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Wild bee and floral diversity co-vary in response to the direct and indirect impacts of land use

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Abstract. Loss of habitat area and diversity poses a threat to communities of wild pollinators and flowering plants in agricultural landscapes. Pollinators, such as wild bees, and insect-pollinated plants are two groups of organisms that closely interact. Nevertheless, it is still not clear how species richness and functional diversity, in terms of pollination-relevant traits, of these two groups influence each other and how they respond to land use change. In the present study, we used data from 24 agricultural landscapes in seven European countries to investigate the effect of landscape composition and habitat richness on species richness and functional diversity of wild bees and insect-pollinated plants. We characterized the relationships between the diversity of bees and flowering plants and identified indirect effects of landscape on bees and plants mediated by these relationships. We found that increasing cover of arable land negatively affected flowering plant species richness, while increasing habitat richness positively affected the species richness and functional diversity of bees. In contrast, the functional diversity of insect-pollinated plants (when corrected for species richness) was unaffected by landscape composition, and habitat richness showed little relation to bee functional diversity. We additionally found that bee species richness positively affected plant species richness and that bee functional diversity was positively affected by both species richness and functional diversity of plants. The relationships between flowering plant and bee diversity were modulated by indirect effects of landscape characteristics on the biotic communities. In conclusion, our findings demonstrate that landscape properties affect plant and bee communities in both direct and indirect ways. The interconnection between the diversities of wild bees and insect-pollinated plants increases the risk for parallel declines, extinctions, and functional depletion. Our study highlights the necessity of considering the interplay between interacting species groups when assessing the response of entire communities to land use changes.

Key words: arable land cover; flowering plants; functional diversity; habitat richness; land use; piecewise structural equation models; pollination; species richness; wild bees.

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INTRODUCTION

Land cover change is a major threat to biodiversity and ecosystems leading to changes in species richness, abundance, and composition (Sala et al. 2000, Millennium Ecosystem Assessment 2005, Newbold et al. 2015). Species diversity is commonly linked to ecosystem processes such as long-term resilience of ecosystem services (Oliver et al. 2015), and its loss due to intensified land use can impair ecosystem functioning (Allan et al. 2015). Additionally, diversity at multiple trophic levels can support the maintenance of ecosystem services with impacts comparable to those of abiotic factors (Soliveres et al. 2016).

Animal-mediated pollination is one of the ecosystem services with high economic interest (Gallai et al. 2009, Lautenbach et al. 2012, Klatt et al. 2014) which is strongly affected by changes in land use (Weiner et al. 2014). Almost 90% of flowering plants in wild communities and crops depend, at least to some extent, on animal-mediated pollination (Ollerton et al. 2011), and plant reproductive success benefits from diverse communities of pollinators (Albrecht et al. 2012). Several species from different taxa contribute to pollination (Rader et al. 2016), but bees are considered the principal groups of pollinators for both wild and crop plants (Potts et al. 2016). As a consequence, recent declines in bee diversity observed at large geographic extent (Biesmeijer et al. 2006, Kerr et al. 2015) increase the potential for negative impacts on pollination.

Habitat loss and degradation, following agricultural intensification, have a negative impact on the diversity of pollinators and flowering plants in agricultural landscapes (Firbank et al. 2008, Stoate et al. 2009, Potts et al. 2016). By contrast, agricultural landscapes with a large number of different habitats provide a wide range of resources and promote more diverse communities of pollinators and insect-pollinated plants (Billeter et al. 2008). Therefore, habitat diversity promotes higher bee species richness (Aguirre-Gutiérrez et al. 2015). Increasing distance from semi-natural areas has been found to decrease species richness and abundance of several pollinator groups (Krewenka et al. 2011, Ekroos et al. 2013) and the visitation rate and reproductive output of commercial crops (Ricketts et al. 2008, Garibaldi et al. 2011). Additionally, decreasing cover of semi-natural areas leads to declines in wild bee species richness and abundance (Steffan-Dewenter et al. 2002, Le Féon et al. 2010, Papanikolaou et al. 2017) and to reduced wild bee visitation rates and fruit set of different crops (e.g., Holzschuh et al. 2012, Klein et al. 2012). Although less is known regarding the effect of semi-natural areas on native plant diversity and pollination success, increased cover of semi-natural habitats has been shown to be associated with higher plant species richness (Billeter et al. 2008) and increased visitation rates of native plants (Steffan-Dewenter et al. 2001), while increasing proximity to semi-natural areas has been found to increase seed production of native plants (Schmucki and de Blois 2009, Jakobsson and Agren 2014) with potential positive effects on wild plant communities.

Recent studies demonstrate that pollinator species richness alone is not the determining factor for pollination success (Kleijn et al. 2015, Winfree et al. 2015), since not all potential pollinators contribute equally to pollination (Kwak et al. 1998). According to other studies, functional diversity seems to play a key role; increasing functional diversity of bee communities has been found to increase seed production of crops (Hoehn et al. 2008, Martins et al. 2015) and wild plants (Fründ et al. 2013), highlighting the importance of functional complementarity. In any case, the presence of, and vicinity to, semi-natural habitats seems to benefit wild bee functional diversity (Martins et al. 2015, Geslin et al. 2016), while high diversity of land cover types in the landscape can reduce functional homogenization of communities (Gamez-Virues et al. 2015). However, species richness and functional diversity of wild bees have also been shown to respond differentially to land use (Forrest et al. 2015).

