



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



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ARTICLE INFO

Keywords:

Apiformes
Vineyard
Tillage
Landscape
Floral resources
Ecosystem services

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 (\pm SD) of 29 (\pm 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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<https://doi.org/10.1016/j.agee.2018.07.018>

Received 2 November 2017; Received in revised form 14 July 2018; Accepted 24 July 2018

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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 (Connolly 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 m² 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 m² 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; Gokcezaade 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-tetragonal distance (ITD) of 1–5 individuals per species according to Cane (1987)

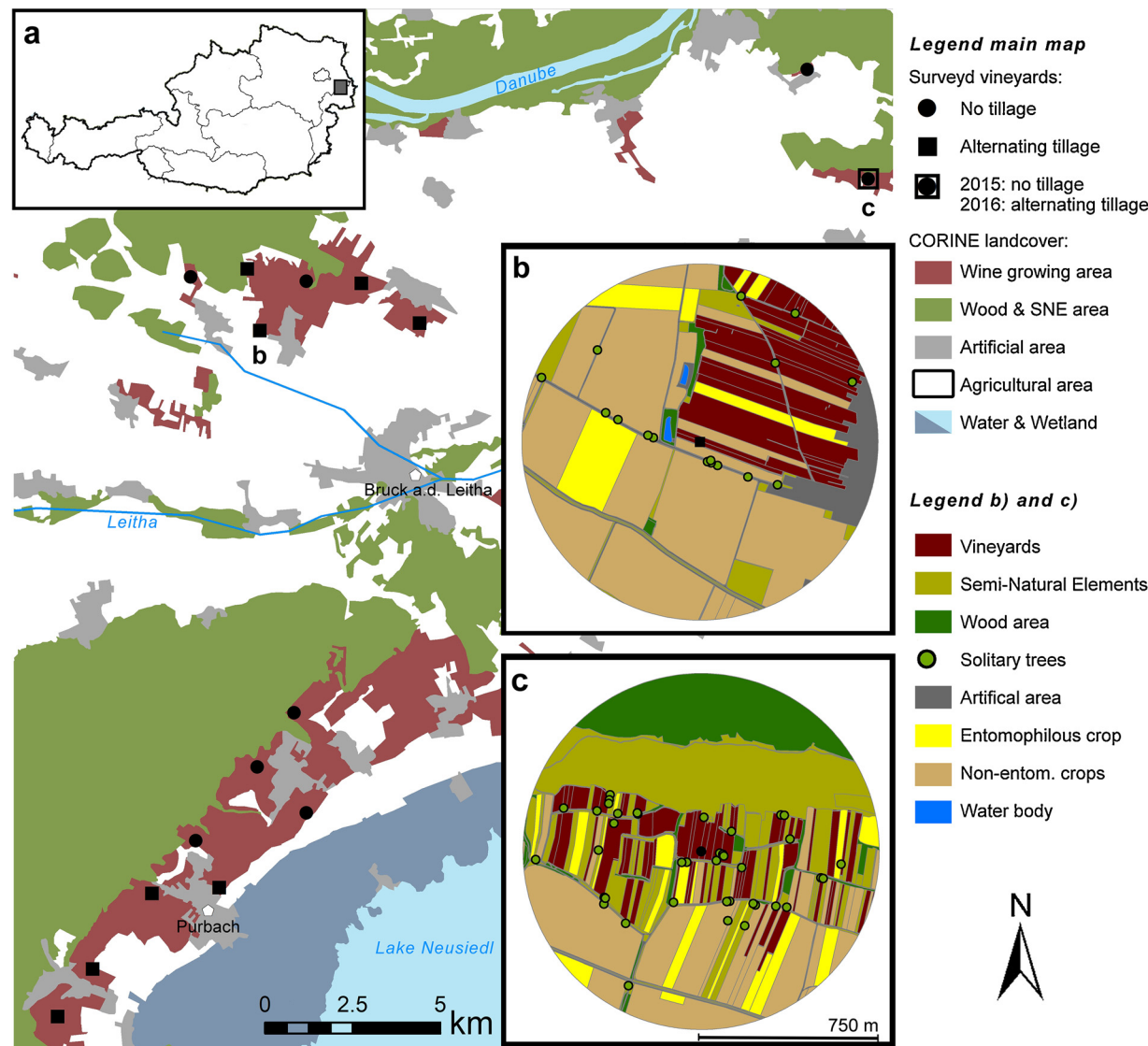


Fig. 1. Location of study area in (a) Eastern Austria in the viticultural areas Carnuntum (north of the Leitha) and Neusiedlersee-Hügelland (south of the Leitha river). Main map with locations of the studied vineyards including respective tillage regime, expansion of wine growing-, wood-, SNE-, artificial-, 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. <i>Bombus</i> spp.)	
	Parasitic	♀ lay their eggs in nests of specific host species	
Sociality	Solitary	♀ nests and breeds alone	Less efficient pollinators (Garibaldi et al., 2015) but indicates vital host populations (Hudson et al., 2006)
	Eusocial	♀ nesting and breeding in colonies (unfertile workers and fertile females)	
ITD (mm)	Continuous	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

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

K Number of estimated parameters.

AICc Second order Akaike Information Criterion.

$\Delta AICc$ Difference between AICc to the next most parsimonious model.

ω_i Akaike's weight.

LL Laplace Likelihood.

R²m R²marginal.

R²c R²conditional.

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 $\text{cor} \geq 0.3$. 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 ($\text{cor} = 0.66$, $P < 0.001$) of these parameters. Overall (mean \pm 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 (\pm SD) CWM of inter-tetragonal-distance was $2.13 (\pm 0.37)$ mm and was significantly associated with untilled vineyards (Random permutation test; $P = 0.016$). On the landscape scale, the ITD increased with the

