

LETTER

Density of insect-pollinated grassland plants decreases with increasing surrounding land-use intensity

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Abstract

Pollinator declines have raised concerns about the persistence of plant species that depend on insect pollination, in particular by bees, for their reproduction. The impact of pollinator declines remains unknown for species-rich plant communities found in temperate seminatural grasslands. We investigated effects of land-use intensity in the surrounding landscape on the distribution of plant traits related to insect pollination in 239 European seminatural grasslands. Increasing arable land use in the surrounding landscape consistently reduced the density of plants depending on bee and insect pollination. Similarly, the relative abundance of bee-pollination-dependent plants increased with higher proportions of non-arable agricultural land (e.g. permanent grassland). This was paralleled by an overall increase in bee abundance and diversity. By isolating the impact of the surrounding landscape from effects of local habitat quality, we show for the first time that grassland plants dependent on insect pollination are particularly susceptible to increasing land-use intensity in the landscape.

Keywords

Agricultural intensification, bee specificity, canopy height, insect dependence, leaf dry matter content, mutualism disruption, plant–pollinator interactions, specific leaf area.

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INTRODUCTION

Disruption of mutualisms through global environmental change is threatening plant biodiversity worldwide (Aslan *et al.* 2013). Wild bee declines in regions dominated by intensive agriculture have raised concerns that plants that depend on pollination for their reproduction may face similar declines (Biesmeijer *et al.* 2006; but see Carvalheiro *et al.* 2013). Recent manipulative studies show that the diversity and community composition of pollinators can significantly affect reproductive success and persistence of plants (Fontaine *et al.* 2006; Albrecht *et al.* 2012; Fründ *et al.* 2013). In agricultural landscapes, wild bees are affected by nesting habitat and food resource availability (Winfree *et al.* 2009; Kennedy *et al.* 2013). Land-use intensification can therefore distort plant–pollinator mutualisms, causing pollen limitation for plants (Aguilar *et al.* 2006) and lack of pollen and nectar resources for bees (Cussans *et al.* 2010). Pollination dependence has been suggested as one of the main drivers for stronger declines in species richness of insect-pollinated plants with increasing

management intensity, compared to wind- and self-pollinated plants (Gabriel & Tscharnke 2007; Batáry *et al.* 2013).

Seminatural grasslands are habitats of major conservation concern in Europe and elsewhere. In addition to effects of local management and patch size, the presence of suitable habitat within the surrounding landscape is known to be very important for the diversity of wild bees (Heard *et al.* 2007; Bommarco *et al.* 2010; Kennedy *et al.* 2013) and plants (Öckinger *et al.* 2012; Reitalu *et al.* 2012; Schmucki *et al.* 2012) and crop pollination (Garibaldi *et al.* 2011). Increasing landscape simplification can therefore also be expected to have indirect negative effects on plants that depend on insect pollinators. Despite the need to inform conservation and restoration projects, pollinator-mediated impacts of surrounding land use on grassland plant communities are relatively poorly studied (Potts *et al.* 2010).

Some recent studies comparing insect- with wind- and self-pollinated plant species richness along landscape gradients found little or no effect of landscape context on pollination mode in plant communities (Ekroos *et al.* 2010;

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Power *et al.* 2012; Batáry *et al.* 2013). However, these studies only investigated species richness, which per se does not account for changes in abundance which can better reflect effects of pollinator declines on plant species and their subsequent effects on bee communities. Secondly, the dependence on insect pollination is usually treated as a binary variable, although many insect-pollinated plants can self-fertilise or persist by vegetative reproduction to varying extents (Kleyer *et al.* 2008). Thirdly, previous studies have not distinguished between plants dependent on different functional subsets of pollinators. Different functional groups of bees do not show equally strong declines (Bommarco *et al.* 2010; Williams *et al.* 2010), and bees with narrow diet breadth, such as long-tongued bumble bees, are particularly sensitive to loss of flower patches in agricultural landscapes (Goulson *et al.* 2008; Bommarco *et al.* 2012). Hoverflies are also important pollinators, but do not show consistent declines with increasing landscape simplification (Jauker *et al.* 2009; Ekroos *et al.* 2013). Plants dependent on long-tongued bees can therefore be expected to face greater pollen limitation than plants pollinated by hoverflies and a wide array of bees. Finally, plant communities are to a large extent determined by local management practices and site fertility, and this needs to be fully accounted for to detect landscape-scale effects.

Gathering primary plant and bee data from 239 seminatural grassland sites across central and northern Europe, we studied how the degree of specialisation between plant and bee communities is shaped by land use in the surrounding landscape. We address this by: (i) investigating whether shifts in bee dependence of plants can be detected using the species richness of plants in the communities, or if weighting by the abundance of the species is necessary to detect shifts; (ii) using continuous indices of bee dependence and insect dependence derived, respectively, by combining species-specific information on dependence of insect pollination, i.e. the ability to self-pollinate in the absence of insect pollination, and on the identity of the pollinators based on flower-type classifications following Kugler (see Klotz *et al.* 2002); and (iii) using the plant functional traits specific leaf area, leaf dry matter content and canopy height averaged at the community scale as a means to characterise and account for local land-use management (following the 'trait-gradient analysis' in Ackerly & Cornwell 2007; Pfestorf *et al.* 2013).

