



## Landscape context and habitat type as drivers of bee diversity in European annual crops

Gabriel Carré<sup>a,\*</sup>, Philip Roche<sup>b</sup>, Rémy Chifflet<sup>a</sup>, Nicolas Morison<sup>a</sup>, Riccardo Bommarco<sup>c</sup>, Jenn Harrison-Cripps<sup>d</sup>, Kristin Krewenka<sup>e</sup>, Simon G. Potts<sup>f</sup>, Stuart P.M. Roberts<sup>f</sup>, Guy Rodet<sup>a</sup>, Josef Settele<sup>g</sup>, Ingolf Steffan-Dewenter<sup>h</sup>, Hajnalka Szentgyörgyi<sup>i</sup>, Thomas Tscheulin<sup>j</sup>, Catrin Westphal<sup>h</sup>, Michal Woyciechowski<sup>i</sup>, Bernard E. Vaissière<sup>a</sup>

<sup>a</sup>INRA, Pollinisation et Ecologie des Abeilles, UMR 406 Abeilles et Environnement, 84914 Avignon cedex 9, France

<sup>b</sup>Cemagref, UR EMAX, 3275 Route de Cézanne, CS 40061, 13182 Aix-en-Provence cedex 5, France

<sup>c</sup>Department of Ecology, Swedish University of Agricultural Sciences, SE-75007 Uppsala, Sweden

<sup>d</sup>School of Biological & Environmental Sciences, University of Stirling, FK9 4LA Stirling, UK

<sup>e</sup>Department of Agroecology, Georg-August-University, Göttingen, Germany

<sup>f</sup>Centre for Agri-Environmental Research (CAER), School of Agriculture, Policy and Development, University of Reading, RG6 6AR Reading, UK

<sup>g</sup>UFZ, Helmholtz-Centre for Environmental Research, Department of Community Ecology, Theodor-Lieser-Str. 4, 06120 Halle, Germany

<sup>h</sup>Department of Animal Ecology I, Population Ecology Group, University of Bayreuth, 95440 Bayreuth, Germany

<sup>i</sup>Institute of Environmental Sciences, Jagiellonian University, ul. Gronostajowa 7, 30-387 Kraków, Poland

<sup>j</sup>Laboratory of Biogeography and Ecology, Department of Geography, University of the Aegean, University Hill, GR-81100 Mytilene, Greece

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### ABSTRACT

To better understand the dynamics of bee populations in crops, we assessed the effect of landscape context and habitat type on bee communities in annual entomophilous crops in Europe. We quantified bee communities in five pairs of crop-country: buckwheat in Poland, cantaloupe in France, field beans in the UK, spring oilseed rape in Sweden, and strawberries in Germany. For each country, 7–10 study fields were sampled over a gradient of increasing proportion of semi-natural habitats in the surrounding landscape. The CORINE land cover classification was used to characterize the landscape over a 3 km radius around each study field and we used multivariate and regression analyses to quantify the impact of landscape features on bee abundance and diversity at the sub-generic taxonomic level. Neither overall wild bee abundance nor diversity, taken as the number of sub-genera, was significantly affected by the proportion of semi-natural habitat. Therefore, we used the most precise level of the CORINE classification to examine the possible links between specific landscape features and wild bee communities. Bee community composition fell into three distinct groups across Europe: group 1 included Poland, Germany, and Sweden, group 2 the UK, and group 3 France. Among all three groups, wild bee abundance and sub-generic diversity were affected by 17 landscape elements including some semi-natural habitats (e.g., transitional woodland-shrub), some urban habitats (e.g., sport and leisure facilities) and some crop habitats (e.g., non-irrigated arable land). Some bee taxa were positively affected by urban habitats only, others by semi-natural habitats only, and others by a combination of semi-natural, urban and crop habitats. Bee sub-genera favoured by urban and crop habitats were more resistant to landscape change than those favoured only by semi-natural habitats. In agroecosystems, the agricultural intensification defined as the loss of semi-natural habitats does not necessarily cause a decline in evenness at the local level, but can change community composition towards a bee fauna dominated by common taxa.