Previous studies have established a relationship between the diversity of plant and pollinator communities (e.g., Potts et al. 2003). In an experimental study, Ebeling et al. (2008) demonstrated a positive effect of plant species richness on species richness of bumble bees, solitary bees, and other pollinators. Furthermore, bee diversity was found to increase with higher plant diversity in meadows (Fründ et al. 2010) and apple orchards (Rosa García and Miñarro 2014). Additionally, functional diversity of both plants and pollinators seems to benefit plant recruitment, promoting the persistence of plant communities

(Fontaine et al. 2006). Such relationships indicate that changes in plant and pollinator communities could be interconnected. In fact, Biesmeijer et al. (2006) found parallel declines of bees and insect-pollinated plants in Britain and The Netherlands, while Weiner et al. (2014) demonstrated that the effects of land use on plant–pollinator networks are accelerated by the mutual dependence of plants and pollinators that results in interdependent losses.

Plant–pollinator networks usually have more animal than plant species, and an assumed higher level of functional redundancy in the bee community makes the networks better buffered against bee than plant extinction (Memmott et al. 2004, Schleuning et al. 2016). In addition to the often observed redundancy of pollinators (Schleuning et al. 2015), the development of alternative regeneration methods such as clonal propagation, self-pollination, and soil seed bank (Brodie et al. 2014) may reduce the level of dependence of plants on pollinators. Based on the above, the relationship between plants and wild bees seems more likely to be bottom-up (i.e., from plants to bees) instead of top-down.

In the present study, we focus on the effect of landscape composition on species richness and functional diversity of insect-pollinated plants and wild bees. Additionally, we investigate the relationship between wild flowering plant and wild bee diversity and expect that bee diversity depends on plant diversity rather than vice versa. Taking into account the interdependence of flowering plants and their pollinators, we expect that landscape composition and habitat diversity have both direct and indirect effects on plant and bee diversity; that is, changes in plant diversity caused by altered landscape properties (direct effect) may subsequently cause changes in bee diversity (indirect effect) or the other way around.

MATERIALS AND METHODS

Study sites

Twenty-four study sites in agricultural landscapes distributed over seven European countries originally being part of the EU FP5 project GREENVEINS were selected for our analysis: Belgium (four sites), Czech Republic (two), Estonia (four), France (three), Germany (four), The Netherlands (four), and Switzerland (three). The sites measured 4×4 km^2 each and covered a large gradient in landscape composition and structure, that is, ranging from 43 to 96% arable land and from 18 to 34 distinct habitat types (Bailey et al. 2007, Billeter et al. 2008).

Digitized habitat maps derived from aerial photographs and updated by field observations were used to obtain landscape metrics. The percentage cover of arable land per site was calculated to assess landscape composition, while the number of European Nature Information System (EUNIS) habitats (http://eunis.eea.europa.eu) was used as a proxy of habitat richness. We used a modified EUNIS classification scheme which allowed us to measure and classify linear elements such as grassy field or road margins, hedgerows, or lines of trees in addition to the usually patchy elements (Appendix S1). Although there might be some systematic differences in the use of arable land, we consider arable land to be more comparable among countries than semi-natural habitat types (e.g., grassland). Thus, we have chosen arable land cover instead of semi-natural habitat cover to improve consistency.

Biodiversity sampling

The plant data were collected based on a stratified random sampling scheme. Between 79 and 314 plots of 2×2 m^2 were sampled per site, with a constant ratio of 1:4:5 among plots distributed in agricultural, patches of semi-natural, and linear semi-natural elements across all sites (for classification, see Appendix S1). The average percentage cover of each plant species within all plots of the same site was used as a proxy for abundance. Only plant species specified as insect-pollinated in the TRY database (Durka 2002, Poschlod et al. 2003, Diaz et al. 2004, Kühn et al. 2004, Green 2009, Kattge et al. 2011) were considered in the analyses (plant species list in Appendix S2). TRY is a global database of plant traits (morphological, anatomical, biochemical, physiological, phenological) comprising more than 250 datasets (www.try-db.org).