We first tested whether increasing agricultural land-use intensity in the surrounding landscape affects the degree of bee dependence of plants in the local communities. We additionally tested whether bee-dependent plants are more sensitive to changes in agricultural land cover in the surrounding landscape than plants relying on a wider array of pollinators. Finally, we analysed whether abundance, species richness and evenness of bees are affected by habitat size and landscape composition, and whether they correlate with the bee dependence index of the plant community while controlling for other factors (e.g. altitudinal and spatial gradients in both plants and pollinators) (Pellissier *et al.* 2010). We allowed for stronger relationships between long-tongued than short-tongued species to landscape gradients and abundance of bee-dependent plants as long-tongued bees are likely to be more sensitive to land-use change (Goulson *et al.* 2008) and deliver

most pollination benefits to bee-dependent plants. We expected that: (i) increasing agricultural land-use intensity in landscapes surrounding the focal grasslands decreases the abundance of bee-dependent plants, but not necessarily their species richness; (ii) plants dependent on bees for pollination are more sensitive to landscape composition than plants dependent on a wider array of pollinators; (iii) abundance and diversity of bees (abundance, species richness and evenness) reflect landscape patterns found in bee-dependent plants.

MATERIAL AND METHODS

Field data

We used six data sets collected in different types of seminatural grasslands in five European countries (Hungary, Germany, Switzerland, Sweden and Finland; see Table 1 and Appendix S1–S2). All data sets were collected over one season during 2001–2010 in discrete habitat patches situated in landscapes with varying proportions of agricultural land use. Data were collected based on either transect counts or sweep-netting (bees) and area-based proportions of plant cover (except in Germany and Sweden, where plant data were measured as the number of flower heads/ha, and presence/absence of plant species in each of 10 subplots per site respectively (see Appendix S1).

Plant trait data and community descriptors

For each plant species in the data sets, we calculated an index for dependence on bee visitors (hereafter termed bee dependence) by combining indices for insect pollination dependence and the relative importance of bees as pollen vectors according to the BioFlor database (Klotz *et al.* 2002). Bee dependence was calculated as the product of the indices insect dependence and bee specificity. Insect dependence was assessed based on: (i) pollination syndromes after Kugler (see Klotz *et al.* 2002), listing the following pollination mode categories in the BioFlor database: 'cleistogamy', 'geitonogamy', 'insects', 'pseudocleistogamy', 'selfing', 'slug', 'water' and 'wind'; and, (ii) the frequency at which the above pollination modes are expected to occur ('always', 'at failure of outcrossing', 'never', 'mostly', 'often', 'possible', 'rare', 'the rule' and 'unknown'). Categorisations of the pollination mode other than insect-, self- and wind-pollination formed only a fraction of all entries on the observed species and were dropped from the dataset.

Several entries were available for most species, reflecting the different primary sources of information listed in BioFlor. We categorised each plant as being strongly dependent on insect-, self- or wind-pollination if the pollination mode was consistently characterised as 'always', 'the rule', or 'mostly'. In some cases, the entries were conflicting: for two species, we found strong dependence on both insect- and wind-pollination (*Plantago media* and *Salsola kali*), whereas for 59 species entries suggested strong dependence on both insect pollination and self-pollination. Following this, we set our index of insect pollination to 1 when the plant was strongly dependent on insects, to 0.5 when strong dependence on insect pollination and another mode (i.e. either wind- or self-pollination) was

Table 1 Description of the data sets included in this study

Data-set	Habitat type	N species*	Survey rounds	Site area (ha) [†]	Arable (%) [‡]	N sites
Finland (a)	Dry seminatural grasslands	B: 116 (19.1 ± 8.5)	B: 4	1.14 (0.07–4.74)	30.7 (0–92.4)	40
		P: 148 (28.8 ± 8.0)	P: 1			
Finland (b)	Mesic seminatural grasslands	B: 104 (16.6 ± 5.3)	B: 4	1.26 (0.25–6.0)	26.5 (0–72.5)	47
		P: 154 (36.8 ± 9.4)	P: 1			
Germany	Calcareous grasslands	B: 188 (50.8 ± 6.3)	B: 5	2.98 (0.23–11.78)	24.8 (0–50.6)	23
		P: 156 (48.1 ± 7.5)	P: 5			
Hungary	Seminatural pastures	B: 124 (7.4 ± 5.5)	B: 3	62.4 (2.51–277.73)	25.3 (0–67.2)	42
		P: 238 (32.8 ± 15.3)	P: 1			
Sweden	Dry and mesic seminatural pastures	B: 81 (10.2 ± 4.5)	B: 4	4.71 (1.9–16.3)	59.2 (0–100)	45
		P: 149 (35.6 ± 7.7)	P: 1			
Switzerland	Hay meadows	B: 49 (4.7 ± 2.6)	B: 3	0.94 (0.3–3.0)	31.2 (0–97.6)	42
		P: 157 (31.0 ± 9.9)	P: 1			

Habitat type, number of observed species (B = bees, P = plants, excluding grasses, trees, bushes and ferns), number of survey rounds for bees and plants, site area, percentage arable in the surrounding landscapes and number of sites included in each data set.

