaleb*. Auf Kreta, im Nordosten der Levka Ori, im Anstieg vom Dorf Ammoudari zum Kastro, fing der Erstautor mehrere Weibchen des *L. laterale* auf *Asphodelus fistulosus*. Die Exemplare waren völlig frisch, gerade geschlüpft und versorgten sich mit Nektar; Pollen hatten sie noch nicht gesammelt.

Eine palynologische Analyse der Pollenhöschen des in Purbach gefangenen Exemplars zeigt überwiegend Pollen von *Taraxacum officinale*. In geringerer Zahl wurden *Veronica* sp., *Senecio* sp. und ein Vertreter der Familie Caryophyllaceae festgestellt. *Lasioglossum laterale* ist daher wie die Mehrzahl der *Lasioglossum*-Arten polylektisch.

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5. Discussion

In European vineyard inter-rows, both field and landscape parameters determined the total wild bee diversity and abundance. However, functional traits showed different responses. Eusocial species benefitted from undisturbed conditions in permanently vegetated inter-rows and high proportion of woods in the surrounding landscape. Solitary species better coped with low-intensity disturbances in vineyard inter-rows and were positively affected by solitary trees in the landscape context. Bare soil management affected wild bees negatively, regardless of functional traits.

5.1. Field scale

Floral resource availability was the most important factor and increased wild bee diversity and abundance in vineyard inter-rows across Europe. The high importance of floral resources (quantitatively and qualitatively) is also reported from vineyards in South Africa (Kehinde and Samways, 2014b) and California (Wilson et al., 2018), other agro-ecosystems (Scheper et al., 2015; Westphal et al., 2009) as well as natural or semi-natural habitats (Haaland et al., 2011; Rollin et al., 2013). The interacting positive effect of extensive inter-row management and floral resource availability on the total wild bee abundance as well as on the solitary species richness and abundance was explained by the high proportion of ground nesting wild bees in inter-rows with undisturbed soil conditions and thus undisturbed nesting sites (I, II). Similar effects of low tillage frequency on ground nesting wild bees are reported from other crop systems (Shuler et al., 2005). Further, it was shown that the infrequent disturbance in temporary vegetated inter-rows increased wild bee diversity and abundance in Austria (I), due to higher floral resources and less grass cover. This makes sense, because flower strips should be renewed after some years to avoid dominance of non-entomophilous grass species (Schmid-Egger and Witt, 2014).

Other organisms that are relevant for biodiversity-based ES sampled in the same vineyard inter-rows were similarly affected by vegetation management in Austria. For example, springtails are important decomposers and mobilize nutrients (Rusek, 1998) and their activity was higher in temporary compared to permanently vegetated inter-rows. However, it has been shown too, that site conditions like soil quality or plant biomass influenced springtail and earthworm communities to a greater extent than inter-row vegetation management or landscape structures (Buchholz et al., 2017). Spiders are important generalist predators in various agro-ecosystems. Their diversity was higher in permanently than in temporary vegetated inter-rows and their activity in permanently vegetated inter-rows increased further with higher proportions of SNE in the surrounding landscape (Pfingstmann et al., 2019).

5.2. Landscape scale

In contrast to other studies (e.g. Kleijn and van Langevelde, 2006), landscape diversity had only a weak positive effect on the total wild bee diversity and no effect on the total abundance in vineyards across Europe. This was attributed to the superior effect of floral resources in combination with extensive management practices (II). In Spain the landscape was least diverse and the vineyard inter-rows were managed in high intensity (due to the hot Mediterranean climate). These circumstances led to the unexpected low wild bee diversity in Spanish vineyards (II), although the southern part of Spain is known to be a wild bee diversity hot spot (Nieto et al., 2015). Landscape diversity compensated low floral resource availability for eusocial wild bee abundance in vineyards across Europe.

In Austria, the different landscape structures were analysed in more detail (I). The higher proportion of woods and artificial structures such as villages and towns increased wild bee diversity and abundance in vineyard inter-rows. This was explained by the impact of these structures on different functional traits. Eusocial species seem to benefit from the structurally diverse forests of the Leithagebirge which are part of the Natura 2000 network (Burgenländische Landesregierung, 2018). The herbaceous margins of wood edges can provide undisturbed nesting habitats and diverse floral resources (Nicholson et al., 2017; Rollin et al., 2013). Especially, eusocial wild bees require complex landscapes with adequate food resources, because of their higher vulnerability to habitat fragmentation (Williams et al., 2010) and dependence on floral resources throughout the vegetation period for successful sexual reproduction (Westphal et al., 2009).

The positive effect of villages and towns on wild bee diversity and abundance (reviewed in Hernandez et al., 2009) as well as the increase of pollination services to plants in agro-ecosystems in the vicinity of towns (Samnegård et al., 2011), was also reported in other studies. These man-made landscape structures are particularly important for above ground nesting wild bees because they extend the landscape with vertical structures that include pre-existing cavities and represent nesting habitats (e.g. Cane, 2005). Additionally, residential gardens and allotments can provide higher floral resource availability compared to other urban land uses (e.g. cemeteries, parks or road verges) and potentially enhance bee species richness and abundance (Baldock et al., 2019). The association of solitary wild bees with solitary trees in Austrian vineyards was explained by their role as nesting habitat for both above- and ground nesting solitary species. Above the ground, trees provide pre-existing cavities or dead wood parts for cavity nesting bees. At the ground level undisturbed soil conditions may attract ground nesting wild bees (I). Further, *Prunus* species are traditionally planted between vineyards in the Austrian study region (Burgenländische Landesregierung, 2018) and provide pollen and nectar resources in spring.

5.3. Pollen resources and pollination

Even though, not all possible pollen samples were analysed, first conclusions can be propound which plant taxa are relevant for wild bees in viticultural landscapes. *Quercus* sp. and *Prunus* sp. are characteristic tree taxa in the Leithagebirge forests (Willner and Fischer, 2015) and were found to be important pollen resources for spring active wild bees such as *Lasioglossum marginatum* and *Osmia cornuta* (IV). *O. cornuta* was not sampled in the inter-rows but high amounts of *Sorbus*-group pollen, which comprised very likely mainly *Prunus* species (Heigl, verbal message 13 February 2018), were found in the trap nests mounted in the viticultural landscape. So far, almost only *Lasioglossum* species were included in the inter-row pollen samples from April. Therefore, the pollen collected by other species in April (e.g. *Andrena* spp. or *Bombus* spp.), which are expected to forage on *Prunus* species is underrepresented here. Pollen samples from *Bombus* spp. are expected to include considerable amounts of *Sorbus*-group pollen, because young bumble bee queens, which are active in April, also forage on flowering fruit trees (Schwantzer, 2016). The high amounts of pollen from the *Crepis*-type, *Galeopsis*-type and *Stellaria graminea*-group in the samples from April showed that *Taraxacum officinale* agg. (*Crepis*-type), *Stellaria media* (*Stellaria graminea*-group) and *Lamium purpureum* (*Galeopsis*-type), which flowered in the majority of the Austrian inter-rows during April, were important pollen resources for wild bees in vineyards. This demonstrated the high relevance of spontaneous vegetation, because none of these plant taxa are included in seed mixtures which were used by some of the winegrowers.

The pollen loads of 40 % of the bee species sampled in the inter-rows during June were analysed so far. This gives a more complete picture of which plants were pollinated by wild bees in vineyard inter-rows and in the Austrian viticultural landscape. Two types of *Trifolium* pollen, *Astragalus*-type and *Vicia*-type pollen represented over 70 % of the pollen in the samples, which can be explained by the high proportions of *Trifolium incarnatum*, *Trifolium pratense*, *Medicago lupulina* (*Astragalus*-type) and different *Vicia* species in vineyard seed mixtures. Even a very plant species rich seed mixture (e.g. “Wolff”-Mischung) includes over 85 % legumes, while other plant families like Asteraceae, Brassicaceae or Lamiaceae are underrepresented (Austrosaat, 2012). Apart from *Lasioglossum lineare*, all other species included in this analysis so far, collected pollen at least from one of the legume pollen types and therefore play an important role in the pollination of these nitrogen fixing plants.

Flowers of commercial grapevine are relatively unattractive for bees. Although, grapevine flowers provide high amounts of pollen during the short flowering period (Vorwohl, 1977), they don’t appear in attractive colours or provide nectar and are therefore less important foraging resources for wild bees. This is emphasised by the results of the additional transect walks in June, because only 15 bee individuals were sampled directly from the grapevine within the two study years in Austria. Additionally, only 3 out of 31 pollen samples from bees in the inter-rows in June comprised considerable amounts of *Vitis vinifera* pollen. Perhaps a female wild bee coincidently finds out about the vast pollen resource during a foraging trip and then starts to collect pollen from grapevine. Honey bees were observed collecting pollen from grapevine flowers, but results of previous studies assessing the additional benefit of cross-pollination to grape yield are controversial. In the short review by Mandl and Sukopp (2011), the pollination mode of different cultivars reportedly varies extremely between completely self-fertile and completely self-sterile. Some of the reviewed studies, observed decreased fruit and seed formation of bagged grapevines compared to open flowers (Olmo, 1943 cited in Mandl and Sukopp, 2011). Other Authors cited in Mandl and Sukopp’s (2011) work documented no difference of grape quantity between bagged and open grapevine flowers (e.g. Marletto and Manino, 1979 cited in Mandl and Sukopp, 2011). The setting of this study was not feasible to study whether additional cross-pollination by insects led to higher yields or increased must quality. This depends to a great extent on the “terroire”; for example the actual vineyard management like pruning, shoot trimming, the training system or soil management, and further on site characteristics like physical soil properties, nutrient and water supply or temperature (reviewed in: Poni et al., 2018). Further, comparing grape quality or yield along different inter-row treatments the same grapevine variety has to be studied (c.f. Pou et al., 2011; Smith et al., 2008). These parameters were too heterogeneous, especially in the Austrian study area where in some vineyards two different varieties were cultivated.

5.4. Rare wild bee species

Dry-warm climate conditions are characteristic for viticultural areas and are preferred by many wild bee species (Scheuchl and Willner, 2016). These conditions not only favour common wild bee species but also comply with the habitat preferences of the rare wild bee taxa reported in this study. Further, not only the climate but also the soil characteristics in the Austrian study region matched the preferences of many rare ground nesting species presented in chapter 4.4. Given the low activity range of some of these rare species due to their small inter-tegular distance (Greenleaf et al., 2007), they are assumed to nest in or in the vicinity of the vineyards. In fact, nests of the common *Lasioglossum marginatum* and *L. lineare*, both eusocial species, were documented in Austrian vineyard inter-rows. In Spain, the high abundance of *Andrena tenuistriata* indicates that this species may also nest in vineyard inter-rows, especially because of its small body size and therefore low activity range. Other rare species that were present in vineyard inter-rows demand plant stems from e.g. raspberries, blackberries, thistles or mulleins where they gnaw in nesting tunnels. The proximity of shrubs, hedges, wood edges or herbaceous margins along fields and roads may offer nesting habitats for these species, while the inter-rows provide foraging resources.

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6. Conclusions and recommendations

The results of this thesis showed that winegrowers can improve habitat quality for wild bees, because vineyard inter-rows can provide nesting and/or foraging habitats for wild bees, including rare species. The inter-rows can be considered as wildflower strips. If extensively managed, and if entomophilous wild plants are re-established from time to time to increase floral resource availability, wild bees can definitely benefit from inter-row vegetation. Winegrowers could therefore enhance pollination provision for wild plants and crops in viticultural agro-ecosystems. However, activities must be critically evaluated, because the input of pesticides (mostly fungicides and herbicides) is rather high in some viticultural regions and knowledge about the effects of these substances on different wild bee species is scarce (Sanchez-Bayo and Goka, 2014) and should therefore be the subject of further research. There exist several measures to reduce pesticides in viticulture in the Austrian agri-environment scheme (ÖPUL), whereby winegrowers receive incentives for refraining from the use of herbicides (AMA, 2015a) and/or insecticides (AMA, 2015b), or adapt to organic farming (AMA, 2015c). The first two measures are linked and mandatory to the erosion mitigation measure in the scheme, which prescribes the cultivation of cover crops in the inter-rows (AMA, 2015d). If this measure is to also benefit wild bees some points should be reconsidered for the next program period. The current program demands the cultivation of more than one plant species in the inter-row (AMA, 2015d), but the quality (in terms of plant species richness) of the cover crop mixture is not specified. Considering species rich seed mixtures to provide continuous flowering aspects by cultivating a variety of plant taxa over the vegetation period would provide floral resources for many different wild bee species (e.g. Goulson et al., 2015). The seed mixtures currently used by many winegrowers include high proportions of legumes. This was reflected in the pollen samples and in the high abundance of wild bees specialised on, or preferring Fabaceae compared to the lower occurrence of wild bees with preference or specialisation on other plant taxa. Seed mixtures which contain higher amounts of Asteraceae, Lamiaceae, or Brassicaceae species could help to improve the floral resource availability for wild bee species with preferences for these foraging plants. Additionally, the result of the pollen analysis highlighted the necessity of permitting spontaneous vegetation in the inter-row cover crop, which is not eligible in the current program (AMA, 2015d).