Flight traps combining the properties of window and yellow pan traps (Duelli et al. 1999) were used for wild bee sampling. Each study site was divided into 16 squares of 1 km^2, and a trap set, comprising two combined flight traps located between 25 and 50 m apart from each other, was placed within each square at a randomly chosen transition zone between a semi-natural habitat and an agricultural field. Therefore, 32 combined flight traps, grouped into 16 trap sets, were installed per site. To minimize sampling and identification effort while maximizing efficiency, we adopted a rapid biodiversity assessment protocol suggested by Duelli (1997). Taking into account the differences in climatic conditions and, thus, phenological properties among countries, the full bloom of *Taraxacum officinale* Wiggers was used as a reference point to initiate sampling at two periods. The first part of the sampling took place in late summer 2001 starting 15 weeks after the full bloom of *T. officinale*, and the second part took place in spring 2002 at full bloom. Over all countries, the traps were kept open for seven weeks in late summer and five weeks in spring and emptied weekly. To account for differences in weather conditions among the sites during the sampling periods, only the samples with most specimens were retained in the analyses, namely four weeks in autumn and three weeks in spring. The samples of each trap set were merged, and the specimens were identified to the species level (bee species list in Appendix S3).

Biodiversity metrics

Two metrics of diversity were assessed at the site level: species richness and abundance-weighted functional diversity.

Species richness was calculated as the total number of species found in a site across all samples, corrected with rarefaction curves (Chao et al. 2014), as the number of vegetation plots surveyed and trapped bee specimens was quite different among the countries. For flowering plants, percentage cover was translated to presence/absence data per plot and plot-based rarefaction curves were generated. We used a threshold of three times the smallest number of plots per site to cut or extrapolate the rarefaction curves (Colwell et al. 2004). For richness estimates of bee communities, we used abundance-based rarefaction based on accumulated specimen numbers per site. Here, we also truncated or extrapolated rarefaction curves at a threshold of three times the smallest number of overall bee abundance per site.

To calculate functional diversity, nine pollination-related traits were derived from the TRY database (Kattge et al. 2011) for flowering plants (Table 1a) and six relevant traits were obtained from a database hosted at the University of Reading for wild bees (Table 1b).

In total, we obtained trait data for 673 flowering plant (out of 1321 species in total, only 673 were insect-pollinated according to the TRY database) and all 181 bee species occurring at our study sites. However, not all traits were available for the mentioned species with the problem being especially pronounced for plants. In order to deal with the issue, we first excluded species lacking information about more than half of the selected traits and we then imputed the missing trait values for the remaining species, before quantifying functional diversity based on the imputed dataset. Following this approach, we excluded all plant species with missing values for at least four traits, retaining 603 out of 673 species. The 70 excluded species belonged in 29 (out of 71) families and no taxonomic bias was detected. Next, the missing data were imputed using a regularized iterative principal component analysis (PCA) algorithm (Josse and Husson 2012). We first attributed the mean value of each variable to the missing values of the variable and then performed a PCA on the complete dataset. Using cross-validation criteria, we specified the number of components to be retained. Finally, the missing values were imputed with the fitted matrix of the regularized scores and loadings of the PCA. The procedure was performed with the functions estim_ncpPCA and imputePCA from the R package missMDA (Josse and Husson 2016). For the sake of consistency, we repeated the same procedure for the bee trait data, although only few values were missing and no bee species had to be excluded from the analysis.

A PCA was then performed on the completed datasets. The factor loadings of all axes cumulatively explaining 70% of the data variation were retained for the calculation of functional diversity, namely 13 axes for plants and 7 for bees. Functional diversity was calculated as abundance-weighted Rao’s quadratic entropy, that is, Rao’s Q (Botta-Dukát 2005, Laliberté and Legendre 2010).

Abundance-weighted functional diversity is often confounded by species richness and abundance. In order to obtain an unbiased metric, we applied a null model approach (Gotelli and Graves 1996) and relied on the standardized effect size (Gotelli and McCabe 2002). In particular, we

Table 1. Description of the functional traits used in this study for calculation of functional diversity.

Trait	Description	References
(a)		
UV light reflectance of flower center	Percentage	1, 2
UV light reflectance of flower periphery	Percentage	1, 2
UV reflectance pattern	Presence/absence	1, 2
Flower color	Four categories: blue-violet, red-pink, white-green, yellow-orange	1, 2, 3
Flower type	Eleven categories: bell-shaped flowers, brush flowers, disk flowers, ray flowers, ray and disk flowers, flag blossom, flower heads, funnel flowers, lip flowers, pollen flowers, spike flowers	1, 2
Nectar availability	Five categories: no nectar, open nectar, partly hidden nectar, totally hidden nectar, nectar present with no information about accessibility	1, 2
Self-compatibility	Self-compatible/self-incompatible	1, 2
Insemination	Three categories: allogamous, autogamous, mixed mating	1, 2
Sex timing	Three categories: homogamous, protandrous, protogynous	1, 2
(b)		
Sociality	Five categories: solitary, communal, primitively eusocial, cleptoparasite, social parasite	–
Pollen transfer to nest	Five categories: legs, legs and body, underside of abdomen, crop, accidental transfer only	–
Lecty	Two categories: oligolectic, polylectic	–
Preferred flower morphology	Three categories: open, restricted, open and restricted access to nectar or pollen	–
Activity period	Overall expected presence/absence as dummy-coded variable for each month from March till October	–
Body size	Intertegular distance (mm)	–