*Total number in data set (mean ± SD per site).

†Mean (min–max).

‡Mean (min–max) within a circular landscape with 1-km radius, based on CORINE land-cover data (see Materials and methods for details).

recorded, and to 0 when no strong dependence on insect pollination was recorded. Similarly, we set our index of bee specificity to 1 if visitors included bumblebees, bees or Hymenoptera in general, but not Lepidoptera, hoverflies or Diptera in general. We set the index value to 0.5 when visitors included bumblebees, bees or Hymenoptera in general, and also Lepidoptera, hoverflies or Diptera in general. Finally, we set our index of bee specificity to 0 if visitors did not include bumblebees, bees or Hymenoptera in general (see Klotz *et al.* 2002 for pollinator classification). To account for multiple entries per species in the trait database, we calculated the species mean for the insect pollination and bee specificity trait attributes. An overview of common species with different values for the bee dependence index is given in Appendix S3. To test whether the ability of vegetative reproduction can offset the effect of landscape context, we computed modified indices of bee and insect dependence by multiplying the values of the indices above by indices of relative seed dependence for reproduction, ranging between 1 (reproduction only by seeds) and 0 (reproduction only vegetative; see Appendix S1).

To isolate effects of local habitat quality from the impact of the surrounding landscape on plant and bee communities, we generated covariates using a community trait-based approach (Ackerly & Cornwell 2007). We first compiled data from the LEDA plant trait database (Kleyer *et al.* 2008) on traits related to plant responses to land-use change and competitive ability (see Appendix S1 for additional details). Traits were as follows: canopy height (CH; in metres), leaf dry matter content (LDMC; $\text{mg}\cdot\text{g}^{-1}$) and specific leaf area (SLA; $\text{mm}^2\cdot\text{g}^{-1}$). CH reflects plant competitive ability (Gross *et al.* 2007), while SLA and LDMC are significantly related to multiple indicators of grassland land-use intensification, including fertiliser use, cutting and grazing intensity (Pfeister *et al.* 2013). In Appendix S1, using the three data sets for which management and soil data were available, we demonstrate that the covariates chosen are effective in isolating effects of local habitat quality from the impact of the surrounding landscape. We did not attempt to include phylogenetic relationships within plant communities, since functional plant diversity has recently been shown to be poorly predicted by phylogenetic diversity (Purschke *et al.* 2013). Finally, as an additional covariate, we used the proportion of grass over herb cover, which is also strongly affected by management.

Based on the species-specific trait indices described above, we estimated the community-weighted mean (CWM) for each plant trait and local plant community (Violle *et al.* 2007), where each trait index was weighted by the abundance of that particular plant species in the community. As abundance measures we used the proportional cover in Hungary and Finland, the proportion of total number of subplots (10 in total) per site containing the species in Sweden, and proportion of the number of flower units in Germany. To assess the importance of accounting for plant abundance using weighted means for the pollination-related traits, we also calculated un-weighted mean values across species for each trait and plant community. Complete trait data were available for 468 of 544 herb species, and 101 of 108 grass species. Community-weighted traits characterised 82 and 92% or more of the total vegetation at all sites for LDMC and SLA, respectively, except for

one site (Germany, Bieberbach), in which LDMC and SLA were available for only 65% of the vegetation.

Bee trait data and community descriptors

We separated bee species, excluding the honey bee, into short-tongued (Colletidae, Andrenidae, Melittidae, Halictidae) and long-tongued species (Apidae, Megachilidae) following Biesmeijer *et al.* (2006). For each of the two groups, we calculated total abundance (i.e. the number of bees/site), species richness, rarefied species richness (Gotelli & Colwell 2001) and Pielou's evenness index.

Landscape variables

Since all studies did not include landscape data, and since the ones which did so included different types of landscape variables and/or considered different spatial scales, we used CORINE Land Cover vector data provided by the European Environmental Agency (<http://www.eea.europa.eu/data-and-maps/data/corine-biotopes>) to obtain an internally consistent set of landscape variables. We calculated two proxies for agricultural land-use intensity, the percentage of arable fields and the percentage of non-arable agricultural land (see Appendix S4) in a radius of 1000 m around the coordinates of the focal grasslands in Quantum GIS (Quantum GIS Development Team 2013). The CORINE-based arable cover variable showed consistent correlations with available independent measures of arable cover surrounding the study sites in Germany (at 1,000 m radius; $r = 0.66$), Hungary (at 500 m radius; $r = 0.78$) and Sweden (at 2,000 m radius; $r = 0.94$). Given the grain size of the CORINE Land Cover data, the radius of 1,000 m is an adequate scale to describe landscapes relevant to pollinators (Walther-Hellwig & Frankl 2000). We used the percentage of arable fields as a proxy of the cover of intensively managed agricultural land, whereas the percentage of non-arable agricultural land described less intensive agriculture including high-quality habitats for bees, such as orchards and seminatural habitats. The majority of non-arable agricultural land was permanent grasslands (for full details, see Appendix S4). We used land-cover data from 2000 for data recorded 2003 and earlier, and land-cover data from 2006 for data recorded 2004 and later, except regarding Switzerland, for which the only available CORINE data were from 2006. Altitudes were extracted from the GTOPO30 Digital Elevation Model (available from the U.S. Geological Survey, <https://lta.cr.usgs.gov/GTOPO30>).