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## 1. Introduction

Insect pollination is both a key ecosystem service that contributes to human well-being (Zhang et al., 2007) and a

production practice used extensively by farmers worldwide. The contribution of wild bees to the pollination of a large array of crops is now well recognised (Klein et al., 2007; Kremen et al., 2007; Winfree et al., 2007; Zhang et al., 2007). Insect pollination is also a management tool in that colonies of managed bees (e.g., *Apis mellifera* and *Bombus terrestris*) are often introduced by farmers to supplement the local pollinator fauna in large agricultural settings (Free, 1993; Velthuis and van Doorn, 2006; Stokstad, 2007). Yet

\* Corresponding author. Tel.: +33 06 76 63 77 13; fax: +33 04 32 72 26 02.  
E-mail address: [carre@avignon.inra.fr](mailto:carre@avignon.inra.fr) (G. Carré).

declines have been reported in many countries for honeybees (Stokstad, 2007) and wild bees (Biesmeijer et al., 2006; Nat. Res. Coun., 2006), and such a decline may alter the stability of entomophilous pollination services (Chapin et al., 2000; Loreau et al., 2001). Bees are the major pollinators of crops worldwide (Klein et al., 2007), and in Europe, 80% of crop species are dependent upon, or benefit from, pollination by insects, and mostly bees (Williams, 1994). It is therefore essential to better understand the relationship between bee abundance and biodiversity and the environment in agroecosystems to be able to maintain or enhance bee populations and the services they provide.

The bee diversity in agroecosystems is explained by biogeographic drivers at different scales. At a continental scale, climate and topographic conditions shape species distribution (Michener, 2000). At a landscape scale, the habitats around fields, defined as the landscape context, and especially semi-natural habitats are the main driver of bee diversity (e.g., Kremen et al., 2002; Steffan-Dewenter, 2002), as these provide food, nesting, and overwintering site resources within the flight range of the species. Land use change modifies the spatial and temporal distribution of these resources and thereby affects crop pollinator communities (Westrich, 1996). At a local scale, the bee biodiversity depends on abiotic and biotic factors such as competition, predation or disease (Kremen et al., 2007).

Agricultural intensification, which results in an increase of arable area combined with the loss and fragmentation of semi-natural habitats, is thought to be a key driver of crop pollinator loss (e.g., Kremen et al., 2002, 2007; Klein et al., 2007). Indeed, several studies have shown that agricultural intensification correlates with decreasing bee species richness (Steffan-Dewenter and Tschardt, 1999; Kremen et al., 2002; Steffan-Dewenter, 2003). Yet a few other studies found that some bee species can be favoured by anthropic areas such as agricultural or urban areas (Westphal et al., 2003; Winfree et al., 2007).

Recently, Ghazoul (2005) questioned the generalisation of pollinator decline and suggested that some bees were resistant to environmental changes. To further test this idea, we aimed to characterize the response of bee taxa to perturbations and land use changes by identifying landscape features (habitat types and structures) and their associated bee communities. Authors to date have generally considered only a small number of habitat types selected *a priori* or only a coarse-grain of semi-natural habitats (Roubik, 2000; Kremen et al., 2002; Klein et al., 2002; Steffan-Dewenter, 2002, 2003; Steffan-Dewenter et al., 2002; Westphal et al., 2003; Herrmann et al., 2007). Studies that have quantified the influence of other landscape features on bee diversity did not consider the diversity of agricultural and urban habitats (Kivinen et al., 2006; Hendrickx et al., 2007).

The objectives of our study were to (i) characterize the overall response of the wild bee fauna to the proportion of semi-natural habitat in the landscape, (ii) assess which habitat types and landscape features explained the abundance and diversity patterns of different bee taxa, and (iii) quantify the response of bee taxa to landscape features.