The two types of extensive management practices (permanently vegetated and temporary vegetated inter-rows) benefit different functional traits, therefore I recommend to maintain or realize a small scale diversity of different management methods at the landscape scale. This is apparent in the Austrian study region, because vineyard size is rather small (I) and as each winegrower has his/her own idea what is best for the vineyard, a wide variety of management methods are applied. On the viticultural landscape scale, the conservation of structurally diverse woods including tree species that are relevant pollen resources for bees (e.g. oaks, willows) as well as the conservation of solitary trees (i.e. fruit trees) should be prioritised. Other landscape structures, such as fallows, shrubs, hedges, or herbaceous margins interspersing the (viti-) cultural landscape and are reported as high quality habitats providing food resources for a range of beneficial organisms in other (agro-) ecosystems (e.g. Cole et al., 2015; Lentini et al., 2012; Woltz et al., 2012). Unfortunately, these patches are under increasing pressure, due to increasing agricultural intensification or soil sealing. Both the conservation or re-establishment of these important landscape structures, and the preservation of their habitat quality in the future, are necessary to counter the current decrease of biodiversity and ecosystem function (Hampicke, 2013). Since there is also growing evidence of the benefit of human settlements on enhancing wild bee diversity and abundance (e.g. Banaszak-Cibicka and Zmihorski, 2012), actions should be implemented there too. For example, public green spaces can be managed to be more pollinator friendly (e.g. by extensive mowing), and garden maintenance should have a target to provide floral resource availability throughout the year (Baldock et al., 2019).

7. Schlussfolgerungen und Empfehlungen

Die Ergebnisse der vorliegenden Dissertation zeigen, dass WinzerInnen die Habitatqualität für Wildbienen in Weingärten verbessern können. Die Fahrgassen können von Wildbienen zur Nahrungssuche als auch Nisthabitat genutzt werden und sind daher am ehesten mit Blühstreifen vergleichbar. Wildbienen profitieren durch ein extensives Begrünungsmanagement und die Einsaat von insektenblütigen Pflanzen in den Fahrgassen, was schlussendlich zu einer erhöhten Bestäubung von Wild- und Kulturpflanzen führen sollte. Eine kritische Betrachtung der Maßnahmen ist jedoch, in Bezug auf den Einsatz von Pestiziden (meist Fungizide und Herbizide) im Weinbau notwendig. Das Wissen über die genauen Auswirkungen vieler Agro-Chemikalien auf unterschiedliche Wildbienenarten ist gering oder nicht vorhanden (Sanchez-Bayo und Goka, 2014) und sollte daher in Zukunft besser erforscht werden. Im österreichischen Agrar-Umweltprogramm (ÖPUL) sind einige Maßnahmen zur Reduktion des Pestizideinsatzes verankert. Für den Verzicht auf Herbizide (AMA, 2015a) und/oder Insektizide (AMA, 2015b) oder auch den Umstieg auf biologische Bewirtschaftung (AMA, 2015c), können WinzerInnen Ausgleichszahlungen geltend machen. Die ersten beiden genannten Maßnahmen sind verpflichtend an die Maßnahme „Erosionsschutz Wein“ geknüpft (AMA, 2015d), welche die Begrünung der Fahrgassen mit mehr als einer Pflanzenart vorschreibt (AMA, 2015d). Damit diese Maßnahme in Zukunft auch Wildbienen fördert, ist es notwendig artenreiche Saatgutmischungen, die potentiell ein kontinuierliches Blütenangebot über die Vegetationsperiode zur Verfügung stellen, in der Maßnahme zu verankern. Damit könnten verschiedene Wildbienenarten, die zu unterschiedlichen Jahrzeiten auftreten, gefördert werden (e.g. Goulson et al., 2015). Die derzeitig von WinzerInnen verwendeten Saatgutmischungen, enthalten einen hohen Anteil an Leguminosen. Dies spiegelte sich beispielsweise in der hohen Abundanz an Wildbienenarten in den Fahrgassen wieder, die bei der Sammlung von Nahrung auf Fabaceen spezialisiert sind oder diese bevorzugen. Verglichen dazu, waren Arten die andere Pflanzentaxa (z.B. Asteraceae, Brassicaceae oder Lamiaceae) bei der Nahrungssammlung präferieren oder auf diese spezialisiert sind, in geringerem Ausmaß in den Weingärten vertreten. Auch die Pollenanalyse der im Juni gesammelten Wildbienen zeigte den hohen Anteil an unterschiedlichen Fabaceen in Weingartenfahrgassen auf. Pflanzenarten aus den Familien der Asteraceae, Brassicacea oder Lamiaceae sollten daher in höheren Anteilen in die Saatgutmischungen eingehen. Die Pollenproben vom April zeigten die Relevanz der Spontanbegrünung als Futterpflanzen für Wildbienen in Fahrgassen auf. Es wird daher geraten auch Spontanbegrünung, als förderbare Begrünungsalternative, in die Maßnahmen der nächsten ÖPUL Förderperiode miteinzubinden.

Unterschiedliche ökologische Wildbienengruppen profitierten von den beiden Varianten extensiver Fahrgassenbewirtschaftung (permanente und temporäre Begrünung). Es wird daher empfohlen diese Varianten kleinräumig umzusetzen oder zu erhalten umso eine Diversifizierung der Bewirtschaftung auf der Landschaftsebene zu erreichen. Die unterschiedliche Bewirtschaftungsintensität der Fahrgassen auf kleinem Raum, ist in Teilen des österreichischen Untersuchungsgebietes noch vorzufinden, weil die einzelnen Weingärten geringe Flächenausmaße aufweisen und von unterschiedlichen WinzerInnen bewirtschaftet werden.

Auf der Landschaftsebene stehen für die österreichischen Gebiete die Erhaltung der strukturreichen Wälder am Leithaberg und der Schutz von Einzelbäumen im Vordergrund. Die Eichen, Weiden und Obstbäumen in diesen Landschaftsstrukturen bieten wichtige Nahrungsressourcen für Wildbienenarten die im Frühling aktiv sind. Andere Landschaftsstrukturen, wie zum Beispiel Brachen, Hecken oder Feld- und Wegränder, sind weitere nachgewiesene wichtige Lebensräume für Wildbienen und verschiedene andere Nützlinge in Agrar-Ökosystemen (z.B. Cole et al., 2015; Lentini et al., 2012; Woltz et al., 2012). Die Erhaltung einer hohen Habitatqualität oder auch Wiederherstellung dieser Strukturen gilt als wichtige Maßnahme um der Biodiversitätsabnahme zu begegnen (Hampicke, 2013). Ein höherer Anteil an Siedlungsgebieten hatte einen positiven Effekt auf die Wildbienenartenvielfalt und Abundanz in den Weingärten. Daher wird angeraten in dörflichen und urbanen Gebieten Maßnahmen zur Förderung von Wildbienen umzusetzen. Diese könnten Beispielsweise auf die extensive Pflege von öffentlichen Grünflächen oder auf ein durchgängiges Blütenangebot über die gesamte Vegetationsperiode in Gärten abzielen (Baldock et al., 2019).

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Appendix Table A 1

Table A 1 Determined pollen types and groups from pollen samples taken from wild bees in vineyards. Number of plant species and list of genera according to Beug (2015) within the respective type or group. Examples of entomophilous plant species that flowered in Austrian vineyard inter-rows attributed to the respective type or group according to Beug (2015).

Pollen types/groups (number of plant species associated)	Attributed genera/ subfamily/ family	Flowering in inter-row	% per month (inter-row)	
			April	June
Allium ursinum-type (19 spp.)	Allium spp.	-	5.1	0.0
Asteraceae liguliflorae	Carduoidea		<1	0.0
Asteraceae tubiflorae	Cichorioideae		<1	0.0
Astragalus-type (43 spp.)	*Astragalus* spp.		0	1.5
	Colutea arborescens			
	Melilotus spp.	*M. albus*		
	Ononis spp.	*M. officinalis*		
	Oxytropis spp.			
Brassicaceae (174 spp.)	56 genera e.g.		7.0	<1
	Alyssum spp.			
	Arabis spp.			
	Brassica spp.			
	Capsella spp.	*C. bursa-pastoris*		
	Cardaria draba	*C. draba*		
	Draba spp.			
	Erysimum spp.			
	Lepidium spp.			
	Raphanus spp.	*R. sativus*		
	Sisymbrium spp.	*S. loeselii*		
	Thlaspi spp.			
Convolvulus arvensis-type (3 spp.)	*Convolvulus* spp.	*C. arvensis*	0.0	<1
Centaurea cyanus (1 sp.)	*Centaurea cyanus*	*C. cyanus*	0.0	<1
Crepis-type (75 spp.)	*Chondrilla* spp.		36.3	0.0
	Cicerbita spp.			
	Cichorium intybus	*C. intybus*		
	Crepis sp.	*C. foetida*		
	Hieracium sp.	*C. setosa*		
	Hypochaeris sp.	*C* sp.		
	Lapsana communis			
	Leontodon spp.			
	Picris spp.	*P. hieracioides*		
	Prenanthes purpurea			
	Taraxacum spp.	*T. officinale* agg.		
	Tolpis staticifolia			
	Willemetia stipitata			
Fabaceae unident.			0.0	2.2
Galeopsis-*Ballota*-group (34 spp.)	*Ajuga* spp.	*A. genevensis*	6.5	0
	Ballota nigra			
	Betonica spp.			
	Galeopsis spp.			

Pollen types/groups (number of plant species associated)	Attributed genera/ subfamily/ family	Flowering in inter-row	% per month (inter-row)	
			April	June
	Lamium spp.	*L. amplexicaule*		
	Leonurus spp.	*L. purpureum*		
	Melittis melissophyllum			
	Phlomis spp.			
	Scutellaria spp.			
	Stachys spp.			
Phacelia tanacetifolia (1 sp.)	*Phacelia tanacetifolia*	*P. tanacetifolia*	0	<1
Lathyrus-*Vicia*-type	*Lathyrus* spp.		0	<1
	Vicia spp.			
Matricaria-type (37 spp.)	*Achillea* spp.	*A. millefolium*	1.4	2.9
	Anthemis spp.	*A. arvensis*		
	Chrysanthemum spp.			
	Cotula coronopifolia			
	Leucanthemopsis alpine			
	Leucanthemum spp.			
	Matricaria spp.	*M. discoidea*		
	Tanacetum spp.			
	Tripleurospermum spp.	*T. inodorum*		
Plantago lanceolata-type (4 spp.)	*Plantago* spp.	*P. lanceolate*	0	<1
Poaceae			0	<1
Quercus rubor-pubes.-type (4 spp.)	*Quercus* spp.	-	2.6	0
Ranunculus acris-type (66 spp.)	*Anemone* spp.		0	<1
	Callianthemum spp.			
	Clematis spp.			
	Myosurus minimus			
	Pulsatilla spp.			
	Ranunculus spp.	*R. bulbosus*		
Robinia pseudoacacia (1 sp.)	*Robinia pseudoacacia*	-	0	4.5
Sorbus-group (49 spp.)	*Amelanchier ovalis*	-	10.8	0
	Cotoneaster spp.			
	Crataegus spp.			
	Cydonia oblonga			
	Dryas octopetala			
	Eriobotrya japonica			
	Malus spp.			
	Mespilus germanica			
	Prunus spp.			
	Pyracantha coccinea			
	Pyrus spp.			
	Sorbus spp.			
	Rubus spp.			
	Lycium spp.			
Senecio-type (126 spp.)	34 genera e.g.:		7.8	3.1
	Aster spp.			
	Bellis perennis	*B. perennis*		
	Calendula spp.	*C. officinalis*		
	Erigeron spp.	*E. annuus* *E. canadensis*		
	Helianthus annuus			