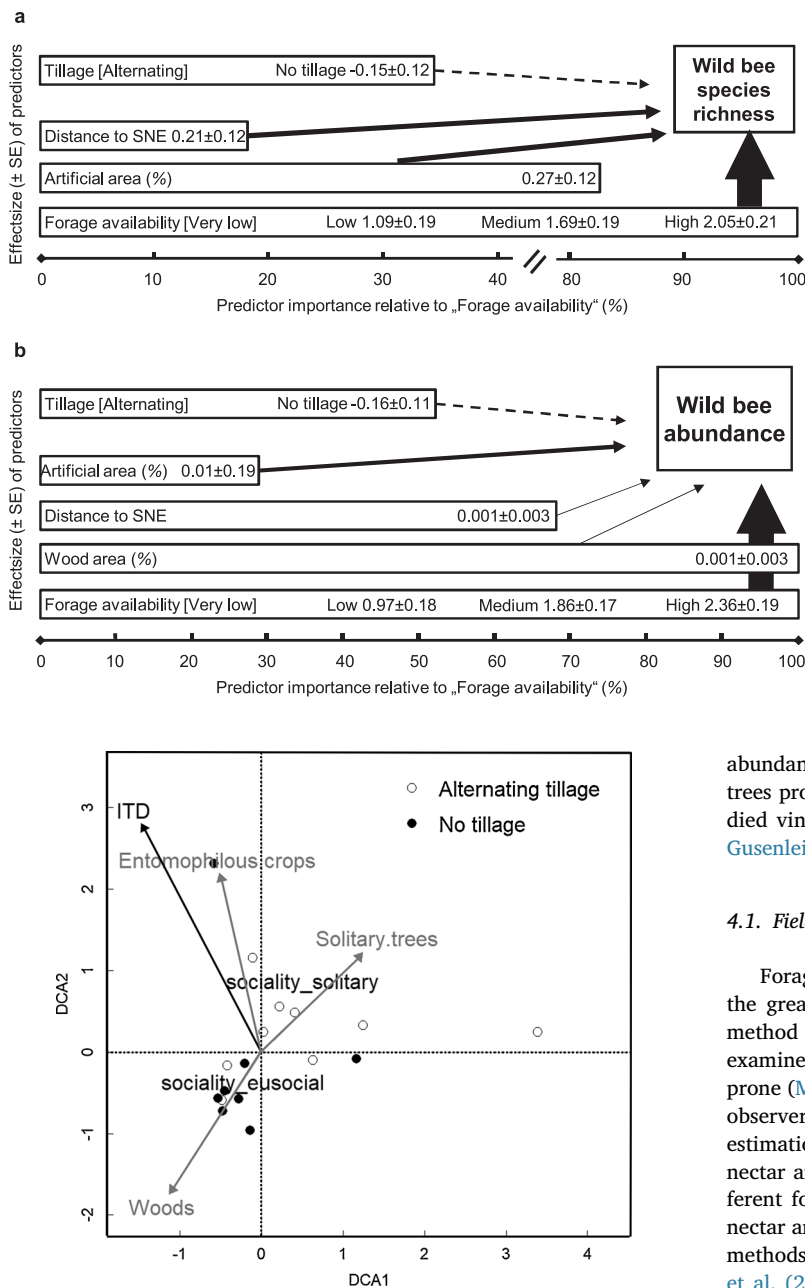


Fig. 2. Parameters affecting (a) wild bee species richness and (b) wild bee abundance in Austrian vineyards derived from model averaging including effect size (estimate values \pm SE). Bar length = relative importance of a predictor in relation to the most important predictor (forage availability); full 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-tetragonal 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 Gusenleimer 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 Szegedy 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

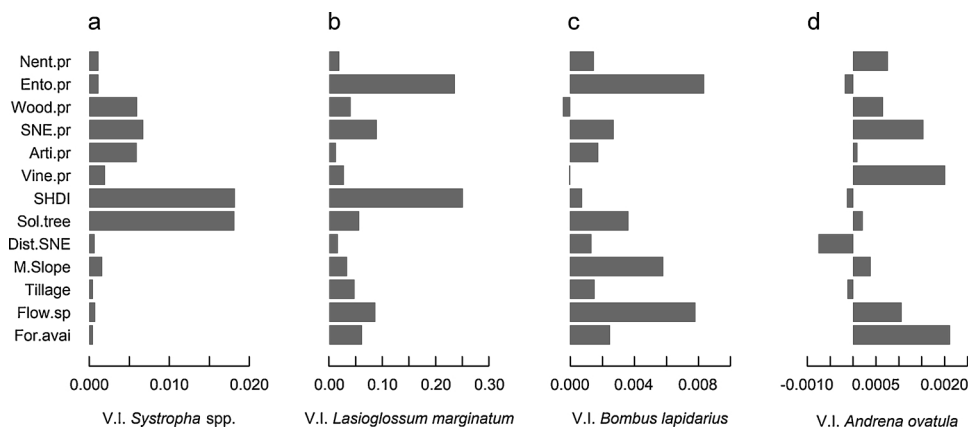


Fig. 4. Conditional variable importance (V.I.) of field (forage availability (For.avai), entomophilous plant species richness (Flow.sp), tillage regime (Tillage)) and landscape parameters (mean slope (M.slope), distance to SNE (Dist.SNE), number of solitary tree (Sol.tree), Shannon Landscape Diversity 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-entomophilous 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.

Acknowledgements

This research is part of the BiodivERsA project VineDivers (www.vinedivers.eu) and was funded through the BiodivERsA/FACCE JPI (2013–2014 joint call) for research proposals, with the national funders: Austrian Science Fund (grant number I 2044-B25FWF), French National Research Agency (ANR), Spanish Ministry of Economy and Competitiveness (MINECO), Romanian Executive Agency for Higher Education, Research, Development and Innovation Funding (UEFISCDI) and Federal Ministry of Education and Research (BMBF/Germany). The open access funding was provided by the Austrian Science Fund: I 2044-B25. We are grateful to Johann Grassl and to the winegrowers in the Neusiedlersee-Hügelland and Carnuntum region for allowing us to study their vineyards. Thanks to Andreas W.P. Ebmer and Karl Mazzucco for help with wild bee identification. Further, we thank Naroa Barea Aranzabe for measuring ITD, Martin Wittner for help with wild bee preparation, David Horner for proof reading and Michael

Melcher (IASC, BOKU Vienna) for his support with Random Forest analysis. Last, but not least we thank the Reviewers and the Editor for their help to improve this manuscript.

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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