## 2. Methods

### 2.1. Study area and field sites

The study was conducted in five European countries: France, Germany, Poland, Sweden and UK (Fig. 1). The field sites were located in different environmental regions following Metzger et al. (2003): Mediterranean north (France), Atlantic central (Germany and the UK), continental (Poland), and nemoral (Sweden).

In each country, we selected a different annual entomophilous crop species: buckwheat *Fagopyrum esculentum* (Poland), cantaloupe

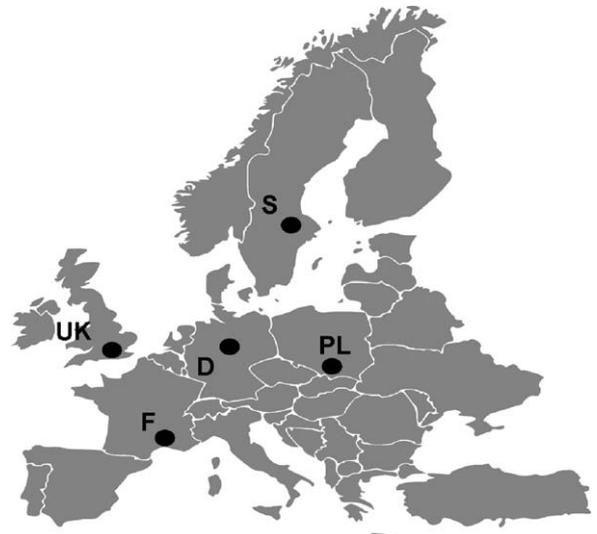


Fig. 1. Location of the study sites in France (F), Germany (D), Poland (PL), Sweden (S), and the United Kingdom (UK) (map: <http://www.mygeo.info/landkarten/europa>).

*Cucumis melo* (southern France), field beans *Vicia faba* (UK), spring rape *Brassica napus* (Sweden), and strawberry *Fragaria × ananassa* (Germany). Four of these crops have open-access flowers while field bean has papilionaceous flowers with restricted-access, thereby limiting the range of flower visitors (Free, 1993). The crops considered were the dominant entomophilous cultivated annual species in each region. Perennial crops such as forage and orchards were not considered as, from a land use standpoint, these areas are less disturbed than those of annual crops. Our goal was not to isolate crop and country as separate factors as we wanted to test the stability of the wild bee response to landscape context over a range of contrasting situations. We thus considered the five pairs of country and crop model as independent replicates.

We selected 10 sites in each country. In France and Poland, data from 1 and 4 field sites, respectively, were unavailable because crops were destroyed by hail storms. In each country, the fields were located along a gradient of landscape context with varying proportions of semi-natural habitat in a 3 km radius around the target field. The gradient went from landscapes dominated by agriculture to landscapes dominated by semi-natural habitats. The fields were separated by a minimum distance of 6 km from each other in order to be independent replicates as this distance is the maximum nesting and foraging range of most bees (Gathmann and Tschardt, 2002; Westphal et al., 2006).

### 2.2. Bee sampling and identification

Only bees were considered in this study because they represent the most important pollinator group for crops in Europe (Free, 1993). Bees were sampled in a 50 m × 25 m plot located in a homogeneous area in each field. This plot was centred in the middle of the field for those <2 ha, and, for larger fields, it was located between the geometric centre of the field and its margins. This design was selected to provide an average situation representative of each field.

Two methods were used to assess bee abundance and diversity: standardized transect walks and pan traps (Westphal et al., 2008). In each plot, a 150 m standardized transect line was set and an observer walked this line in 30 min and captured all flower-visiting bees with a net within a 4-m wide corridor. The walks were conducted at different times of day to avoid bias due to bee diurnal activity patterns (Dafni et al., 2005). In each site, two sets of pan traps of three colours (yellow, white and blue) were placed with a

5 m distance between traps within each set. The traps were made of 500 ml plastic bowls (<http://www.pro-pac.de/>) with the inside sprayed with a UV-reflecting paint (Sparvar Leuchtfarbe, Spray-Colour GmbH, Merzenich, Germany). They were filled with 400 ml of water with a drop of detergent and then exposed for 24 h. We conducted four rounds of bee sampling using both methods during the main flowering period for each crop from May to August 2005.