Pollen types/groups (number of plant species associated)	Attributed genera/ subfamily/ family	Flowering in inter-row	% per month (inter-row)	
			April	June
	Inula spp. *Senecio* spp. *Silphium perfoliatum*	*S. vernalis*		
Stellaria graminea-group (9 spp.)	*Stellaria* spp.	*Stellaria media*	14.9	0
Tilia (8 spp.)	*Tilia* spp.	-	0	<1
Trifolium pratense-type (5 spp.)	*Trifolium* spp.	*T. incarnatum* *T. pratense*	<1	14.0
Trifolium repens-type (21 spp.)	*Trifolium* spp. *Trigonella* spp.	*T. campestre* *T. hybridum* *T. repens* *T. resupinatum*	<1	33.6
Veronica-type (33 spp.)	*Pseudolysimachion* spp. *Veronica* spp.	*V. arvensis* *V. hederifolia* *V. persica* *V. polita*	5.0	<1
Vicia-type (17 spp.)	*Pisum sativum* *Vicia* spp.	*V. angustifolia* *V. faba* *V. hirsute* *V. pannonica*	<1	24.1
Vitis vinifera (2 spp.)	*Vitis* spp.	*V. vinifera*	0	9.3

Notes:

Asteraceae liguliflorae / Asteraceae tubiflorae: Summarizes Asteraceae species which were impossible to identify to a pollen type or group; exine structure allows attribution to the according subfamilies

Brassicaceae: High variability within species; association to pollen types questionable (Beug, 2015)

Fabaceae unident: Summarizes Fabacea which were impossible to associate to a pollen type / group

Lathyrus-*Vicia*-type: Due to exine structure variability association to *Lathyrus*- or *Vicia*-type not possible

Tripleurospermum inodorum, *Erigeron canadensis*: Not cited in Beug (2015) but associated to the respective type by comparison with ponetweb.ages.at (AGES, 2016)

Poaceae: Very similar pollen types; discrimination between wild and cultivated taxa possible (Beug 2015); not implemented due to low relevance as foraging resource for bees

Appendix Table A 2

Table A 2 Quantities of pollen types (according to Beug 2015) from wild bees in Austrian vineyard inter-rows in April and June and from grapevine flowers. Notes: L=Location the wild bee was sampled; M=Month in which the wild bee was sampled; m=vegetation management intensity: t=temporary vegetated, p=permanently vegetated; Wild bee genera were abbreviated: *A=Andrena*, *Ap=Apis*, *B=Bombus*, *Eu=Eucera*, *H=Halictus*, *L=Lasioglossum*, *O=Osmia.*

L	**T**	**m**	**Pollen types** **Bee species**	*Allium ursinum*-type	Asteraceae liguliflorae	Asteraceae tubiflorae	Brassicaceae	*Convolvulus arvensis*	*Centaurea jacea*-type	*Crepis*-type	Fabaceae	*Galeopsis*-type	*Phacelia tanacetifolia*	*Lathyrus*-*Vicia*-type	*Matricaria*-type	*Melilotus*-type	*Plantago*-type	Poaceae	*Quercus*	*Ranunculus*	*Robinia pseudoacacia*	*Sorbus*-group	*Senecio*-type	*Stellaria graminea*-group	*Tilia*	*Trifolium pratense*-type	*Trifolium repens*-type	*Veronica*-type	*Vicia*-type	*Vitis vinifera*	Unidentified; fragments
Inter-row	**April**	p	*A.flavipes*				273			35														4							1
		p	*L.calceatum*									6										4	313								0
		t	*L.fulvicorne*							59		176			55									8							2
		t	*L.laterale*							365		3											1					22			8
		p	*L.marginatum*							300																					7
		p	*L.marginatum*	1						315																					1
		t	*L.marginatum*	205						49														3				3			50
		t	*L.marginatum*				9			1												33		266							4
		p	*L.marginatum*									11										131		141							27
		t	*L.marginatum*		10					23									29			181		55					2		0
		t	*L.marginatum*			3	2			6		52										87		90				37			23
		p	*L.marginatum*							315												1									0
		p	*L.nigripes*									17							78			2		39			1	140			38

L	T	m	Pollen types / Bee species	*Allium ursinum*-type	Asteraceae liguliflorae	Asteraceae tubiflorae	Brassicaceae	*Convolvulus arvensis*	*Centaurea jacea*-type	*Crepis*-type	Fabaceae	*Galeopsis*-type	*Phacelia tanacetifolia*	*Lathyrus*-*Vicia*-type	*Matricaria*-type	*Melilotus*-type	*Plantago*-type	Poaceae	*Quercus*	*Ranunculus*	*Robinia pseudoacacia*	*Sorbus*-group	*Senecio*-type	*Stellaria graminea*-group	*Tilia*	*Trifolium pratense*-type	*Trifolium repens*-type	*Veronica*-type	*Vicia*-type	*Vitis vinifera*	Unidentified; fragments
	June	t	*A.ovaluta*																								370				0
		t	*A.ovatula*								22												1			37	229		22		9
		t	*A.ovatula*													112		2								7	157				22
		p	*A.ovatula*																		23					109	148				34
		p	*A.ovatula*																								307				0
		t	*B.lapidarius*					2			40						1	2								93	163				13
		t	*B.lapidarius*											45				2			48				35	90	87				10
		p	*B.pascuorum*														8	11			31		1				265				22
		t	*B.pascuorum*																		6				3		59		210		23
		t	*Eu.nigrescens*																										344		8
		t	*Eu.nigrescens*																										355		10
		t	*Eu.nigrescens*																										379		3
		t	*Eu.nigrescens*																										425		6
		p	*H.quadricinctus*					2	1						1		6	4			29					29	214				37
		p	*H.simplex*															8			14					234	52				15
		p	*H.simplex*								75																127				13
		t	*H.simplex*						66				19		209													23		12	15
		t	*H.subauratus*												16								222			66					18
		t	*H.subauratus*					5										2			126		16				155				10

L	**T**	**m**	**Pollen types** / **Bee species**	*Allium ursinum*-type	Asteraceae liguliflorae	Asteraceae tubiflorae	Brassicaceae	*Convolvulus arvensis*	*Centaurea jacea*-type	*Crepis*-type	Fabaceae	*Galeopsis*-type	*Phacelia tanacetifolia*	*Lathyrus*-*Vicia*-type	*Matricaria*-type	*Melilotus*-type	*Plantago*-type	Poaceae	*Quercus*	*Ranunculus*	*Robinia pseudoacacia*	*Sorbus*-group	*Senecio*-type	*Stellaria graminea*-group	*Tilia*	*Trifolium pratense*-type	*Trifolium repens*-type	*Veronica*-type	*Vicia*-type	*Vitis vinifera*	Unidentified; fragments
		t	*L.discum*																		23					181	111				9
		p	*L.lineare*					43					25																	233	13
		p	*L.lineare*				12						23																	267	6
		t	*O.aurulenta*					4			37						5				0		1			240	17				7
		t	*O.caerulescens*																										129	206	9
		t	*O.caerulescens*													6		1		7	50						140				116
Grapevine flower	**June**	p	*A.dorsata*																						27					339	14
		t	*Ap.mellifera*																				1							305	0
		t	*L.laticeps*																											232	6
		t	*L.lineare*										4																	318	8
		t	*L.lineare*																											307	7
		p	*L.lineare*										182																	136	6
Total				206	10	3	296	56	67	1468	174	265	253	45	281	118	20	32	107	7	350	439	556	606	65	1086	2602	225	1866	2355	546
Total inter-row April				206	10	3	284	0	0	1468	0	265	0	0	55	0	0	0	107	0	0	439	314	606	0	0	1	202	2	0	161
Total inter-row June				0	0	0	12	56	67	0	174	0	67	45	226	118	20	32	0	7	350	0	241	0	38	1086	2601	23	1864	718	428
Total grapevine flower				0	0	0	0	0	0	0	0	0	186	0	0	0	0	0	0	0	0	0	1	0	27	0	0	0	0	1637	41

Appendices – Publications

Appendix I – Core Publication I: Kratschmer et al. (2018) AEE 266

APPENDIX TABLES:

Table A.1 Habitat classification based on landscape features and related EUNIS (European Nature Information System) habitat codes (if applicable; NA – not included in EUNIS code) used for field mapping and digitalization. The range of landscape features across all landscape circles is given in percentage of the total area per landscape circle (750 m radius). Solitary trees are given in numbers.

Habitat classification	Landscape features for mapping	EUNIS Code	Range over all circles	Definition
Semi-Natural Elements (SNE)	Orchard	G1.D	0.0-8.9 %	Cultivation of fruit trees; often extensively managed
	Tree row	G5.1	0.0-0.7 %	+/- continuous line of trees; > 5m high
	Grassland	E	0.0-23.9 %	Vegetation dominated by grasses and non-woody plants
	Pasture	E2.1	0.0-8.3 %	Regularly grazed area
	Hedgerow	FA	0.1-1.9 %	Woody vegetation forming strips; < 5 m high
	Sparsely wooded grassland	E7	0.0-2.9 %	Grassland; <10 % wooded overstorey
	Wetland	D	0.0-0.5 %	Water table min. 1/2 year; accompanied by herbaceous vegetation
	Fallow	I1.5	2.1-12.4 %	Abandoned or left to rest fields/arable land
	Unsealed path and road	J4.1	0.0-1.0 %	Dirt roads, rarely used; colonised by herbaceous weed vegetation
	Grass strip, field margin	X07	0.7-2.2 %	Road verges, field edges, < 1m width
Wood area	Woodland	G	0.0-55.3 %	Woodland, forests; tree height > 5 m; canopy cover at least 10 %
Solitary tree	Solitary tree	NA	14-101 trees	Single tree; no element of a group of trees or tree row
Vineyard	High proportion of vegetation cover	FB4.1	2.5-33.0 %	Characteristic accompanying flora present; lightly treated; permanent vegetation cover
	Medium proportion of vegetation cover	FB4.2	0.6-30.6 %	Cleared of herb layer; temporary vegetation cover
	Bare soil	NA	0.0-4.1 %	Completely cleared of herb layer
Entomophilous crop	Entomophilous crop	I1	0.8-27.2 %	Annually or regularly harvested insect pollinated crops (sunflower, oilseed)
Non-entom. crop	Non-entomophilous crop	I1.1	1.2-54.8 %	Cereals and other crops (no insect pollination; wheat, maize)
Water body	Ponds and Rivers	C	0.0-0.6 %	Inland surface water incl. artificial constructed and seasonal waterbodies
Artificial and constructed entities	Constructed, industrial and other artificial habitats	J	<0.1-4.7 %	Other man-made structures than J1, J2, J4.2
	Town and village	J1	<0.1-37.6 %	Buildings and other impermeable surfaces occupy > 30 % coverage
	Settlement	J2	0.0-4.5 %	Buildings and other impermeable surfaces occupy < 30 % coverage
	Roads	J4.2	<0.1-2.5 %	Impermeable road surface, gravel roads and car parks

Table A.2 Proximity measures per vineyard and slope measures per landscape circle.

Vineyard/ Circle	Distance to water source (m)	Distance to SNE (m)	Mean (±SD) slope (%)	Minimum slope (%)	Maximum slope (%)
1	304.25	3.41	3.3 ± 1.7	0.3	17.8
2	230.37	7.42	4.2 ± 3.9	0.4	38.0
3	91.20	18.48	8.5 ± 7.9	0.2	59.1
4	497.41	4.16	15.7 ± 9.4	0.5	66.8
5	171.48	6.49	3.2 ± 2.9	0.0	32.9
6	>750.00	18.34	4.1 ± 3.5	0.0	28.7
7	>750.00	17.24	13.7 ± 7.9	0.0	46.3
8	511.74	26.75	9.8 ± 7.2	0.1	73.2
9	117.20	13.06	5.0 ± 4.4	0.0	47.5
10	165.99	51.30	9.5 ± 5.8	0.1	50.6
11	>750.00	39.77	9.3 ± 7.2	0.0	42.3
12	>750.00	3.26	6.3 ± 4.0	0.2	35.4
13	356.28	15.35	3.9 ± 7.1	0.0	41.7
14	156.77	43.03	3.3 ± 5.9	0.1	29.3
15	>750.00	8.28	4.2 ± 7.8	0.5	37.0
16 (2015)	132.23	35.43	7.9 ± 4.9	0.3	38.7
16 (2016)	154.90	34.70	7.9 ± 4.9	0.3	38.7

Note Vineyard in landscape circle 16 was changed for the 2nd year survey after tillage of the untilled plot in spring 2016.

Table A.3 List of sampled wild bee species in Austrian vineyards including traits and total abundance.