Notes: (a) Traits related to pollination derived from the TRY database (Kattge et al. 2011) for 673 insect-pollinated plants. (b) Traits for 181 wild bees derived from a database hosted at the University of Reading and updated ITD measures by Michael Kuhlmann. References for TRY data: (1) Kühn et al. (2004); (2) Durka (2002); and (3) Green (2009).

kept the number of species and abundances the same as that observed in the real assemblages but randomized the trait associations by drawing from the entire species pool while conserving the observed trait co-variance, that is, by reshuffling the species in the species–trait matrix. This model assumes that the occurrence and abundance of the species is independent of their traits. Based on 999 repetitions of this procedure, we recalculated Rao's Q and obtained the standardized effect size of functional diversity (from now on richness-corrected FD) by subtracting the mean randomized Rao's Q from the observed one and dividing the resulting number by the standard deviation of the randomized Rao's Q. All further analyses presented here focus on the richness-corrected functional diversity (from now on FD). Additional analyses on the uncorrected functional diversity metrics are presented in Appendix S4.

Data analysis

First, we wanted to identify the biotic and abiotic variables affecting each biodiversity metric. To this end, we developed a linear mixed-effects model for each biodiversity metric. The landscape metrics habitat richness and percentage cover of arable land were included as fixed effects in all models and country was specified as random effect to control for systematic differences (e.g., different climate, different preferences in crop selection). In a preliminary analysis, we also included nitrogen input (associated with soil fertility) and climate variables (i.e., temperature and precipitation that could potentially be used to assess soil humidity), but none of these variables explained the observed patterns of our biodiversity metrics. Additionally, bee biodiversity metrics (bee species richness, bee FD) were included as predictors to the models fitted to plant metrics (plant species richness, plant FD) and vice versa. All variables were standardized to zero mean and unit standard deviation to obtain comparable coefficient estimates (Quinn and Keough 2002). Additionally, all explanatory variables were tested for collinearity by estimating pairwise Pearson's correlation coefficient and checking whether its absolute value exceeds the commonly used threshold of 0.7 (Dormann et al. 2013). No pair demonstrated such a high correlation value.

Subsequently, we followed a multi-model inference approach (Burnham and Anderson 2002) to identify relevant predictors for each metric. For each one of the four global models, all candidate models were developed and compared in terms of the second-order Akaike Information Criterion corrected for sample size (AICc). The best model was defined as the one with the lowest AICc value, and the remaining models were compared to it based on their difference in AICc value (δAICc). All models with a δAICc lower than 2 were considered equivalent to the best model, and the explanatory variables included in the set of equivalent models were seen as the most important factors affecting the modeled metric in each case.

The outcome of the multi-model inference was used to construct a piecewise structural equation model (piecewise SEM). In the context of piecewise SEMs, paths are first estimated in individual models and then assembled to the full SEM (Shipley 2000). Fisher's C statistic was used for evaluating the fit of piecewise SEM (Shipley 2009). The statistic is calculated based on the significance of all missing paths, and a X^2 test on it determines whether the model has a good fit (the model is not rejected when $P > 0.05$). Direct and indirect effects can be specified in piecewise SEMs. The strength of a direct effect is equivalent to the coefficient estimate of the link connecting the two variables, while the strength of an indirect effect is calculated by multiplying the coefficient estimates of all the relationships included in the path connecting the two variables. The total effect of one variable on another can be specified by adding up the direct effect and the indirect effects obtained by all paths between them.

We constructed the piecewise SEM based on the multi-model inference. When the direction of an arrow could not be clearly deduced from the multi-model inference results, separate SEMs were created changing only the arrow direction and were then compared using Fisher's C and AIC.

Results

Direct effects of landscape on the diversity of bees and insect-pollinated plants

The percentage of arable land directly negatively affected only plant species richness (Table 2a), while habitat richness had a positive

Table 2. Selected models for each biodiversity variable.

Variable	Intercept	Percentage arable	Habitat richness	Bee/plant species richness	Bee/plant functional diversity	AICc	δAICc	Weight
(a) Plant species richness	172.40	−1.37		1.79 (bee)		213.25	0.00	0.63
(b) Bee species richness	9.10	–	–	0.20 (plant)		166.15	0.00	0.34
	0.47	–	0.74	0.13 (plant)		166.85	0.70	0.24
(c) Bee functional diversity	−2.07		0.04			32.88	0.00	0.23
	−1.02					33.00	0.12	0.22
	−1.67			0.004 (plant)		34.22	1.34	0.12
	−0.89				0.19 (plant)	34.86	1.98	0.09
(d) Plant functional diversity	−0.70					33.31	0.00	0.36
	−0.49				0.20 (bee)	35.10	1.80	0.15

Notes: Eight global models were built and a multi-model inference approach was followed to compare all submodels and select those that provided the best fit. The selection threshold in all cases was δAICc < 2. Two landscape variables (habitat richness and percentage cover of arable land) were included as fixed effects in all the global models. (a) Flowering plant species richness modeled with landscape, bee species richness, and bee functional diversity; (b) Bee species richness modeled with landscape, plant species richness, and flowering plant functional diversity; (c) Bee functional diversity modeled with landscape, plant species richness, and plant functional diversity; and (d) Plant functional diversity modeled with landscape, bee species richness, and bee functional diversity.

effect on bee diversity (bee species richness: Table 2b; bee FD: Table 2c). On the contrary, plant FD was not affected by either of the landscape variables (Table 2d).