Statistical analyses

We first tested whether the CWM bee dependence of plants was affected by percentage of arable fields and percentage of non-arable agricultural land in the landscape. We constructed MCMC-based linear mixed models with a random structure reflecting the spatial grouping of sites (for details and implementation see Supplementary Material). In three studies (Hungary, Sweden and Switzerland), distinct, non-overlapping regions were sampled, and therefore we included the grouping of sites within region and regions within studies. All other

studies included a single region. Models included the landscape variable of interest (i.e. percentage arable land or percentage non-arable agricultural land) as well as the covariates altitude, area of the focal grassland (\log_e -transformed), proportion of grass species in the plant community and community-weighted means for CH (\log_e -transformed), SLA and LDMC. By including these covariates we obtained a conservative estimate of the effect of the landscape composition on CWM bee dependence, while controlling for potential confounding relationships between landscape effects, CWM traits related to management and pollinator-related traits. Latitude and longitude were indirectly accounted for by including random variables for study and region within study. Strong (multi-)collinearity in the predictors was only detected for altitude and landscape variables in Switzerland (variance inflation factor > 5 ; Appendix S5). Therefore, we repeated the analyses once without altitude as a covariate, and once without the Swiss data included, and ensured that this did not affect our conclusions (results not shown).

Generally, given the lack of orthogonality between explanatory variables inherent to the observational nature of this study, estimates should be interpreted with caution. For instance, parameter estimates should not be used for predictions in other regions (Dormann *et al.* 2013). The most complex formulation of random effects included random slopes for regions within studies. We proceeded in a stepwise manner to simplify the models, first attempting to remove the region-in-study random slope, and secondly the study-level random slope, based on the difference between the values of the Deviance Information Criterion (Δ DIC). We set a conservative threshold (one DIC unit difference) below which random slopes were removed. In the results, Δ DIC values are shown for the inclusion of study-level random slopes only, as the variation accounted for by region-in-study slopes always approached zero. We tested the hypotheses pertaining to the impact of landscape on bee dependence by examining MCMC P -values for the fixed effects of the landscape variables. All explanatory variables were centred and standardised before analyses, and focal grassland area was \log_e -transformed prior to centring. For means and standard deviations of original variables, see Appendix S6.

Secondly, we repeated these analyses using un-weighted trait means to see whether weighting by plant species abundance improved the detectability of plant community shifts in terms of bee-dependent species. We tested for the interaction between the landscape variable and the identity of the pollinator dependence variable (CWM bee dependence, or un-weighted mean bee dependence). We did this using both estimates as response variables while using site as an additional random variable to reflect that values of CWM and un-weighted mean bee dependence were not independent. Interactions between the identity of the pollinator dependency variable and the covariates were included to allow for relationships specific to the pollinator dependency variables. We tested the significance of the interaction between the identity of the pollinator dependency variable and the landscape term using the MCMC P -value.

Thirdly, we assessed whether the abundance of honeybees mediated the effect of landscape on bee dependence, by testing

the significance of the interaction between landscape variables and honeybee abundance (\log_{10} -transformed), excluding studies for which honeybee data were not available (Hungary and Switzerland). We also assessed whether plant vegetative reproduction offsets the effect of landscape context, by testing for the interaction between the landscape variable and the identity of the bee dependence variable (CWM bee dependence, or CWM bee and seed dependence).

Fourth, we tested whether insect dependence of local plant communities was affected by percentage of arable fields and percentage of non-arable agricultural land in the landscape, using the approach described above for bee dependence. To formally test whether bee-dependent plants were more sensitive to increasing arable cover in the surrounding landscape than plants dependent on a wider array of pollinators, we used the approach described above, testing for the interaction between the landscape variable and the identity of the pollinator dependency variable (bee dependence or insect dependence).

Fifth, we examined whether including interactions between landscape variables and community-weighted mean plant

traits, which are amongst other surrogates for local fertility and land-use intensity, improved model fits. Significant interactions would provide evidence that bee- or insect-dependency, mediated by lack of pollinators in certain landscape types, is affected by plant nutrient availability.