Trait Taxa	Nesting type	Lecty	Sociality	ITD	Total abundance
Apis mellifera LINNAEUS 1759	A	pl	social	2.68	150
Andrena dorsata (KIRBY 1802)	G	pl	solitary	2.04	1
Andrena flavipes PANZER 1800	G	pl	solitary	2.12	14
Andrena fulvago (CHRIST 1791)	G	ol	solitary	2.15	1
Andrena gravida IMHOFF 1833	G	pl	solitary	2.82	6
Andrena labialis (KIRBY 1802)	G	ol	solitary	2.32	3
Andrena minutula (KIRBY) 1802	G	pl	solitary	2.21	1
Andrena ovatula (KIRBY 1802)	G	pl	solitary	2.07	28
Andrena polita SMITH 1847	G	ol	solitary	2.26	1
Andrena simontornyella NOSKIEWICZ 1940	G	pl	solitary	1.28	5
Anthidium strigatum (PANZER 1805)	A	pl	solitary	1.01	1
Anthophora plumipes (PALLAS 1772)	G	pl	solitary	3.76	2
Bombus haematurus KRIECHBAUMER 1870	A	pl	eusocial	3.65	1
Bombus hortorum (LINNAEUS 1761)	A	pl	eusocial	3.41	3
Bombus lapidarius (LINNAEUS 1758)	A	pl	eusocial	4.02	40
Bombus pascuorum (SCOPOLI 1763)	A	pl	eusocial	3.24	11
Bombus sylvarum (LINNAEUS 1761)	A	pl	eusocial	3.03	3
Bombus terrestris (LINNAEUS 1758)	A	pl	eusocial	3.66	29
Ceratina chalybea CHEVRIER 1873	A	pl	solitary	1.83	2
Ceratina cyanea (KIRBY 1802)	A	pl	solitary	1.27	2
Ceratina nigrolabiata FRIESE 1896	A	pl	solitary	1.33	2
Eucera chrysopyga (PÉREZ, 1879)	G	pl	solitary	3.31	2
Eucera longicornis (LINNAEUS 1758)	G	ol	solitary	3.21	1
Eucera nigrescens PÉREZ 1880	G	ol	solitary	3.17	14
Halictus kessleri BRAMSON 1880	G	pl	eusocial	1.27	5
Halictus maculatus SMITH 1849	G	pl	eusocial	1.32	10
Halictus quadricinctus (FABRICIUS 1776)	G	pl	solitary	2.67	3
Halictus rubicundus (CHRIST 1791)	G	pl	eusocial	2.05	1
Halictus seladonius (FABRICIUS 1794)	G	pl	eusocial	1.48	2
Halictus simplex BLÜTHGEN, 1923	G	pl	solitary	1.71	21
Halictus smaragdulus VACHAL 1895	G	pl	eusocial	1.19	1
Halictus subauratus (ROSSI 1792)	G	pl	eusocial	1.41	8

Halictus tumulorum (LINNAEUS 1758)	G	pl	eusocial	1.31	1
Heriades truncorum (LINNAEUS 1758)	A	ol	solitary	1.32	3
Hylaeus annularis (KIRBY 1802)	A	pl	solitary	1.34	1
Hylaeus brevicornis NYLANDER 1852	A	pl	solitary	1.01	2
Hylaeus communis NYLANDER 1852	A	pl	solitary	0.96	1
Hylaeus confusus NYLANDER 1852	A	pl	solitary	1.17	1
Hylaeus gibbus SAUNDERS 1850	A	pl	solitary	1.26	3
Hylaeus imparilis FÖRSTER 1871	A	pl	solitary	0.99	1
Hylaeus trinotatus PÉREZ 1895	A	pl?	solitary	1.48	1
Lasioglossum aeratum (KIRBY 1802)	G	pl	eusocial	0.92	2
Lasioglossum calceatum (SCOPOLI 1763)	G	pl	eusocial	1.74	10
Lasioglossum discum (SMITH 1853)	G	pl	NA	2.14	3
Lasioglossum glabriusculum (MORAWITZ 1872)	G	pl	eusocial	0.78	4
Lasioglossum griseolum (MORAWITZ 1872)	G	pl	NA	1.07	3
Lasioglossum interruptum (PANZER 1798)	G	pl	eusocial	1.40	1
Lasioglossum laevigatum (Kirby 1802)	G	pl	solitary	2.21	1
Lasioglossum laterale (BRULLÉ 1832)	G	pl	NA	1.86	1
Lasioglossum laticeps (SCHENK 1869)	G	pl	eusocial	1.58	1
Lasioglossum lativentre (SCHENCK 1853)	G	pl	solitary	1.50	4
Lasioglossum leucozonium (SCHRANK 1781)	G	pl	solitary	1.63	3
Lasioglossum lineare (SCHENCK 1869)	G	pl	eusocial	1.23	27
Lasioglossum malachurum (KIRBY 1802)	G	pl	eusocial	1.48	7
Lasioglossum marginatum (BRULLÉ 1832)	G	pl	eusocial	1.78	99
Lasioglossum mesosclerum (PÉREZ 1903)	G	pl	NA	1.22	2
Lasioglossum minutissimum (KIRBY 1802)	G	pl	solitary	0.80	6
Lasioglossum nigripes (LEPELETIER 1841)	G	pl	eusocial	1.94	3
Lasioglossum pauxillum (SCHENCK 1853)	G	pl	eusocial	1.16	5
Lasioglossum punctatissimum (SCHENCK, 1853)	G	pl	solitary	1.14	1
Lasioglossum pygmaeum (SCHENCK 1853)	G	pl	solitary	1.00	2
Lasioglossum quadrinotatum (KIRBY 1802)	G	pl	solitary	1.72	1
Lasioglossum xanthopus (KIRBY 1802)	G	pl	solitary	2.21	4
Lasioglossum zonulum (SMITH 1848)	G	pl	solitary	2.18	1
Melitta leporina (PANZER 1799)	G	ol	solitary	1.95	1
Nomada bifasciata OLIVIER 1811	P	pl	P	1.92	1
Nomada flavoguttata (KIRBY 1802)	P	pl	P	1.07	1
Nomada zonata PANZER 1798	P	pl	P	1.60	1
Osmia aurulenta (PANZER 1799)	A	pl	solitary	2.89	2
Osmia caerulescens (LINNAEUS 1758)	A	pl	solitary	2.17	5
Osmia claviventris THOMSON 1872	A	pl	solitary	2.01	1
Osmia leucomelana (KIRBY 1802)	A	pl	solitary	1.41	2
Osmia rufohirta LATREILLE 1811	A	pl	solitary	2.12	1
Osmia spinulosa (KIRBY 1802)	A	ol	solitary	1.84	1
Panurgus calcaratus (SCOPOLI 1763)	G	ol	eusocial	1.64	5
Rhophitoides canus (EVERSMANN 1852)	G	ol	solitary	1.67	2
Sphecodes ephippius (LINNÉ 1767)	P	pl	P	1.36	2
Sphecodes ferruginatus HAGENS 1882	P	pl	P	1.59	1
Sphecodes gibbus (LINNAEUS 1758)	P	pl	P	1.27	2
Sphecodes ruficrus (ERICHSON 1835)	P	pl	P	1.03	1
Sphecodes rufiventris (PANZER 1798)	P	pl	P	1.20	3
Sphecodes sp.	P	pl	P	NA	4
Stelis minuta LEPELETIER & SERVILLE 1825	P	pl	P	1.20	2
Systropha curvicornis (SCOPOLI 1770)	G	ol	solitary	1.98	22
Systropha planidens GIRAUD 1862	G	ol	solitary	2.29	4

A	above-ground nesting	*pl*	polylectic
G	ground-nesting	*ol*	oligolectic
P	parasitic		
ITD	Inter-Tegular Distance (mm) from 1-5 specimen (the mean ITD was calculated if more than 1 specimen of a species were present)		

Table A.4 Entomophilous plant species list documented in vineyard inter-rows of different tillage regimes in 2015 and 2016.

Tillage regime / Plant species	Alternating tilled vineyards	Untilled vineyards	Total vineyards
Achillea millefolium agg.	7	7	14
Anthemis arvensis	1	1	2
Bellis perennis	0	1	1
Capsella bursa-pastoris	7	4	11
Carduus acanthoides	2	0	2
Carum carvi	0	1	1
Centaurea cyanus	1	2	3
Cerastium sp. 1	0	2	2
Cerastium sp. 2	2	0	2
Cichorium intybus	2	0	2
Cirsium arvense	0	2	2
Consolida sp.	1	2	3
Convolvulus arvensis	8	8	16
Conyza canadensis	3	2	5
Crepis foetida	1	3	4
Crepis sp.	2	1	3
Daucus carota	2	2	4
Erigeron annuus	5	6	11
Erigeron canadensis	0	3	3
Erodium cicutarium	1	2	3
Fagopyrum esculentum	2	0	2
Falcaria vulgaris	1	1	2
Geranium pusillum	6	5	11
Hypericum sp.	1	1	2
Lactuca serriola	2	0	2
Lamium amplexicaule	1	2	3
Lamium purpureum	7	8	15
Lathyrus sativus	0	1	1
Lotus corniculatus	2	1	3
Malva neglecta	3	0	3
Malva sp.	1	2	3
Matricia discoidea	2	0	2
Medicago lupulina	7	3	10
Medicago sativa	5	2	7
Melilotus albus	1	1	2
Melilotus officinalis	5	0	5
Muscari sp.	0	2	2
Myosotis arvensis	1	1	2
Nonea pulla	0	1	1
Onobrychis viciifolia	4	1	5
Papaver rhoeas	1	1	2
Phacelia tanacetifolia	6	0	6
Plantago lanceolata	5	6	11
Polygonum aviculare	1	2	3
Prunella vulgaris	0	1	1
Raphanus sativus	4	1	5
Sanguisorba minor	2	2	4
Sisymbrium loeselii	2	0	2
Sonchus sp.	2	0	2
Stellaria media	9	8	17
Taraxacum officinale agg.	8	8	16

Tragopogon sp.	1	1	2
Trifolium campestre	1	3	4
Trifolium hybridum	0	3	3
Trifolium incarnatum	7	1	8
Trifolium pannonicum	1	1	2
Trifolium pratense	6	5	11
Trifolium repens	7	6	13
Tripleurospermum inodorum	2	0	2
Valerianella sp.	1	2	3
Veronica persica	8	6	14
Veronica sp. 1	5	7	12
Veronica sp.2	2	3	5
Vicia angustifolia	2	4	6
Vicia faba	0	2	2
Vicia hirsuta	2	0	2
Vicia pannonica	3	2	5
Viola arvensis	2	2	4

Numbers Indicate the amount of vineyard per tillage regime and in total the respective plant species was documented in.

Table A.5 Community weighted means for functional trait analysis per vineyard.

Vineyard	Nesting type	Lecty	Sociality	ITD (mm)
1	Ground-nesting	pl	solitary	1.580
2	Above-ground nesting	pl	eusocial	2.737
3	Ground-nesting	pl	solitary	2.592
4	Above-ground nesting	pl	eusocial	2.572
5	Ground-nesting	pl	solitary	2.168
6	Ground-nesting	pl	solitary	2.446
7	Ground-nesting	pl	eusocial	1.841
8	Ground-nesting	pl	solitary	1.919
9	Ground-nesting	pl	eusocial	1.807
10	Ground-nesting	pl	eusocial	1.986
11	Ground-nesting	pl	eusocial	2.014
12	Ground-nesting	pl	eusocial	1.815
13	Ground-nesting	pl	eusocial	2.614
14	Ground-nesting	pl	solitary	1.771
15	Ground-nesting	pl	eusocial	1.838
16 (2015)	Ground-nesting	pl	eusocial	2.499
16 (2016)	Ground-nesting	pl	eusocial	1.941

CWM Community weighted mean

ITD Inter-tegular-distance

Note Vineyard in landscape circle 16 was changed for the 2nd year survey after tillage of the untilled plot in spring 2016.