It is noteworthy that the intercept-only model occasionally ranked high in the model selection procedure (best and second-best for plant and bee functional diversity, respectively), indicating that the selected direct effects are probably not very strong in those cases. However, all the global models satisfactorily fit the data. The data variance explained by the models (conditional R^2) was 80% in the case of plant species richness, 88% for bee species richness, 70% for plant FD, and 30% for bee FD. The fixed effects explained 80%, 31%, 9%, and 17% (marginal R^2), respectively.

Interdependencies of flowering plant and bee diversity aspects

Our results indicate strong positive relationships between bee and flowering plant diversity. Plant and bee species richness were strongly interconnected (Table 2a, b). The version of the piecewise SEM that included an arrow pointing from bee species richness toward plant species richness (version 2) provided better fit than the version with an arrow to the opposite direction (Table 3). Additionally, bee FD was positively affected by increasing plant species richness (Table 2c).

Bee FD and plant FD were also related (Table 2c, d). In that case, when comparing piecewise SEMs to decide on the directionality of the relationship, it is evident that the model versions 1 and 2 with the relationship directed from plant FD to bee FD performed much better than the other two, with version 2 (arrow from bee species richness to plant species richness) being the best (Table 3). Thus, bee FD was found to depend on plant FD.

Indirect effects of landscape on the diversity of bees and insect-pollinated plants

The interdependence between bee and flowering plant diversity resulted in indirect effects of the landscape on both species groups (Figs. 1, 2). The indirect effects and their strengths differed among the model versions (Table 4).

All the models included a negative indirect effect of percentage of arable land on bee FD mediated by plant species richness. The version with the best fit (version 2) indicated positive indirect effects of habitat richness on plant species richness mediated by bee species richness and on bee FD mediated by plant and bee species richness.

Discussion

We found strong relationships between insect-pollinated plant and wild bee diversity; there are indications for both bottom-up and top-down effects, contrary to our expectations that the effect of flowering plants on bees would be more pronounced than vice versa. Overall, we found not only direct effects of landscape structure on wild bees and insect-pollinated plants but also indirect ones, resulting from the interdependence of these two groups.

Table 3. Fit evaluation for the different versions of the piecewise structural equation model (SEM).

Version	Arrow direction	Fisher's C	P	AICc
1	Plant species richness → Bee species richness Plant functional diversity → Bee functional diversity	10.24	0.60	100.24
2	Bee species richness → Plant species richness Plant functional diversity → Bee functional diversity	6.33	0.90	96.33
3	Plant species richness → Bee species richness Bee functional diversity → Plant functional diversity	11.37	0.79	184.17
4	Bee species richness → Plant species richness Bee functional diversity → Plant functional diversity	8.49	0.93	181.29

Notes: The relationships in the SEM were specified based on the results of the multi-model inference. When the directionality of the relationship was unclear, two different versions of the SEM were created by changing the direction of the relationship in question while keeping everything else unchanged. The different versions were subsequently compared in terms of AIC to identify the version that provides a better fit.