Finally, we tested whether the abundance, species richness and evenness of long-tongued and short-tongued bees were (i) affected by agricultural land-use intensity, and (ii) correlated with the bee dependence or insect dependence indices of the plant community. For each response variable, we compared four models, each containing one of four combinations of the two pollinator dependence variables (bee dependence and insect dependence on one hand), and the two proxies for agricultural land-use intensity (arable or non-arable agricultural land-use cover in the surrounding landscape). Each model included study and region within study as random variables, and focal grassland area and altitude as fixed explanatory variables. We interpreted the results based on the direction of the effects and P -values of the models with $\Delta\text{DIC} < 2$. Given the low numbers of pollinators in some

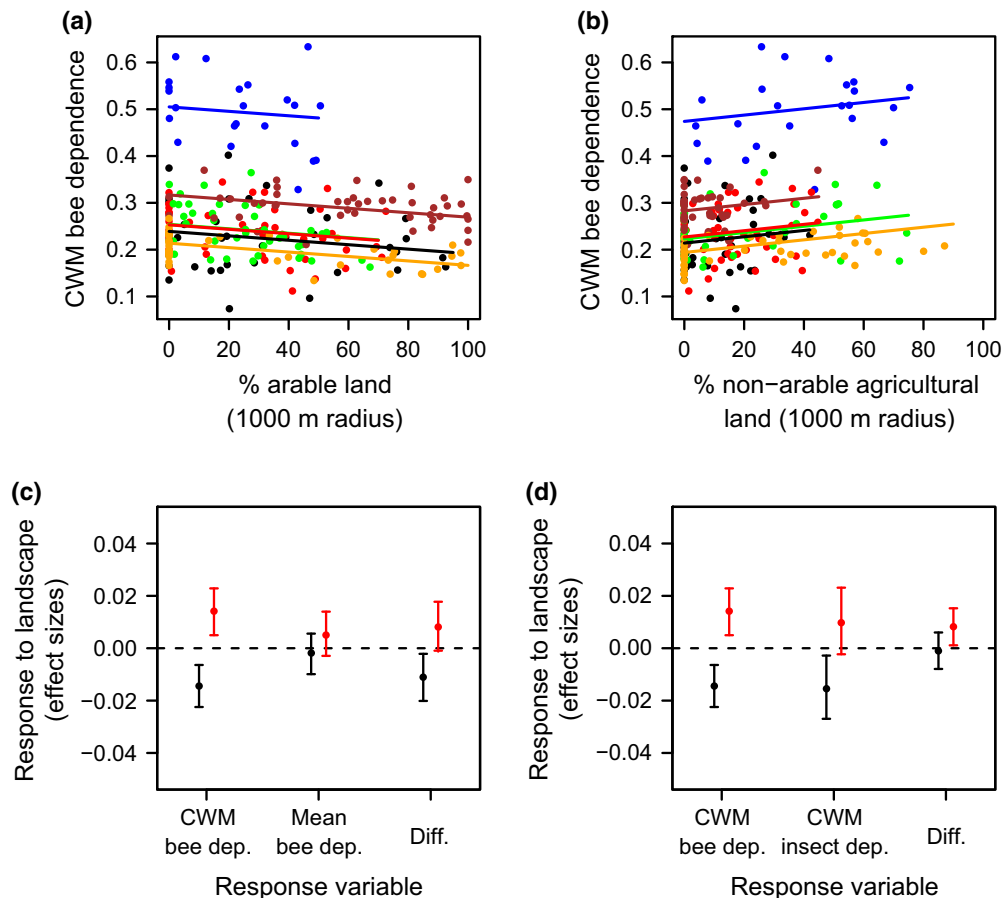


Figure 1 (a) Relationships between community-weighted mean (CWM) bee dependence of plants and arable land cover. (b) Relationships between community-weighted mean (CWM) bee dependence of plants and non-arable agricultural land cover. Colour in (a) and (b) indicates the source of the data (blue = Germany, brown = Sweden, red = Finland (Study b), black = Finland (Study a), yellow = Switzerland, green = Hungary). (c) Estimates for CWM bee dependence, un-weighted mean bee dependence, and the difference in the effect size between these two response variables and 95% highest posterior density (HPD) intervals for the effect of arable land cover (black, left points and whiskers), and non-arable agricultural land cover (in red, right point and whiskers). (d) Estimates and 95% HPD intervals for the effect of arable land cover (black, left points and whiskers) and non-arable agricultural land cover (in red, right point and whiskers) for CWM bee dependence, CWM insect dependence, and the difference in the effect size between these two response variables.

Table 2 Linear mixed model for community-weighted bee dependence in grassland plants including arable land use in the landscape and covariates related to local environment as explanatory variables

	MCMC means	Lower 95% CI bound	Upper 95% CI bound	<i>N</i> effective samples	<i>P</i>
Intercept	0.281	0.174	0.397	2000	
Proportion arable	-0.014	-0.022	-0.006	2000	0.001
Area	-0.011	-0.023	0.001	2000	0.081
Altitude	0.001	-0.025	0.028	2000	0.948
Proportion grass	-0.074	-0.088	-0.059	2182	<0.001
CWM_CH	0.019	0.011	0.029	2000	<0.001
CWM SLA	-0.021	-0.035	-0.007	2000	0.002
(CWM SLA) ²	0.017	0.010	0.025	2378	<0.001
CWM LDMC	-0.042	-0.055	-0.030	2000	<0.001
(CWM LDMC) ²	-0.012	-0.019	-0.004	2000	0.002
Study/region SD	0.003	0.000	0.006	649	
Study SD	0.138	0.051	0.228	1856	
Residual SD	0.054	0.049	0.058	2000	