Appendix Figures

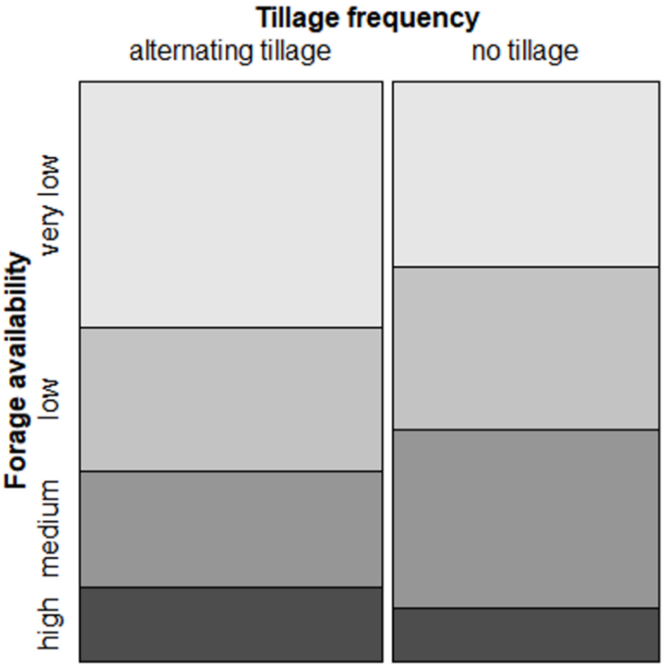

Fig. A.1 Forage availability represented in untilled and alternating tilled vineyard inter-rows in Austria (2015-2016). The Mosaic plot (R package "vcd"; Meyer et al., 2016) visualizes the proportion of forage availability categories per tillage regime and observation date.

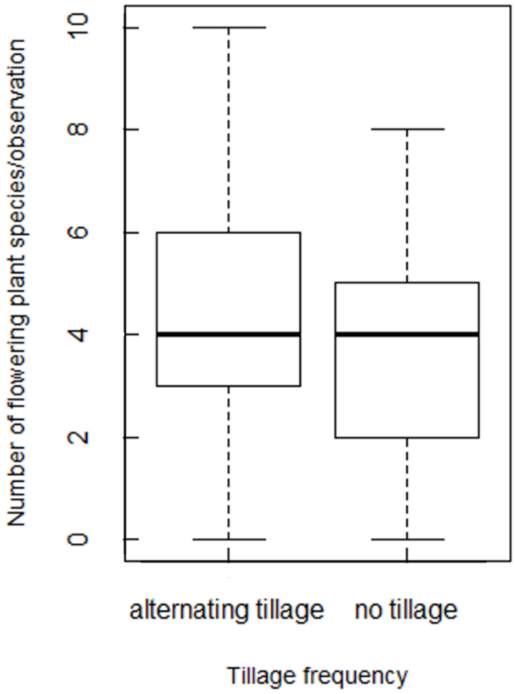

Fig. A.2 Number of entomophilous flowering plant species (per observation) represented in untilled and alternating tilled vineyard inter-rows in Austria (2015-2016).

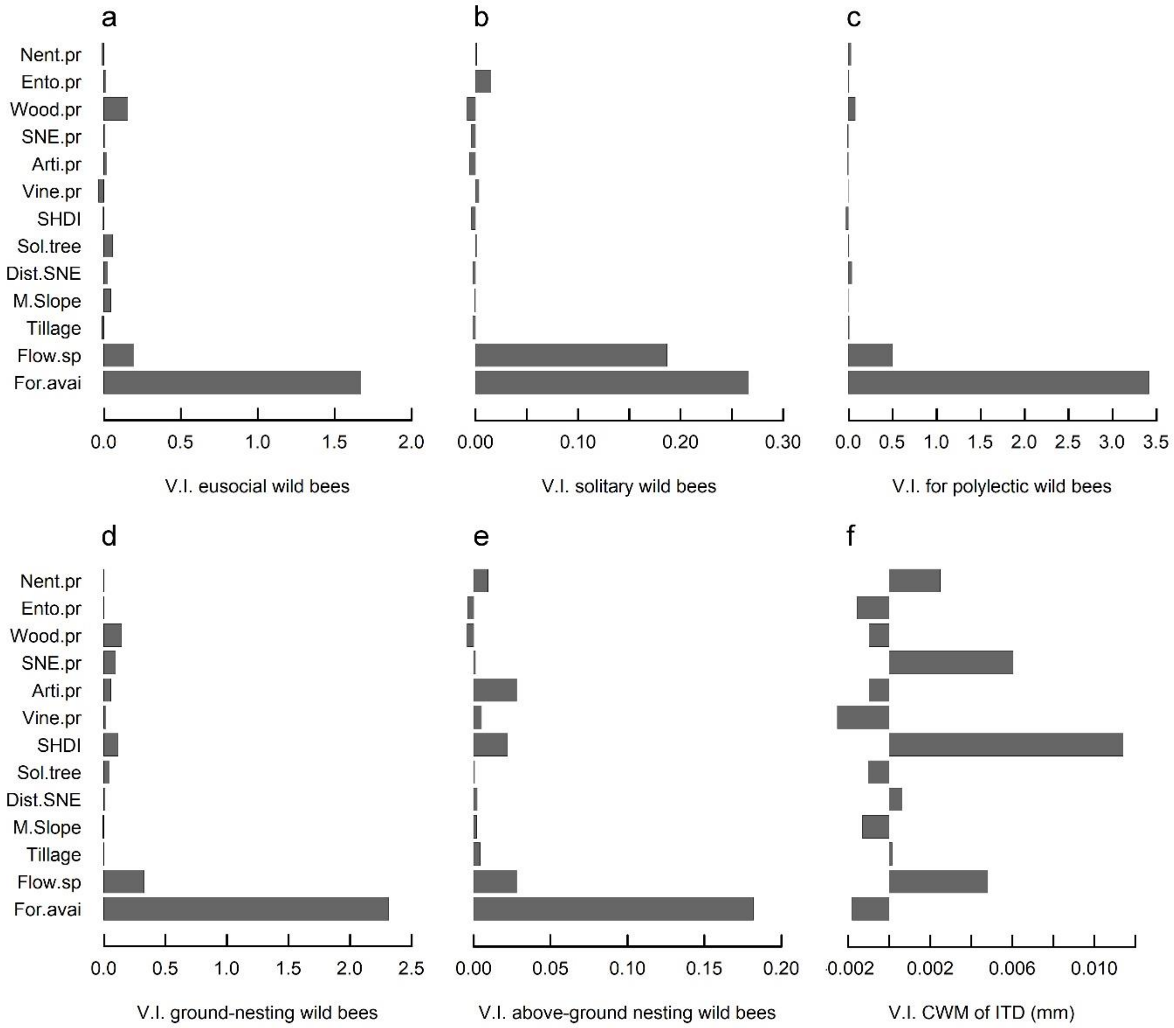

Fig. A.3. Conditional variable importance (V.I.) of field (forage availability (For.avai), entomophilous plant species richness (Flow.sp), tillage regime (Tillage)) and landscape parameters (mean slope (M.slope), distance to SNE (Dist.SNE), number of solitary tree (Sol.tree), Shannon Landscape Diversity Index (SHDI), the proportions of vineyards (Vine.pr), artificial entities (Arti.pr), semi-natural elements (SNE.pr), woods (Wood.pr), entomophilous crops (Ento.pr), non-entomophilouse crops (Nent.pr)) for (a-e) the abundance wild bee species traits and (f) the community weighted means (CWM) of inter-tegular distance (ITD) in vineyards each tested separately by random forests.

Appendix II – Core Publication II: Kratschmer et al. (2019) Ecol. Evol. 9

Appendix - Tables

Table S1: Species list of wild bees from vineyards across Europe including information on total abundance, abundance per country and functional traits. Nomenclature after Fauna Europaea (Polaszek and Mitroiu 2013); *A. danuvia* (Stöckhert and Pittioni 1950), *Hylaeus dilatatus* (Notton and Dathe 2008) and *H. intermedius* (Dathe et al. 2016)

Traits Taxa	Nesting type	Sociality	Lecty	ITD (mm)	Abundance				
					Σ	AT	ES	FR	RO
Andrena aerinifrons Dours, 1873	G	solitary	pl	1.59	6	0	6	0	0
Andrena combaella Warncke, 1966	G	solitary	ol	2.34	1	0	0	0	1
Andrena dorsata (Kirby, 1802)	G	solitary	pl	2.04	1	1	0	0	0
Andrena ferrugineicrus Dours, 1872	G	solitary	pl	2.18	2	0	2	0	0
Andrena flavipes Panzer 1799	G	solitary	pl	2.08	17	8	2	1	6
Andrena florentina Magretti, 1883	G	solitary	pl	2.41	3	0	3	0	0
Andrena gravida Imhoff, 1832	G	solitary	pl	2.82	5	5	0	0	0
Andrena labialis (Kirby, 1802)	G	solitary	ol	2.32	2	2	0	0	0
Andrena longibarbis Perez, 1895	G	solitary	pl	1.59	1	0	1	0	0
Andrena nitida (Müller, 1776)	G	solitary	pl	3.02	1	0	1	0	0
Andrena ovatula (Kirby, 1802)	G	solitary	pl	2.07	22	20	0	1	1
Andrena pusilla Perez, 1903	G	solitary	pl	1.10	2	0	1	0	1
Andrena saxonica Stoeckhert, 1935	G	solitary	ol	1.36	1	0	0	0	1
Andrena simontornyella Noskiewicz, 1939	G	solitary	pl	1.30	2	2	0	0	0
Andrena subopaca Nylander, 1848	G	solitary	pl	1.42	2	0	0	0	2
Andrena tenuistriata (Perez, 1895)	G	solitary	pl	1.29	65	0	65	0	0
Andrena varia Perez, 1895 ☼	G	solitary	pl	2.10	6	0	6	0	0
Anthidium manicatum (Linnaeus, 1758)	A	solitary	pl	3.19	1	0	0	0	1
Anthophora crinipes Smith, 1854	G	solitary	pl	3.72	1	0	0	0	1
Anthophora plumipes (Pallas, 1772)	G	solitary	pl	3.74	1	1	0	0	0
Apis mellifera (Linnaeus, 1758)	A	social	pl	n.a.	217	128	7	23	59
Bombus haematurus Kriechbaumer, 1870	A	eusocial	pl	3.65	1	1	0	0	0
Bombus hortorum (Linnaeus, 1761)	A	eusocial	pl	3.35	3	3	0	0	0
Bombus humilis Illiger, 1806	A	eusocial	pl	3.51	1	0	0	1	0
Bombus lapidarius (Linnaeus, 1758)	A	eusocial	pl	3.65	33	30	0	3	0
Bombus lucorum (Linnaeus, 1761)	A	eusocial	pl	3.77	1	0	0	1	0
Bombus pascuorum (Scopoli, 1763)	A	eusocial	pl	3.13	12	9	0	2	1
Bombus pratorum (Linnaeus, 1761)	A	eusocial	pl	3.75	1	0	0	1	0
Bombus sylvarum (Linnaeus, 1761)	A	eusocial	pl	3.32	3	2	0	0	1
Bombus terrestris (Linnaeus, 1758)	A	eusocial	pl	3.82	23	22	0	0	1
Ceratina chalybea Chevrier, 1872	A	solitary	pl	1.83	1	1	0	0	0
Ceratina cyanea (Kirby, 1802)	A	solitary	pl	1.26	3	1	0	2	0
Ceratina dalltorreana Friese, 1896	A	solitary	pl	0.99	1	0	1	0	0
Ceratina nigrolabiata Friese, 1896	A	solitary	pl	1.36	3	2	0	0	1
Chelostoma florisomne (Linnaeus, 1758)	A	solitary	ol	1.57	1	0	0	0	1
Eucera chrysopyga (Perez, 1879)	G	solitary	pl	3.21	2	1	0	0	1
Eucera eucnemidea Dours, 1873	G	solitary	pl	2.35	16	0	16	0	0
Eucera interrupta Baer, 1850	G	solitary	ol	2.79	1	0	0	0	1
Eucera longicornis (Linnaeus, 1758)	G	solitary	ol	3.21	1	1	0	0	0
Eucera nigrescens Perez, 1879	G	solitary	ol	3.16	20	13	0	7	0
Eucera nigrilabris Lepeletier, 1841	G	solitary	pl	3.65	2	0	2	0	0
Eucera numida Lepeletier, 1841	G	solitary	pl	3.28	2	0	2	0	0
Eucera seminuda Brullé, 1832	G	solitary	pl	2.65	1	0	0	0	1
Halictus eurygnathus Bluethgen, 1931	G	solitary	pl	1.77	1	0	0	1	0
Halictus kessleri Bramson, 1879	G	eusocial	pl	1.29	9	3	0	0	6