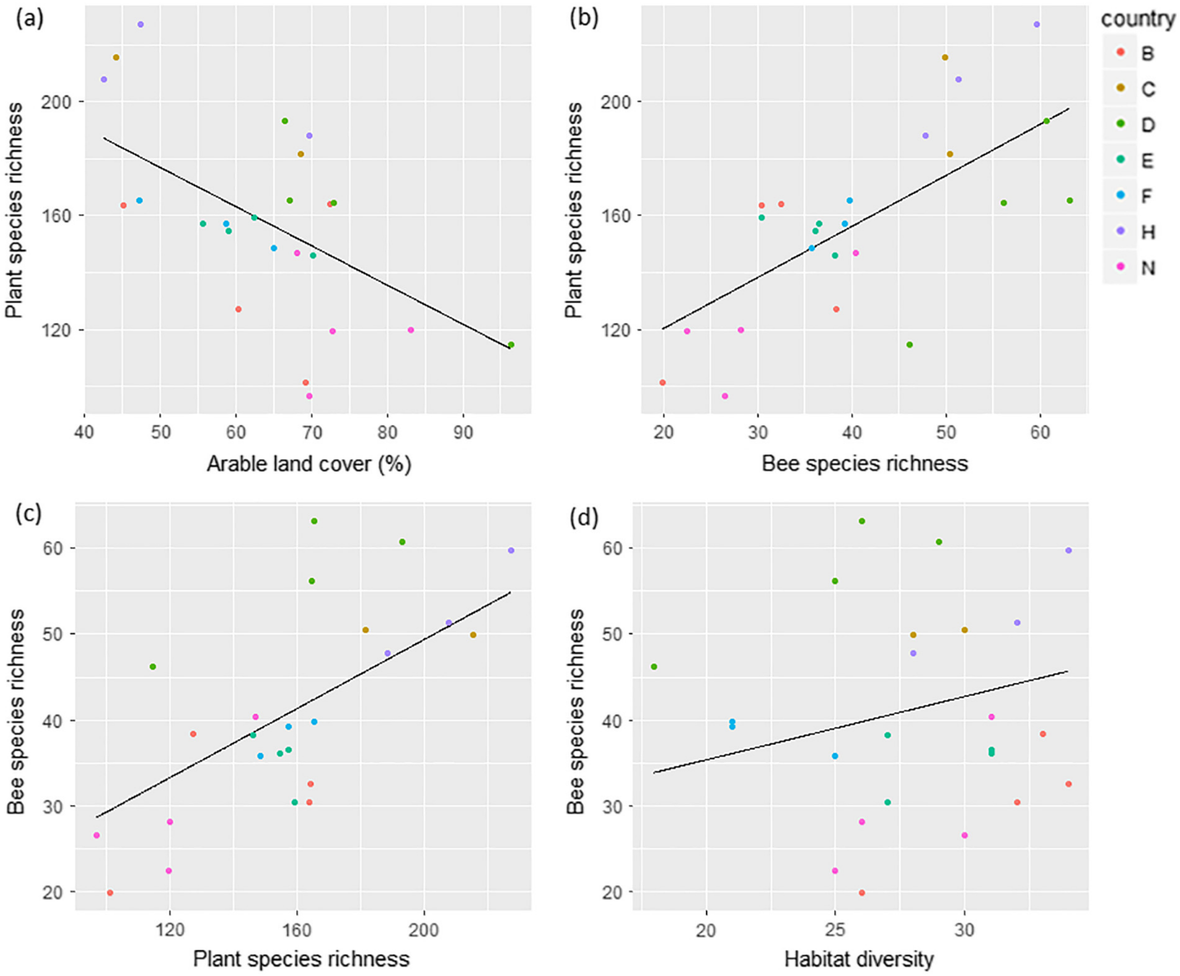
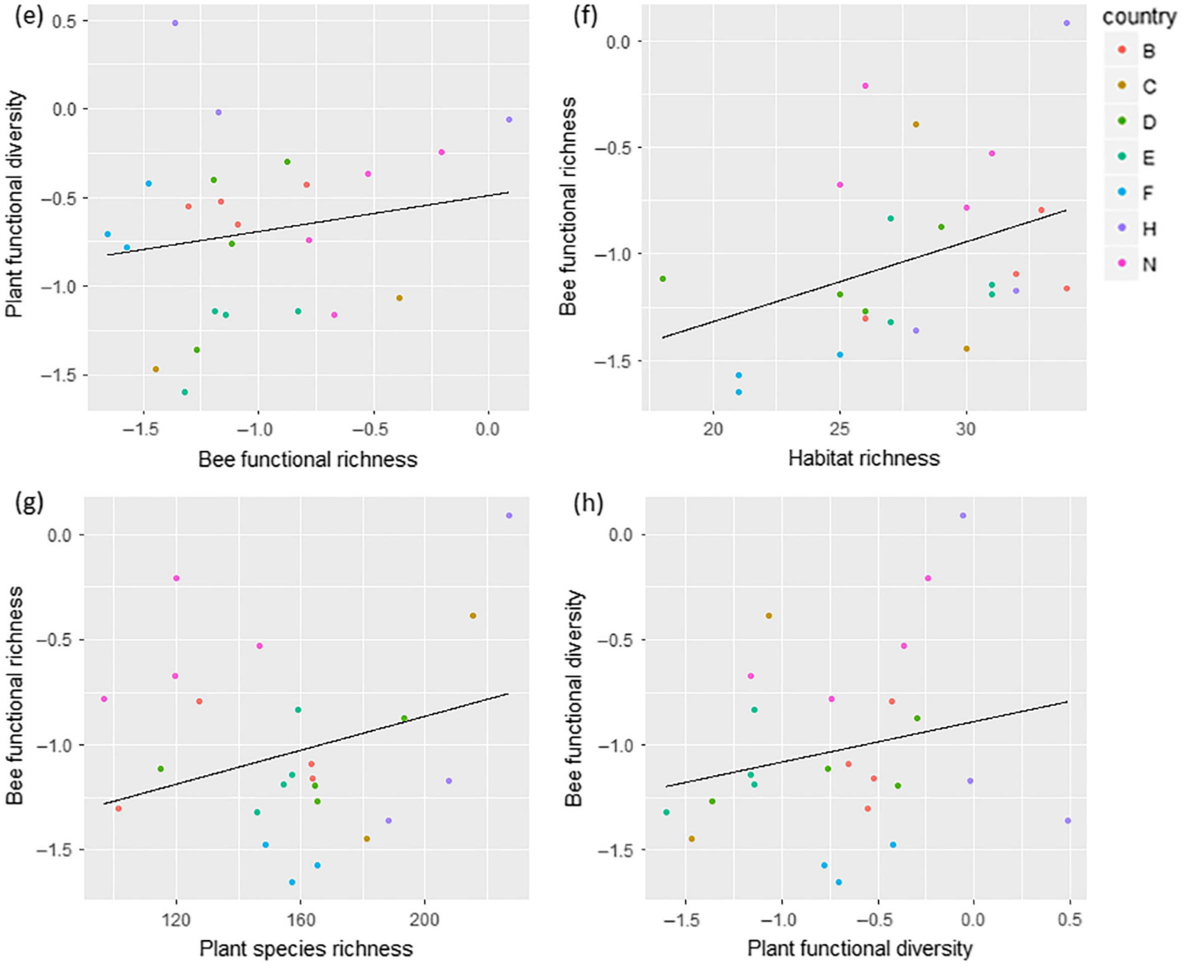