MCMC means, credible intervals (95%) and *P*-values [SD: standard deviation, given for Region within Study, between study and residuals; CWM= community-weighted mean; CH=canopy height (metres); LDMC=leaf dry matter content (mg.g⁻¹); SLA=specific leaf area (mm².g⁻¹)]. All explanatory variables were centred and standardised, CWM CH and area were log_e-transformed prior to that. Means and standard deviations of original variables are reported in Appendix S6.

sites, we performed analyses on pollinator species richness and evenness only on sites with at least 15 bees collected for the overall pollinator community, and 10 and 5 bees for the long- and short-tongued bee community-specific analyses respectively. Species richness was rarefied down to these values. Numbers of sites thereby included in the species richness and evenness analyses were 148 for all bees, 135 for long-tongued bees and 203 for short-tongued bees.

Details of the statistical packages, versions used and further literature references for statistical approaches are given in Appendix S1.

RESULTS

The community-weighted mean (CWM) bee dependence of grassland plant communities decreased consistently with increasing percentage of arable fields in the surrounding landscape ($P_{\text{MCMC fixed arable}} = 0.001$). This effect did not differ among studies ($|\Delta\text{DIC}| < 0.29$; Fig. 1a, Table 2). CWM bee dependence increased with an increasing percentage of non-arable agricultural land cover ($|\Delta\text{DIC}| < 1.04$; $P_{\text{MCMC fixed non-arable agric.}} = 0.006$, Fig. 1b, Appendix S7).

By contrast, the mean values not weighted in relation to the abundance of bee-dependent plants did not relate to any landscape factors (all $P > 0.25$, Appendices S8 and S9). The size of the estimate for the effect of arable land use in the surrounding landscape on bee dependence among plants was significantly larger when community-weighted mean rather than the un-weighted mean bee dependence over the species was used as the response variable ($P_{\text{MCMC fixed arable} \times \text{response type}} = 0.012$). For the effect of non-arable agricultural land cover on bee dependence, the estimate was also lower for the un-weighted bee dependence, but here the interaction was not

significant ($P_{\text{MCMC fixed non-arable agric.} \times \text{response type}} = 0.083$) (Fig. 1c).

The landscape effects were independent of the abundance of foraging honeybees ($P_{\text{MCMC landscape effect} \times \text{honeybee abundance}} > 0.40$ in all cases). Including the ability of vegetative reproduction in the bee dependence index did not result in quantitatively different effects ($P_{\text{MCMC landscape effect} \times \text{response type}} > 0.05$ in all cases). When leaving out grasses from the CWM bee dependence, the strength of the relationship between landscape and bee dependence remained equally strong ($P_{\text{MCMC fixed arable}} < 0.001$).

CWM insect dependence decreased with increasing percentage of arable fields ($|\Delta\text{DIC}| < 0.11$; $P_{\text{MCMC fixed arable}} = 0.010$; Appendix S10) but was not affected by non-arable agricultural land cover in the landscape ($|\Delta\text{DIC}| < 0.51$; $P_{\text{MCMC fixed non-arable agric.}} = 0.166$; Appendix S11). To test whether bee dependence was more strongly affected by landscape than the insect dependence, we tested the interaction

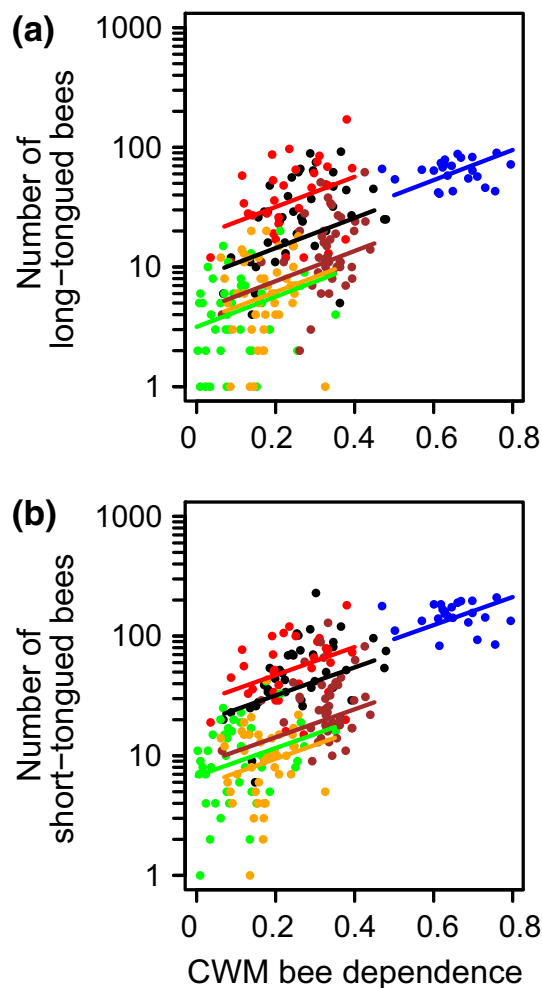


Figure 2 Number of bees caught in seminatural grasslands increases with the community-weighted mean (CWM) bee dependence of plants, both for long-tongued bees (a) and short-tongued bees (b). Colour indicates the source of the data (blue = Germany, brown = Sweden, red = Finland (Study b), black = Finland (Study a), yellow = Switzerland, green = Hungary).