Halictus langobardicus Bluethgen, 1944	G	solitary	pl	1.47	1	0	0	0	1
Halictus maculatus Smith, 1848	G	eusocial	pl	1.37	7	4	0	2	1
Halictus quadricinctus (Fabricius, 1776)	G	solitary	pl	2.70	4	3	0	0	1
Halictus rubicundus (Christ, 1791)	G	eusocial	pl	2.05	1	1	0	0	0
Halictus scabiosae (Rossi, 1790)	G	eusocial	pl	2.58	15	0	0	15	0
Halictus seladonius (Fabricius, 1794)	G	eusocial	pl	1.48	2	2	0	0	0
Halictus simplex Bluethgen, 1923	G	solitary	pl	1.77	26	13	0	2	11
Halictus smaragdulus Vachal, 1895	G	eusocial	pl	1.22	2	1	0	0	1
Halictus subauratus (Rossi, 1792)	G	eusocial	pl	1.42	7	5	0	1	1
Halictus tumulorum (Linnaeus, 1758)	G	eusocial	pl	1.33	4	1	0	1	2
Heriades truncorum (Linnaeus, 1758)	A	solitary	ol	1.32	2	2	0	0	0
Hoplitis claviventris Thomson, 1872	A	solitary	pl	2.01	1	1	0	0	0
Hoplitis leucomelana (Kirby, 1802)	A	solitary	pl	1.43	3	1	0	1	1
Hoplitis tuberculata Nylander, 1848	A	solitary	pl	2.47	2	0	0	2	0
Hoplosmia spinulosa (Kirby, 1802)	A	solitary	ol	1.84	2	0	0	1	1
Hylaeus communis Nylander, 1852	A	solitary	pl	0.96	1	1	0	0	0
Hylaeus dilatatus (Kirby, 1802)	A	solitary	pl	1.20	1	0	0	0	1
Hylaeus intermedius Förster, 1871 ☼	A	solitary	pl	1.33	1	0	0	0	1
Hylaeus variegatus (Fabricius, 1798)	A	solitary	pl	1.37	1	0	0	1	0
Lasioglossum aeratum (Kirby, 1802)	G	eusocial	pl	0.98	2	2	0	0	0
Lasioglossum brevicorne (Schenck, 1870)	G	eusocial	ol	1.43	1	0	0	1	0
Lasioglossum calceatum (Scopoli, 1763)	G	eusocial	pl	1.74	5	4	0	0	1
Lasioglossum discum (Smith, 1853)	G	solitary	pl	2.33	2	2	0	0	0
Lasioglossum glabriusculum (Morawitz, 1872)	G	eusocial	pl	0.81	2	2	0	0	0
Lasioglossum griseolum (Morawitz, 1872)	G		pl	1.00	2	2	0	0	0
Lasioglossum interruptum (Panzer, 1798)	G	eusocial	pl	1.44	4	1	0	2	1
Lasioglossum laevigatum (Kirby, 1802)	G	solitary	pl	2.10	2	1	0	1	0
Lasioglossum laterale (Brullé, 1832)	G		pl	1.86	1	1	0	0	0
Lasioglossum lativentre (Schenk, 1853)	G	solitary	pl	1.38	6	4	0	2	0
Lasioglossum leucozonium (Schrank, 1781)	G	solitary	pl	1.72	3	1	0	2	0
Lasioglossum lineare (Schenk, 1869)	G	eusocial	pl	1.36	20	20	0	0	0
Lasioglossum malachurum (Kirby, 1802)	G	eusocial	pl	1.55	90	6	3	81	0
Lasioglossum marginatum (Brullé, 1832)	G	eusocial	pl	1.65	79	70	0	0	9
Lasioglossum mesosclerum (Perez, 1903)	G		pl	1.22	1	1	0	0	0
Lasioglossum minutissimum (Kirby, 1802)	G	solitary	pl	0.80	6	6	0	0	0
Lasioglossum morio (Fabricius, 1793)	G	eusocial	pl	1.02	9	0	0	5	4
Lasioglossum nigripes (Lepeletier, 1841)	G	eusocial	pl	1.94	1	1	0	0	0
Lasioglossum pauperatum (Brullé, 1832)	G		pl	1.08	2	0	1	1	0
Lasioglossum pauxillum (Schenck, 1853)	G	eusocial	pl	1.18	25	3	0	22	0
Lasioglossum punctatissimum (Schenck, 1853)	G	solitary	pl	1.19	2	0	0	2	0
Lasioglossum puncticolle (Morawitz, 1872)	G	eusocial	pl	1.53	1	0	0	1	0
Lasioglossum pygmaeum (Schenck, 1853)	G	solitary	pl	1.15	1	1	0	0	0
Lasioglossum quadrinotatum (Kirby, 1802)	G	solitary	pl	1.72	1	1	0	0	0
Lasioglossum villosulum (Kirby, 1802)	G	solitary	pl	1.18	11	0	1	10	0
Lasioglossum xanthopus (Kirby, 1802)	G	solitary	pl	2.21	3	3	0	0	0
Lasioglossum zonulum (Smith, 1848)	G	solitary	pl	1.87	6	0	0	1	5
Megachile centuncularis (Linnaeus, 1758)	A	solitary	pl	2.77	1	0	0	1	0
Melitta leporina (Panzer, 1799)	G	solitary	ol	2.20	1	1	0	0	0
Nomada agrestis Fabricius, 1787	P	parasitic	pl	2.74	1	0	1	0	0
Nomada basalis Herrich-Schäffer, 1839	P	parasitic	pl	1.86	1	0	0	0	1
Nomada discrepans Schmiedeknecht, 1882	P	parasitic	pl	1.08	4	0	4	0	0
Nomada flavoguttata (Kirby, 1802)	P	parasitic	pl	1.07	1	1	0	0	0
Osmia adunca (Panzer, 1798)	A	solitary	ol	2.40	1	0	0	1	0
Osmia aurulenta (Panzer, 1799)	A	solitary	pl	2.70	4	1	0	0	3
Osmia caerulescens (Linnaeus, 1758)	A	solitary	pl	2.22	4	4	0	0	0
Panurginus albopilosus (Lucas, 1846)	A	solitary	pl	0.89	13	0	13	0	0
Panurgus calcaratus (Scopoli, 1763)	G	eusocial	ol	1.66	1	1	0	0	0

Panurgus dentipes Latreille, 1811	G	solitary	ol	1.54	2	0	0	2	0
Rophites quinquespinosus Spinola, 1808	G	solitary	ol	2.13	1	0	0	0	1
Sphecodes albilabris (Fabricius, 1793)	P	parasitic	pl	1.82	1	0	0	0	1
Sphecodes ephippius (Linnaeus, 1767)	P	parasitic	pl	1.36	2	2	0	0	0
Sphecodes ferruginatus Hagens, 1882	P	parasitic	pl	1.59	1	1	0	0	0
Sphecodes gibbus (Linnaeus, 1758)	P	parasitic	pl	1.27	1	1	0	0	0
Sphecodes ruficrus (Erichson, 1835)	P	parasitic	pl	1.50	1	0	1	0	0
Sphecodes rufiventris (Panzer, 1798)	P	parasitic	pl	1.25	1	1	0	0	0
Sphecodes schenkii Hagens, 1882	P	parasitic	pl	1.47	1	0	0	0	1
Sphecodes sp.	P	parasitic	pl		4	4	0	0	0
Systropha curvicornis (Scopoli, 1770)	G	solitary	ol	1.97	14	14	0	0	0
Systropha planidens Giraud, 1861	G	solitary	ol	2.06	3	3	0	0	0
Total abundance					719	329	132	181	77
Total species richness					113	64	20	35	38

Nesting: A above-ground nesting; *G* ground nesting; *P* parasitic

Lecty: pl polylectic; *ol* oligolectic; *P* parasitic

ITD Inter-tegular distance from 1-5 specimen per country (averaged if >1 specimen present)

* *Bombus terrestris*: Includes field counts of *B. terrestris* and *B. lucorum* in AT

** *Halictus simplex*: Female specimen represent a species complex including *H. simplex*. *H. eurygnathus* and *H. langobardicus* because female identification features are ambiguous (Amiet et al. 2001). One male *H. langobardicus* was identified in RO and one *H. eurygnathus* was identified in FR.

☼ First record for a country

Table S2: Effect sizes (Estimate ± SE). p-values and model quality assessment (dispersion. R^2_{GLM}) of the most parsimonious models for wild bee diversity. abundance and characteristic traits in vineyards across Europe. The categories “very low” floral resource availability and country “AT” were used as baseline for parameter estimation of the categorical predictor variables.

Response variables	**Predictor variables**		**Estimate ± SE**	**p-value**	**Dispersion**	**R^2_{GLM}**
Species richness						
Total ~	Floral resources	“low”	0.590 ± 0.165	≤ 0.001	1.292	69.6 %
		“medium”	1.096 ± 0.187	≤ 0.001		
	Mean veg. cov. (%)		0.015 ± 0.003	≤ 0.001		
	SHDI		0.089 ± 0.219	0.683		
	Country	“ES”	-0.875 ± 0.225	≤ 0.001		
		“FR”	-0.459 ± 0.148	0.002		
		“RO”	-0.106 ± 0.203	0.601		
Eusocial ~	Floral resources	“low”	0.985 ± 0.266	≤ 0.001	0.884	67.8 %
		“medium”	1.438 ± 0.305	≤ 0.001		
	Mean veg. cov. (%)		0.013 ± 0.006	0.023		
	SHDI		0.341 ± 0.332	0.303		
	Country	“FR”	-0.172 ± 0.203	0.398		
		“RO”	-0.082 ± 0.318	0.796		
Solitary ~	Floral resources	“low”	0.437 ± 0.228	0.056	1.344	49.9 %
		“medium”	1.025 ± 0.257	≤ 0.001		
	Mean veg. cov. (%)		0.014 ± 0.004	0.001		
	SHDI		-0.175 ± 0.311	0.574		

	Country	“ES”	-0.423 ± 0.278	0.077		
		“FR”	-0.596 ± 0.225	0.008		
		“RO”	-0.054 ± 0.278	0.845		
Solitary ~	Mean veg. cov. (%) : Floral resources				3.351	47.0 %
		: “very low”	0.012 ± 0.005	0.009		
		: “low”	0.016 ± 0.005	≤ 0.001		
		: “medium”	0.023 ± 0.004	≤ 0.001		
	Country	“ES”	-0.239 ± 0.254	0.346		
		“FR”	-0.655 ± 0.222	0.003		
		“RO”	-0.023 ± 0.004	0.748		
Abundance						
Total ~	Mean veg. cov. (%) : Floral resources				5.481	63.4 %
		: “very low”	0.011 ± 0.002	≤ 0.001		
		: “low”	0.019 ± 0.002	≤ 0.001		
		: “medium”	0.028 ± 0.002	≤ 0.001		
	Country	“ES”	-0.072 ± 0.120	0.519		
		“FR”	-0.174 ± 0.093	0.067		
		“RO”	-0.264 ± 0.153	0.216		
Eusocial ~	Floral resources	“low”	-0.714 ± 1.271	0.574	3.351	73.9 %
		“medium”	3.831 ± 1.160	≤ 0.001		
	SHDI		0.683 ± 0.688	0.321		
	SHDI : Floral resources					
		: “low”	1.457 ± 0.799	0.068		
		: “medium”	-0.895 ± 0.728	0.219		
Solitary ~	Mean veg. cov. (%) : Floral resources				4.744	44.2 %
		: “very low”	0.013 ± 0.003	≤ 0.001		
		: “low”	0.016 ± 0.003	≤ 0.001		
		: “medium”	0.026 ± 0.003	≤ 0.001		
	Country	“ES”	0.766 ± 0.155	≤ 0.001		
		“FR”	-0.681 ± 0.182	≤ 0.001		
		“RO”	-0.034 ± 0.213	0.873		
Body size						
ITD (mm) ~	Country	“ES”	-0.491 ± 0.186	0.011	0.200	12.6 %
		“FR”	-0.272 ± 0.186	0.149		
		“RO”	-0.254 ± 0.178	0.159		
ITD (mm) ~	Intercept		1.866 ± 0.068	≤ 0.001	0.218	0.0 %
ITD (mm) ~	SHDI		0.292 ± 0.295	0.327	0.199	14.3 %
	Country	“ES”	-0.395 ± 0.209	0.066		
		“FR”	-0.274 ± 0.186	0.145		
		“RO”	-0.189 ± 0.189	0.323		
ITD (mm) ~	SHDI : Country				0.196	15.8 %
		: “AT”	0.378 ± 0.273	0.172		
		: “ES”	0.053 ± 0.351	0.879		
		: “FR”	0.206 ± 0.279	0.463		
		: “RO”	0.257 ± 0.320	0.426		

ITD Inter-tegular distance

SHDI Shannon Landscape Diversity Index

: Interaction of parameters

R^2_{GLM} Explained deviance = How much variation (%) of the response variable is explained by the predictor variable(s)

Appendix – Figures:

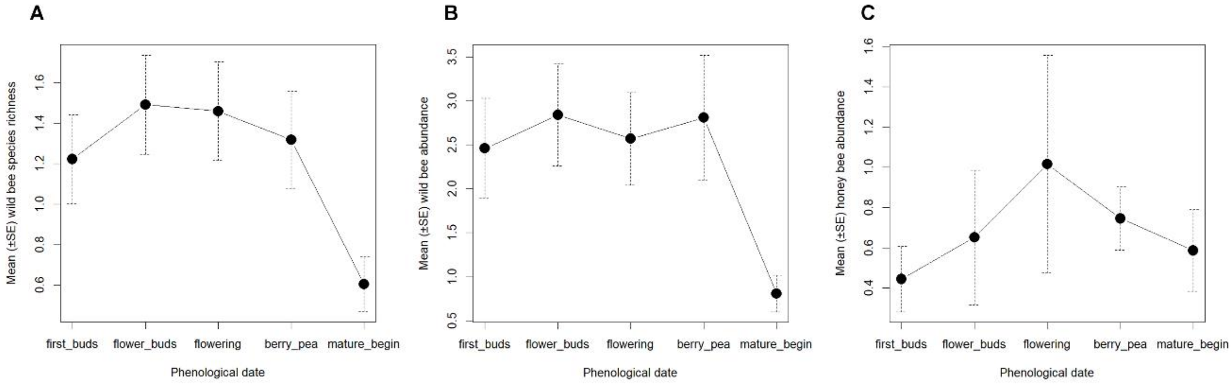

Fig. S1. Mean (±SE) wild bee species richness (a) abundance (b) and honey bee abundance (c) across sampling dates in vineyards that were synchronized to grapevine phenology

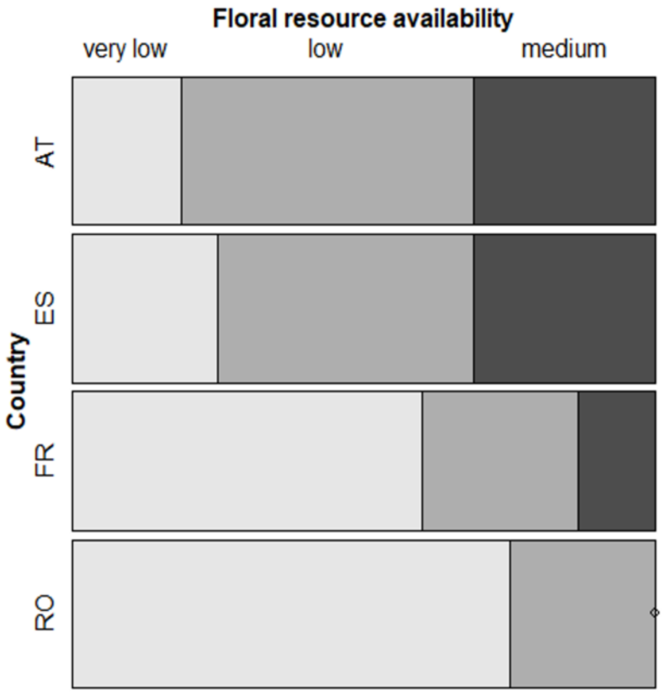

Fig. S2. Average floral resource availability in vineyard inter-rows in four European countries in 2016. The Mosaic plot (R package “vcd”, (Meyer et al. 2016)) visualizes the averaged (per inter-row) proportion of floral resource availability categories per country.

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Appendix III – Publication III: Winter et al. (2018) J Appl Ecol. 55 (5)

The appendices are very long and give extensive information about the methodologies used and datasets included in the meta analysis. This would be out of scope here and therefore these documents are not attached here, but can be downloaded online under:

https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2664.13124

Appendix IV – Publication IV: Kratschmer, Petrović et al. (resub.) Ecol Entomol.

Appendix Table 1. Percentages of each landscape structure in total per site and mean (± SD) per region

Region	Site (%)	Semi-Natural Elements	Agriculture	Green areas	Hedges and trees	Vineyard	Buildings	Wetland	Woodlots	Roads and gravel roads	Water entities	Artificial/ constructed areas
Urban	W1	0.0	0.0	29.5	0.0	0.0	25.3	0.0	0.0	32.8	4.2	8.2
Urban	W2	0.0	21.8	45.3	0.0	0.0	9.8	0.0	5.8	15.5	0.0	1.8
Urban	W3	0.0	0.0	14.8	0.0	0.0	44.6	0.0	0.0	32.7	0.0	7.9
Urban	W4	0.0	0.0	33.9	0.0	0.0	26.7	0.0	0.0	33.4	0.0	6.0
Village	L1	22.3	0.0	22.4	0.1	0.0	22.2	0.0	5.9	9.2	0.6	17.3
Village	L2	1.8	38.3	13.3	0.0	0.0	5.9	4.0	27.3	3.6	3.6	2.2
Village	L3	7.6	28.4	28.2	0.1	0.0	13.8	0.1	9.3	7.5	2.2	3.0
Village	L4	15.1	25.4	25.9	0.1	0.0	12.2	0.1	9.1	6.9	2.3	3.0
Agriculture	M1	2.4	58.1	14.6	0.1	0.0	8.5	0.0	1.7	7.0	4.4	3.1
Agriculture	M2	5.5	69.3	6.4	0.7	0.0	1.8	0.0	3.5	6.8	0.0	6.0
Agriculture	M3	3.0	91.3	0.3	0.7	0.0	0.1	0.0	2.0	2.3	0.0	0.3
Agriculture	M4	2.1	95.5	0.0	0.0	0.0	0.0	0.0	1.9	0.6	0.0	0.0
Viticulture	N1	35.4	5.7	1.5	2.1	20.0	0.3	0.0	33.1	1.8	0.0	0.1
Viticulture	N2	15.5	47.0	0.0	3.0	31.6	0.0	0.0	0.0	2.4	0.0	0.5
Viticulture	N3	11.4	5.4	6.2	1.3	19.1	0.9	0.0	52.8	2.8	0.0	0.1
Viticulture	N4	25.6	22.2	1.2	2.2	25.1	0.3	0.0	19.8	2.3	0.1	1.1
Urban		0.0±0.0	5.5±11	30.75±12.45	0.0±0.0	0.0±0.0	26.75±14.34	0.0±0.0	1.5±3	28.75±8.5	1±2	6±2.88
Village		11.75±8.65	22.75±16.15	22.25±6.65	0.0±0.0	0.0±0.0	13.5±6.61	1±2	12.75±9.6	6.75±2.06	2.25±1.26	6.2±7.18
Agriculture		3±1.41	78.25±17.69	5.25±7.08	0.5±0.58	0.0±0.0	2.25±4.27	0.0±0.0	2.5±1	4.25±3.2	1±2	2.25±2.87
Viticulture		22±10.68	20±19.62	2±2.71	2±0.82	24±5.94	0.25±0.5	0.0±0.0	26.5±22.28	2.25±0.5	0.0±0.0	0.25±0.5

Appendix Table 2. Distance matrix for trap nest sites in different land use regions. Green: Largest distance between sites within a region; Red: Smallest distance between sites within a region.

Reg.		Urban	Urban	Urban	Urban	Village	Village	Village	Village	Agriculture	Agriculture	Agriculture	Agriculture	Viticulture	Viticulture	Viticulture	Viticulture
	Site	W1	W2	W3	W4	L1	L2	L3	L4	M1	M2	M3	M4	N1	N2	N3	N4
Urban	W1	0	7267.7	6220.15	6717.36	45265.91	56008.18	55044.4	55237.69	12565.13	14129.15	14256.9	16844.27	39525.84	40852.65	38535.21	38882.6
	W2		0	8892.97	10269.08	38556.49	49253.7	48250.36	48442.79	12051.64	15660.72	15607.08	17168.38	33218.29	34840.02	32715.92	32852.78
	W3			0	1472.7	42633.12	53356.9	52482.28	52675.79	18259.75	20284.81	20392.09	22847.7	41980.11	43688.11	41596.64	41700.35
	W4				0	43850.97	54559.61	53699.26	53892.62	19099.4	20842.51	20973.63	23540.18	43412.06	45095.9	42984.93	43108.23
Village	L1					0	10751.99	9849.22	10042.71	46927.18	51574.72	51344.3	51205.71	34763.64	37934.87	38639.75	37060.8
	L2						0	1256.78	1125.54	57237.88	61901.94	61655.6	61333.17	41189.11	44198.94	45441.38	43720.17
	L3							0	193.68	56119.28	60784.74	60535.68	60185.78	39937.95	42951.19	44187.14	42466.97
	L4								0	56304.92	60970.49	60721.17	60368.18	40063.98	43073.41	44317.74	42595.83
Agriculture	M1									0	4667.01	4419.2	5131.77	31326.55	31868.56	29242.18	30027.26
	M2										0	381.21	3435.11	34919.49	35161.72	32452.91	33404.66
	M3											0	3108.22	34544.73	34782.15	32072.73	33026.19
	M4												0	32354.79	32392.24	29648.3	30697.26
Viticulture	N1													0	3194.47	4453.05	2653.89
	N2														0	2785.81	1987.76
	N3															0	1799.17
	N4																0

Note: Reg.= Region

Appendix Table 3. Pollen types or groups, attributed plant genera and number of different plant species associated according to Beug (2015) found in *Osmia cornuta* trap nests in four regions of different land use in eastern Austria. If only one plant species from a genera is associated it is fully stated.

Pollen type	Attributed plant genera or family
Acer	*Acer* spp. (6 species)
Aesculus hippocastanum-type	
Allium ursinum-type	*Allium* spp. (18 species)
Allium vineale-type	*Allium* spp. (6 species)
Ballota-type	Lamiaceae (5 genera)
Betula	*Betula* spp. (4 species)
Carpinus betulus	
Crepis-type	Asteraceae (13 genera)
Fagus	*Fagus* spp. (3 species)
Juglans	*Juglans* spp. (2 species)
Muscari	*Muscari* spp. (4 species)
Platanus orientalis	
Quercus	*Quercus* spp. (13 species)
Salix	*Salix* spp. (39 species)
Skimmia japonica	
Sorbus-group	Rosaceae (13 genera), Solanaceae (1 genus)
Pollentypes <1%	
Cannabinaceae	Cannabaceae (2 genera)
Primula veris-type	*Primula* spp. (4 species)
Viola tricolor-type	*Viola* spp. (8 species)

Appendix Table 4. Parameters estimated (± SE) from the most parsimonious models for pollen diversity and number of brood cells. The “urban” region was used as baseline for parameter estimation. Results of a power analysis (z-test) on the 50% effect size of each predictor based on 1000 simulations. C.I. = Confidence Interval

Response variables	Fixed factors	Estimate ± SE (effect size)	Random effect SD		Power analysis (z-test)	
			Trap nest ID (n=16)	Region (n=4)	50 % effect size	Power for predictor (95% C.I.)
Pollen diversity	Region:			-		
	“village”	0.015 ± 0.345	0.401		0.0075	11.60 % (9.68; 13.75)
(	“agriculture”	-1.656 ± 0.478			-0.85	70.80 % (67.87; 73.60)
	“viticulture”	0.026 ± 0.345			0.013	10.90 % (9.04; 13.00)
Pollen diversity	Green areas	0.039 ± 0.011	0.083	0.579	0.020	45.00 % (41.98; 48.14)
Pollen diversity	Agricultural areas	-0.023 ± 0.004	0.533	<0.001	-0.012	66.00 % (62.97; 68.94)
No. of brood cells	Agricultural areas	-0.017 ± 0.002	-	0.384	-0.0085	98.50 % (97.54; 99.16)

Appendix Table 5. Percentage of OTU (operational taxonomic unit) identified based on sequences produced by the trnL-F primers e and f and taxonomic name of nearest match (90%). We also added information if the matching taxa is expected to be found in the sampling sites (native) or not (non native). Percentage values were calculated using read numbers from taxa above 1% of reads. Portions below 1% were summarized. Results for each subsample are in the columns numbered 1 to 6. The results for all sequences for the same site combined are also present.