Fig. 1. Factors affecting each one of the four biodiversity metrics. Regression lines with embedded raw data for each one of the selected variables according to the best supported models for plant species richness (a, b), bee species richness (c, d), plant functional diversity (e), and bee functional diversity (f–h). Countries in the legend: B, Belgium; C, Czech Republic; D, Germany; E, Estonia; F, France; H, Switzerland; N, The Netherlands.

The effects of landscape on the diversity of bees and flowering plants are in line with other studies demonstrating the detrimental effects of habitat loss on communities in agricultural landscapes (e.g., Billeter et al. 2008, Gamez-Virues et al. 2015). However, the indirect effects we found may indicate that some of the impacts reported in those studies actually are indirect influences related to species interactions. For instance, the positive relationship between percentage cover of semi-natural areas and bee diversity, which is often encountered in the literature (Steffan-Dewenter et al. 2002, Le Féon et al. 2010, Papanikolaou et al. 2017), would be translated in our study as a negative relationship between percentage cover of arable land and bee diversity (Russo et al. 2015). Our best SEM included such a negative relationship between arable land cover and bee functional diversity, but this relationship was an indirect one mediated by plant species richness. The diversity, quantity, and quality of floral resources (nectar, pollen) affect bee community composition (Potts et al. 2003), and the lack of floral resources in landscapes devoid of semi-natural habitats was considered a possible mechanism behind the decline of bee diversity in such landscapes. Our findings provide evidence for this mechanism,



(Fig. 1. *Continued*)

since bee species richness and functional diversity declined with decreasing number of insect-pollinated plant species. However, wild bees depend on diverse habitats for nesting and food resources and, thus, they are directly affected by habitat richness. Additionally, percentage cover of arable land strongly affected plant species richness, potentially masking a direct effect of habitat richness on it. Still, plant richness can indirectly benefit from positive effects of linear and patchy habitat diversity on bee species richness (Poschlod and Braun-Reichert 2017).

Investigating plant–pollinator networks, Weiner et al. (2014) demonstrated linked losses in plants and pollinators with increasing grassland management, assessed through three variables: fertilization, mowing, and grazing intensity. According to their findings, land use intensification causes a direct decline in plant diversity which in turn precipitates non-random extinctions of pollinators mediated by limited resources. Although they did not find direct effects of land use on pollinators in the context of their study, they claim that such effects are possible especially for more specialized pollinators such as bees. Our findings support their conclusions about plant-mediated effects of landscape on bee functional diversity and further demonstrate the possibility of bee-mediated effects of landscape on flowering plant species richness. Several other studies have reported that bee species richness increases with increasing plant species richness (Steffan-Dewenter et al. 2001, Holzschuh et al. 2007, Ebeling et al. 2008), while others highlight the importance of bee

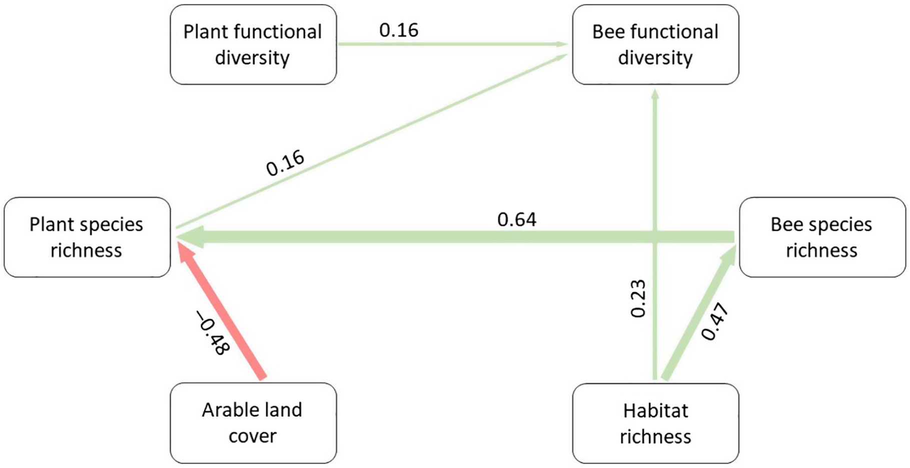


Fig. 2. Representation of the SEM version that demonstrated the best fit (model version 2: Bee species richness → Plant species richness, Plant functional diversity → Bee functional diversity). The green and red arrows indicate positive and negative relationships, respectively. The numbers represent the coefficient estimates that correspond to each relationship, and the arrow width is weighted to indicate the strength of the relationships.