Table 3 Sign and *P*-values for coefficients for predictors of European grassland bee community descriptors (abundance, rarefied species richness and evenness)

Bee group	Community descriptor	% Arable	% Non-arable agric.	CWM bee depend	CWM insect depend	Area (ha)	Altitude (km)
All species	Abundance		+ 0.044	+ <0.001			
	Species		+ 0.011			(−) 0.097	
	Evenness		+ 0.004				
Long-tongued species	Abundance		(+) 0.085	+ <0.001	+ <0.001		
	Species						
	Evenness						
Short-tongued species	Abundance		+ 0.031	+ <0.001			− 0.047
	Species					(−) 0.032	
	Evenness		+ 0.037			(+) 0.082	− 0.030

Predictors are percentage of arable fields and percentage of non-arable agricultural land in a 1000-m radius around the focal grassland, community-weighted bee dependence and insect dependence amongst the grassland plant communities and area of the focal grassland and altitude (CWM = community-weighted mean). *P*-values below 0.10 are shown, marginally non-significant effect signs are in parentheses ($0.05 < P < 0.10$).

between landscape variables and the identity of the pollinator dependence variable (i.e. bee vs. insect dependence; Fig. 1d). This interaction was not significant for either percentage arable fields, nor for percentage non-arable agricultural land cover ($P_{\text{MCMC fixed arable}} = 0.906$; $P_{\text{MCMC fixed non-arable agric.}} = 0.282$), i.e. bee-dependent plants did not respond to landscape context more strongly compared to plants dependent on a wider range of pollinators.

Plant traits related to local habitat quality were consistently significantly related to CWM bee and insect dependence (Table 2, Appendices S7–S11). These variables did not modify the effects of the landscape variable on pollinator dependence irrespective of which combination of CWM pollinator dependence or landscape variable was used, as all models with interactions between these terms had higher DIC values than models without interactions.

Increasing non-arable agricultural land cover increased abundances of all bees as well as abundance of long-tongued species (when analysed separately), overall bee species richness and evenness and evenness of short-tongued bees. Abundances of both long- and short-tongued bees increased with increasing CWM bee dependence of local plant communities (Fig. 2a, b). For long-tongued bees a model containing CWM bee dependence instead of CWM insect dependence had nearly identical DIC ($\Delta\text{DIC} < 0.24$) information content. Detailed results are presented in Table 3.

DISCUSSION

Our results demonstrate consistent negative impacts of increasing land-use intensity on community-weighted mean pollinator dependence of plants in seminatural grasslands across Europe. This result only became evident when controlling for focal grassland size, altitude and community-level plant traits reflecting local habitat quality of the focal grasslands. Our results provide the first large-scale assessment of the extent of landscape-scale management intensity on plant communities in seminatural grasslands across a large number of sites, countries and landscape types. This adds to the growing evidence that environmental change in landscapes surrounding high nature value habitats may have severe impacts on mutualistic species in a diversity of systems such as ant–

plant mutualisms in the Amazon (Emer *et al.* 2013) and tree seed dispersal in Peru (Terborgh *et al.* 2008).

While natural and seminatural grasslands may themselves offer significant resources for pollinators (Bommarco *et al.* 2010; Garibaldi *et al.* 2011; Kennedy *et al.* 2013), the surrounding landscape plays an important role in structuring pollinator communities (Öckinger *et al.* 2012). Assuming that insect pollinator-dependent plants are pollen-limited (Aguilar *et al.* 2006), detrimental effects of increasing land-use intensity in surrounding landscapes on pollinators can cause pollen limitation in grassland plants over time. This may in turn negatively affect the reproductive success of insect pollinator-dependent plants, which has recently been shown for two strongly bee-dependent herb species present in our study regions (Cussans *et al.* 2010). While it is possible that pollinators are also affected via changing plant communities in grasslands over time (e.g. increased dominance of grasses, Kleijn & Verbeek 2000), or that plants are affected by herbivory- rather than pollination-mediated effects (Carson & Root 1999), we isolated pollinator effects on plants as we used non-bee/non-insect-pollinated plants as a control.

Responses in bee dependence and insect dependence of plants were affected in a similar extent by increasing percentage of arable land, which is surprising since hoverflies have not generally declined in agricultural landscapes as much as wild bees (Biesmeijer *et al.* 2006). Hoverflies may be very abundant in homogeneous arable farmland (Jauker *et al.* 2009; Ekroos *et al.* 2013), and hoverfly species richness in grasslands increases with increasing arable land cover in the surrounding landscape (Öckinger *et al.* 2012). Our results suggest that insect-dependent plants in seminatural grasslands do not benefit sufficiently from such changes in the pollinator community. This is in line with studies suggesting that wild bees are more efficient pollinators than hoverflies (Jauker *et al.* 2012).