Unit	Origin	Viticulture region (n = 1)							Urban region (n=1)						
		1	2	3	4	5	6	Σ	1	2	3	4	5	6	Σ
Docyniopsis tschonoskii	non native	0,0	0,0	0,0	0.0	3.2	0.0	0.0	3.3	1.6	2.6	2.3	2.1	1.4	2.2
Malus sp.	native	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.5	2.5	6.9	5.1	4.2	2.3	5.0
Prunus avium	native	5.1	6.7	5.7	13.7	4.0	4.0	6.6	4.7	4.7	2.3	4.2	2.3	3.4	3.8
Prunus domestica	native	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.5	2.3
Prunus fordiana	non native	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	1.0	0.0	1.0	0.0	0.0	0.0
Prunus laurocerasus	native	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	2.5	1.8	1.5	2.1	1.5	1.8
Prunus sp.	-	4.5	6.0	4.1	6.9	3.5	2.2	4.5	48.8	61.0	59.7	47.4	58.1	39.1	51.2
Prunus undulata	non native	0.0	1.0	0.0	0.0	0.0	0.0	0.0	4.5	4.3	2.9	4.3	1.9	1.9	3.4
Prunus virginiana	non native	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	1.6	1.5	1.6	0.0	1.3
Pyrus sp.	native	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	1.3	1.9	2.0	1.3	1.0	1.7
Rosaceae sp.	native	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	1.6	1.1	2.2	0.0	1.3
Salix babylonica	non native	0.0	5.7	0.0	28.4	0.0	4.0	7.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Quercus sp.	native	81.4	61.6	81.6	43.8	70.8	37.6	60.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Abies sp.	native	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Acer cappadocicum	non native	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0
Acer franchetii	non native	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.4	1.2	0.0	0.0
Acer maximowiczianum	non native	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	2.2	0.0	1.4	1.1
Acer pseudoplatanus	native	0.0	0.0	0.0	0.0	2.1	0.0	0.0	4.5	1.5	6.2	0.0	7.3	0.0	2.9
Acer sp.	native	0.0	1.1	0.0	0.0	0.0	2.9	1.2	7.0	7.6	4.7	18.5	5.3	24.6	12.3
Fagus sp.	native	2.0	1.9	2.4	0.0	4.6	0.0	1.8	1.3	1.2	0.0	0.0	1.5	0.0	0.0
Allium ursinum	native	2.4	10.8	0.0	3.1	1.5	46.1	13.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<1% of the reads		4.6	5.2	6.2	4.1	8.0	3.3	5.0	8.7	9.3	6.8	7.5	9.0	9.9	9.8

Curriculum vitae

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Education

Sept. 2015 – present: 788 890 Doctoral Programme in Agriculture; Field of studies: Agriculture (UG 2002/16U) at the University of Natural Resources and Life Sciences, BOKU, Vienna
Thesis working title: Effects of vineyard inter-row management and landscape complexity on wild bees and associated ecosystem services.

May 2015: Master Sc., 033 427 Environment and Bio-Resources Management (UG2002/14U), field: Biodiversity/land use, BOKU, Vienna

August 2012: Bachelor Sc., 066 227 Environment and Bio-Resources Management (UG2002/11U), BOKU, Vienna

June 2005: High-school diploma, HLMW 9, School for Fashion Design and Clothing Techniques

Employment

Scientific research projects:

February 2019 – present: Project: „Urbane Biodiversität“ (Urban diversity on public transport areas in Vienna); Scientific project employee, Institute for Integrative Nature Conservation Research (INF), BOKU, Vienna. Function: Wild bee sampling, species identification, data analysis, publishing.

July 2017 – present: Project: “BINATS 2 BIodiversity NAture Safety – Erfassung der Biodiversität in österreichischen Ackerbaugebieten anhand der Indikatoren Landschaftsstruktur, Gefäßpflanze, Heuschrecken, Tagfalter und Wildbienen – 2. Erhebungsdurchgang”: Scientific project employee, Institute for Integrative Nature Conservation Research (INF), BOKU, Vienna. Function: Wild bee sampling, species identification, data analysis, publishing.

March 2015 – July 2017: Project: “VineDivers – Biodiversity-based ecosystem services in vineyards” (www.vinedivers.eu): Scientific project employee, Institute for Integrative Nature Conservation Research (INF), BOKU, Vienna. Function: Wild bee sampling, species identification, data analysis, publishing.

Contract for work:

March 2016 – present: Leading courses on bumblebee identification and expertise for bumblebee forum support (www.naturbeobachtung.at) for the project 2020 (Hofer AG and |naturschutzbund| partly in cooperation with BOKU).

May 2017 – Sept. 2018: Leading courses on pollinators and pollinator ecology for the Interreg-project "wild und kultiviert" in Salzburg (www.wildundkultiviert.at). Funding extension expected for 2019

Teaching:

October 2015 – present: Co-supervision of master thesis at the Institute for Integrative Nature Conservation Research (INF) BOKU, Vienna:

Gruchmann-Bernau, E (2019) Wildbienen-Diversität auf extensiven Solar-Gründächern („Wild bee diversity on extensive solar-green roofs").

Petrovic, B (2018) Pollenanalyse in unterschiedlichen Landschaften („Pollen analysis in different landscapes").

Kjaer, S (2018) Vergleich der Wildbienendiversität auf Hecken und Brachen in Weinbaulandschaften Ostösterreichs („Comparison of wild bee diversity in hedgerows and fallows in viticulture landscapes in Eastern Austria").

Schwantzer, M (2016) Wechselwirkungen zwischen Obstbäumen und Wildbienen in Weinbaulandschaften Ostösterreichs („Interaction between fruit trees and wild bees in viticulture landscape in Eastern Austria").

May 2015 – present: External teaching entrustment at the BOKU, Vienna for the Course VX 834119 "Naturschutzrelevante Lebensräume" ("Applied vegetation ecology"): Guiding 2-3 excursions per summer semester with 20 students focusing on urban ecosystems and habitats (excursion title: "Going Wild – City hike to habitats under and on the roofs of Vienna").

March 2019 – July 2019: External teaching entrustment at the BOKU, Vienna for the May
2016 – July 2016: Course VS 853327 "Naturschutzfachliche und kulturelle
Bedeutung von Weinbaulandschaften" („Nature conservation and cultural significance of vineyard landscapes"): Lecture, Co-Supervision of student projects. Leading excursions for EX 853328 "Nature conservation and cultural significance of vineyard landscapes"

Other employment:

June 2012 – June 2014: Freelancing and volunteering, GLOBAL 2000, environmental NGO, Austria.

Activities:

- Design and realization of the Green Concept for the GLOBAL 2000 Tomorrow Festival in 2013 and 2014

- Volunteer coordination

June 2010: Internship at the Municipal Department 22 – Environmental Protection in Vienna (MA 22).

Oct. 2005 – April 2008: Tailor for made to measure medical support bandages, Hanusch orthopaedic technic, Vienna.

Publications

Peer-reviewed publications in scientific journals

2019:

Kratschmer, S; Pachinger, B; Schwantzer, M; Paredes, D; Guzmán, G; Goméz, JA; Entrenas, JA; Guernion, M; Burel, F; Nicolai, A; Fertil, A; Popescu, D; Macavei, L; Hoble, A; Bunea, C; T; Kriechbaum, M; Zaller, JG; Winter, S (2019) Response of wild bee diversity, abundance, and functional traits to vineyard inter-row management intensity and landscape diversity across Europe. Ecology and Evolution 9 (7): 4103-4115. DOI: 10.1002/ece3.5039

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Fiera, C; Werner, U; Popescu, D; Buchholz, J; Querner, P; Bunea, C; Hoble, A; Strauss, P; Bauer, T; **Kratschmer, S**; Guernion, M; Winter, S; Zaller, JG (2019) Tillage intensity and herbicide application rather than landscapes structure affects surface active springtail communities in Romanian vineyards. (**in review**)

Lanner, J; **Kratschmer, S**; Petrovic, B; Gaulhofer, F; Meimberg, H; Pachinger, B (2019) City dewelling wild bees: How communal gardens promote species richness (**in review**)

2018:

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2017:

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, JG (2017) Soil biota in vineyards are more influenced by plants and soil quality than by tillage intensity or the surrounding landscape. *Scientific Reports, 7(1),* DOI: 10.1038/s41598-017-17601-w

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Ebmer AW; **Kratschmer, S;** Pachinger B (2019) *Lasioglossum* (*Evylaeus*) *pressithorax* Ebmer, 1974, (Hymenoptera: Apidae), eine sehr seltene ostmediterran-asiatische Halictidae, neu für Österreich und Mitteleuropa. Linzer biologische Beiträge. (**in review**)

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Popular scientific publications:

Kratschmer S, Pachinger B, Winter S (2018) Wildbienen im Weingarten. Wie wirken Bodenbearbeitung, Blütenangebot und Landschaftsstruktur? Der Winzer 11/2018: 20-21 (Populärwissenschaftlicher Beitrag)

Posters & Talks

2019:

Kratschmer, S; Ockermüller, E; Neumayer, J; Hainz-Renetzeder, C; Pascher, K; Pachinger, B (2019) Identifying landscape structures to enhance wild bee diversity in agricultural areas. IALE – World Congress2019 [Poster]

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2018:

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2017:

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2016:

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2015:

Kratschmer, S; Pachinger, B; Paredes, D; Guzmán, G; Nicolai, A; Favreau, M; Popescu, D; Bunea, C; Florian, T; Winter, S (2015) Effects of inter-row management intensity on wild bees in Austrian, Spanish, French and Romanian vineyards. Abstract Band der 108. Tagung der Deutschen Zoologischen Gesellschaft, 42. [Poster]

Kratschmer, S; Pachinger, B; Kriechbaum, M (2015) Summen auf den Dächern Wiens. Wildbienen (Apidae) auf begrünten Dachflächen und Möglichkeiten ihrer Förderung. Entomologica Austriaca 22, 113-114. [Poster]

The list only shows publications for scientific conferences as first author. Contributions to Talks & Posters are available in BOKU FIS-Forschungsinformationssystem: https://forschung.boku.ac.at/fis/suchen.person_publikationen?sprache_in=de&menue_id_n=102&id_in=146491

Thesis

Summen auf den Dächern Wiens. Wildbienen (Apidae) auf begrünten Dachflächen und Möglichkeiten ihrer Förderung (Buzzing on Vienna's roof tops. Wild bees (Apidae) on greenroofs and support opportunities). Master thesis, University of Natural Resources and Life Sciences, Vienna, Austria, May 2015.

Awards:

March 2019:	Preis der Österreichischen Entomologischen Gesellschaft (Price from the Austrian Entomological Society) for the publication: Kratschmer, S; et al. (2018) Tillage intensity or landscape features: What matters most for wild bee diversity in vineyards? Agriculture, Ecosystems and Environment 266: 142-152. DIO: https://doi.org/10.1016/j.agee.2018.07.018

November 2018: BOKU Best Paper Award for the publication: Kratschmer, S; Kriechbaum, M; Pachinger, B (2018) Buzzing on top: Linking wild bee diversity, abundance and traits with green roof qualities. Urban Ecosystems. DOI: 10.1007/s11252-017-0726-6

October 2016: Best Poster on Hymenoptera Meeting 2016 in Stuttgart (see Poster&Talks for details)

November 2015: Scientific promotion price 2015 for the master thesis (Summen auf den Dächern Wiens) awarded by Vienna's municipal department for environmental protection (MA 22)

April 2013: Award for the design and realization of a Green Festival in 2012, awarded by Green Events Austria

Interviews for newspaper articles, TV and radio shows:

Fischer, J (2019) Die Wildbienen aus dem Weingarten. In: Die Presse Wissen & Innovation am 06.April 2019. Available at: https://diepresse.com/home/science/5608157/Die-Wildbienen-aus-dem-Weingarten

Vom Leben der Natur (2019) Hummeln – Bienen im Pelz. Composed by: Renate Pliem. Vienna: Ö1. Broadcast from 23th to 26th April 2019. Available at: https://oe1.orf.at/programm/20190423/550348

Punkt eins (2018) Mut zur bunten Landschaft? Hosted by: Xaver Forthuber. Vienna: Ö1. Live broadcast on 27th March 2018. Available at: https://oe1.orf.at/programm/20180327/509464

Frühstückshonig – Neues vom Imker Franz (2016) Über die Lage der Hummeln in Österreich. Vienna: Radio Orange. Broadcast on 17th June 2016. Information under: https://o94.at/de/programm/sendung/id/1394743

Zurück zur Natur – Spezial (2015) Bienenland Österreich. Presented by: Maggie Entenfeller. Vienna: ORF2. Broadcast on 25th June 2015. Press release: https://www.ots.at/presseaussendung/OTS_20150624_OTS0163/zurueck-zur-natur-spezial-bienenland-oesterreich

Further education & courses:

04-09 March 2018: Participation as trainee at the European Bee Course in Malta (MCAST) COST Action: FA1307

Languages skills

German (mother tongue), English (very good), Spanish (very basic)