We identified all specimens caught in the transects and pan traps to the sub-generic level according to Michener (2000). We used the sub-generic taxonomic level as a good compromise between statistical constraints and biological significance. Concerning statistical constraints, the sub-generic level aggregates species that have similar morphological and behavioral traits, and it also increases the frequencies per modality and decreases the number of null values. Too many null values can result in a low inertia explained by each factor and a bias towards rare modalities (Lebart et al., 1997). Concerning biological significance, at the continental scale of Europe, there are over 2500 bee species (Michener, 2000) which are quite diverse and the sub-generic taxonomic level provided a more comparable level to compare the fauna of the different countries. Indeed, in other research fields, the sub-generic taxonomic level has also often been used to study diversity at similar large scales or for taxonomic groups with high number of species (Ricklefs and Miller, 2005; Lenat and Resh, 2001). Particularly for bees, the sub-generic level is congruent with morphological and behavioral similarities that allow pertinent aggregations (Danforth, 2002).

Bee abundance figures are the cumulative number of individuals from the transects and pan traps as these two methods are complementary in surveying the bee fauna (Westphal et al., 2008). Bee diversity was the number of sub-genera captured by both methods.

### 2.3. Landscape context and geographical data

We used the CORINE Land Cover (2000) database to characterize the landscape context of each field (European Environmental Agency; Corine Land Cover: France, IFEN, 2004; Germany, UBA, 2004; Poland, GIOS, 2004; Sweden, Lantmäteriet, 2004; UK, NERC, 2004). For habitat typology, we used the CORINE land cover classification. The definitions of urban, crop, and semi-natural habitats are those of level 1 CORINE while level 3 was used for more detailed habitat typology. For example, the broad-leaved forest type refers to the level 3 and is comprised within the semi-natural habitats considered at the level 1 of CORINE.

The map resolution was 25 m × 25 m and we extracted raster layers around each field with GRASS 6.2 (Neteler and Mitasova, 2004). Based on these layers, landscape parameters were calculated using FRAGSTAT 3.1 considering class and landscape metrics (Table 1; McGarigal and Marks, 1995). The class metrics referred to habitat patches with the same CORINE classification while landscape metrics referred to all classes. The metrics used belonged to four categories: (i) area, density and edge metrics, (ii) shape metrics, (iii) isolation and proximity metrics, and (iv) contagion and interspersions metrics, and all defining equations are given in the FRAGSTAT documentation (McGarigal and Marks, 1995). The aggregation index (AI) ranges from 0 for maximally disaggregated to 100 when the landscape consists of a single patch. The interspersions and juxtaposition index (IJI) also range from 0 when a patch type is adjacent to only one other category of patch and 100 when a patch is adjacent to all category types.

### 2.4. Statistical analyses

To assess the landscape scale that best explained bee community assemblages, we looked at the strength of the

**Table 1**

Landscape parameters extracted around each field site based on the CORINE Land Cover database.

Classification	Level	Parameter (code)
Area/density/edge metrics	Class metrics per each category	Mean (patch area) (AREA) Mean (patch perimeter) (PERIM) Number of patches (NB)
	Landscape metrics	Number of patches per category (NB) Number of classes (NB)
Shape metrics	Class metrics for each category	Mean (perimeter–area ratio) (PARA)
Isolation/Proximity metrics	Patch metrics	Euclidean nearest neighbour distance (ENN)
Contagion/interspersion metrics	Class metrics	Aggregation index (AI) Interspersion and juxtaposition index (IJI)

relationship between the landscape parameters considered at the CORINE level 1 and bee abundance and diversity over different scales (Steffan-Dewenter et al., 2002). We extracted landscape parameters over 500 m increments from a radius of 500–3000 m. Regression coefficients from the Partial-Least-Square 1 analyses were used to determine the landscape scale that gave the best fit.