Our study is the first to assess the effects of pollinator dependence of plant communities by accounting for the abundance of individual plant species, which provided added analytical power in two respects. Apart from providing effective means to quantify resource availability for pollinators, the measures revealed landscape effects on plant communities

not detectable when using un-weighted average bee dependence across the species in the community. Previous studies may therefore have missed subtle, but important, shifts in pollination trait distributions linked to changes in plant abundance (Gabriel & Tschardt 2007; Ekroos *et al.* 2010; Power *et al.* 2012; Batáry *et al.* 2013). In grasslands, a significant delay in actual extinction of species can be expected after habitat fragmentation, landscape simplification, or both (Kuussaari *et al.* 2009). Therefore, abundance-based measures may provide an important tool for detecting effects on plant communities that occur before individual species go locally extinct, which is critical for timely and effective conservation interventions.

Past studies investigating shifts in the proportion of insect-pollinated plants across plant communities have found local management (e.g. organic vs. conventional farming) to be the most important explanatory factor, with landscape playing a minor or no role (e.g. Ekroos *et al.* 2010; Batáry *et al.* 2013). We show that there are strong correlations between pollinator dependence and traits relevant to resource availability and grassland management intensity. Thus, in an observational study in which site-level conditions are never fully independent of measures of landscape composition, correction for local site conditions is a necessary prerequisite to testing for landscape effects. Here, we show that including CWM functional plant traits in the models for pollinator dependence provides an easy yet effective way to statistically account for local site characteristics (Table A2), which increased our capacity to detect consistent landscape effects. Whilst testing the effect of local agricultural practice on plant and bee communities was not the aim of our study, our results suggested that appropriate grassland management can be used to partly circumvent negative effect of landscape simplification. For instance, specific leaf area and leaf dry matter content are key traits reflecting land-use intensification (Gross *et al.* 2007; Pfestorf *et al.* 2013), and the quadratic effect we found between leaf dry matter content and bee dependence suggests that intermediate land-use intensity can favour the abundance of bee-dependent plants and their pollinators.

Bee abundance, rarefied species richness and evenness consistently decreased with decreasing non-arable agricultural land cover, even when controlling for the dominance of bee-dependent plants in the communities. This further strengthens the hypothesised causal pathway linking landscape-scale agricultural land-use intensity, pollinators and plant communities. Interestingly, whereas both proxies for agricultural land-use intensity were equally strong predictors for plant communities, this was not the case for bee abundance and diversity, where significant effects were only detected for non-arable agricultural cover. Future studies using more detailed data on surrounding land use are needed to address this apparent discrepancy, which may be because of increased pollen limitation of bee-pollinated grassland plants as the proportion of insect pollinator-dependent herbs in arable fields is low (Batáry *et al.* 2013), increased interspecific competition between arable and grassland plants, as insect-pollinated plants in these two systems represent different species (Batáry *et al.* 2013), or because of mass-flowering crops (Westphal *et al.* 2003; Holzschuh *et al.*

2011). Overall, our findings confirm the expectations that open, non-tilled landscapes are beneficial for wild bees, and that less intensive agriculture might counteract unintended negative effects of intensive agriculture on biodiversity in seminatural grasslands as mediated by pollination (Carvalho *et al.* 2013).

Although our study reveals consistent impacts of landscape context on the distribution of insect pollinator dependence of plants in seminatural grasslands, we were unable to address some additional questions raised by our findings. In particular, modelling how pollinating insects respond to landscape change and grassland plants would benefit from more detailed information on agricultural land use in the surrounding landscapes. As an example, high proportions of organic farming are known to benefit flower-visiting insects at large spatial scales (Holzschuh *et al.* 2008; Rundlöf *et al.* 2008), but whether less intensive farming practices can restore grassland plant communities remains to be tested. In addition, trait variability within plant and pollinator species remains a major knowledge gap (e.g. de Bello *et al.* 2011). The degree of self-incompatibility of plants can vary between populations (Thomann *et al.* 2013), which may have important consequences on plant population persistence and community composition in fragmented landscapes.

The parallel declines in pollinating insects and pollinator-dependent plants observed in the past has recently slowed and partially recovered, thereby conferring optimism that conservation initiatives may have had some beneficial effects (Carvalho *et al.* 2013). Here, we show the community-level effects of mutualism disruption in plant communities in seminatural grasslands, where the abundance of pollinator-dependent plants and pollinators decrease in parallel with increasing land-use intensity in the surrounding agricultural landscapes. Our results suggest that management efforts at both local and landscape levels, tailored to pollinating insects and to the wild plants which they pollinate, will be particularly important in arable-dominated landscapes surrounding valuable seminatural grasslands. Our effect sizes suggest that the persistence of pollinator-dependent plants in grassland communities depends on ecological traits that are linked to local management and correlated with pollination-related traits. Our results indicate that plants dependent on insects for pollination could also benefit from implementing landscape-wide management of farmland habitats to support abundant and diverse bee populations.

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AUTHORSHIP

Y.C., J.E., N.G. and H.G.S. developed the conceptual and methodological foundations for this manuscript. P.B., S.H., E.K., R.L., E.Ö. and J.P. provided the empirical data, J.E. compiled plant trait data and Y.C. performed the analyses. Y.C. and J.E. wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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