diversity for the persistence of the plant community (Fontaine et al. 2006) or just identify the positive correlation between the diversity of flowers and flower visitors (Fründ et al. 2010). Biesmeijer et al. (2006) found a relationship between bee and plant species richness, but they were unable to point to which direction it was operating. In our case, we identified bottom-up effects (from plant species richness to bee functional diversity) in accordance with our expectations. Our results further highlight the possibility of top-down (from bee to plant species richness) effects. This finding may be explained by the fact that some plants need specific pollinators and therefore cannot produce seed set in a site where their pollinator does not occur (Steffan-Dewenter and Tscharntke 1999). More importantly, there was stronger evidence for an effect directed from bee to plant species richness, in line with other studies demonstrating that plant diversity benefits from increasing bee diversity (Clough et al. 2014) and pollinator availability (Lundgren et al. 2016). This result supports the idea of a more complex structure where individuals of multiple plant and pollinator species interact and indirectly affect each other (Carvalheiro et al. 2014).

It is worth noting that the richness-corrected plant functional diversity was affected neither by percentage cover of arable land nor by habitat richness. The lack of correlation between landscape variables and corrected plant functional diversity likely results from the traits we selected or from the fact that other variables, such as soil fertility and humidity, have not been included in our analyses. All the selected plant traits are pollination-related. As such, those traits determine

Table 4. Direct and indirect effects of landscape variables on biodiversity metrics derived from the best version of the SEM.

Model version	Cause	Effect on	Direct	Indirect	Total
2: Bee species richness → Plant species richness Plant functional diversity → Bee functional diversity	% arable	Plant species richness	−0.48	0	−0.48
		Bee species richness	0	0	0
		Plant functional diversity	0	0	0
		Bee functional diversity	0	−0.08 (−0.48 × 0.16)	−0.08
	Habitat richness	Plant species richness	0	0.30 (0.47 × 0.64)	0.30
		Bee species richness	0.47	0	0.47
		Plant functional diversity	0	0	0
		Bee functional diversity	0.23	0.05 (0.47 × 0.64 × 0.16)	0.28

the effect of plants on the ecosystem function of pollination, but may not directly impact species response to land use change and associated pressures (Lavorel and Garnier 2002). Although land use is likely to act on plant functional diversity via changes in pollinator diversity, no such effects were detected in our study.

Furthermore, our models show a positive effect of flowering plant species richness on bee functional diversity, suggesting that species-impoverished plant communities can lead to a decline in functional diversity of the bee community. The decrease in the number of flowering plant species caused by high arable land cover seems to act as a filter on the wild bee community by limiting the variety of flowering resources and leading to trait convergence (i.e., lower values of Rao's Q), as previously demonstrated by Forrest et al. (2015) and Ponisio et al. (2016). We also found that decreasing plant functional diversity leads to decreasing bee functional diversity, as well, denoting that parallel declines in functionality occur and trait convergence of the insect-pollinated plant community results in more homogeneous communities also for wild bees. High plant functional diversity could safeguard diverse resources allowing the coexistence of bee species with different traits. Even bee species that are considered generalists (e.g., most bumblebees) tend to prefer specific plant families and species (Fontaine et al. 2006, Fründ et al. 2010, 2013). Fründ et al. (2010) found that the level of pollinator specialization is not affected by flower diversity and suggested the high specialization as a possible mechanism promoting species coexistence. Such a mechanism could explain the positive effect of flowering plant functional diversity on bee functional diversity found in our study. Another possible explanation could be that higher plant species richness promotes niche complementarity (Venjakob et al. 2016), since bees are able to shift their floral niches in order to avoid interspecific competition (Fründ et al. 2013). Plant communities with more species differing in their pollination-related functional traits can support a more diverse wild bee species community, comprising species with different preferences that display increased niche complementarity, meaning that trait divergence in the plant community leads to a more functionally diverse bee community.

To conclude, we demonstrate that landscape composition and habitat richness affect flowering plant and pollinator communities in both direct and indirect ways. The diversity of wild bees and insect-pollinated plants in agricultural landscapes is strongly interconnected, increasing the risks for parallel declines, extinctions, and functional depletion. Therefore, it would be imperative to consider in environmental policy indirect effects mediated by species interactions. Agri-environmental schemes that aim to facilitate pollinators often focus on enhancing the quality of semi-natural elements, such as flower strips (Carvell et al. 2011, Bommarco et al. 2013, Scheper et al. 2015). Here, however, we show the importance of additionally including the indirect effects via the plant species richness that is affected by the amount of agricultural area. Overall, our study emphasizes the necessity of considering the interplay between interacting species groups when assessing their response to agricultural land use.

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