In order to assess which habitat attributes (habitats, patterns) explained the abundance and diversity of different bee taxa, we used a three-step analysis protocol at the landscape scale previously found. First, we tested the hypothesis that an increase in the proportion of semi-natural habitat in the landscape context increased the abundance and diversity of wild bees using linear regressions between the proportion of semi-natural habitat defined according to the level 1 of CORINE classification and bee abundance and diversity. At this initial step, the regression analyses were conducted over all sub-genera. To obtain the global significance of these comparisons over the five crop-country replicates, we combined probabilities from the five regression tests using meta-analysis method (Sokal and Rohlf, 1995).

Second, we examined the relationship between bee abundance and the landscape. To do so, we used a non-metric multi-dimensional scaling (NMDS) analysis that was carried out using the Vegan R package (Faith et al., 1987). NMDS is described as most appropriate for biotic community data analysis in that it carries no assumption of multivariate normality and has been shown to produce the most accurate representation of underlying data structure (Clarke, 1993). The Bray–Curtis index (Bray and Curtis, 1957) was used as dissimilarity metrics and three axes were extracted. At this stage, we did not take into account rare sub-genera because they contribute little interpretive value and add noise to potential underlying patterns (Gauch, 1982) and this methodology is often used in species ordination in ecology (Legendre and Legendre, 1998). Sub-genera with less than 10 captured specimens over all countries represented only 1% of the total number of specimens, and we removed those sub-genera from the analyses. Then, an ascending hierarchical classification analysis using the Ward criteria (Lebart et al., 1997) was done for both sites and sub-genera in order to identify groups. The coordinates on the NMDS axes were used as input variables. Based on this analysis on bee fauna composition, we identified a structure across Europe with different groups of sub-genera. Then, at the landscape scale previously calculated, the significant landscape parameters calculated at the level 3 CORINE classification were determined with Partial-Least-Squares regression analysis (PLS) by bootstrapping ( $P \leq 0.05$ ). PLS analysis was chosen because (i) the directions in the predictor space can be clearly interpreted, (ii) the new predictors used in the analysis are

orthogonal so problems of predictor colinearity are eliminated, (iii) it is possible to have more predictors than observations (De Veaux, 1995; Tenenhaus, 1998). Thus, this method is less restrictive than stepwise regression based on the AIC criteria especially when predictors are correlated (Dortmann et al., pers. comm.; De Veaux, 1995). We made a distinction between the abundance of honeybees and that of other bees because honeybee patterns are likely to reflect beekeeper activities in addition to landscape parameters.

Third, we analysed each sub-genus separately for each country-crop and used a PLS analysis between landscape parameters and bee abundance data. Landscape parameters for each habitat type were considered whenever their effect was significant at  $P \leq 0.05$  as determined by bootstrapping. We considered only the bee sub-genera whose abundance was significantly explained by the landscape parameters. We looked at the parameters of the level 3 CORINE land cover habitat types that significantly affected bee abundance and pooled them on the level 1 CORINE habitat types. These parameters did not give information on the relative importance of the effect of each factor, but they provided for each sub-genus a profile of its response to landscape context. We used a correspondence analysis followed by a cluster analysis, based on the profile of each taxon, to visualize the similarities of their response pattern to the landscape elements.

The NMDS, clustering analyses, and multiple regression analyses were done with R 2.5 (Dalgaard, 2002). For multiple regression analyses, abundance and diversity were analysed after a square-root transformation in order to stabilise the variance among groups (Sokal and Rohlf, 1995). Correspondence analyses were performed with SPAD (Lebart et al., 1997).

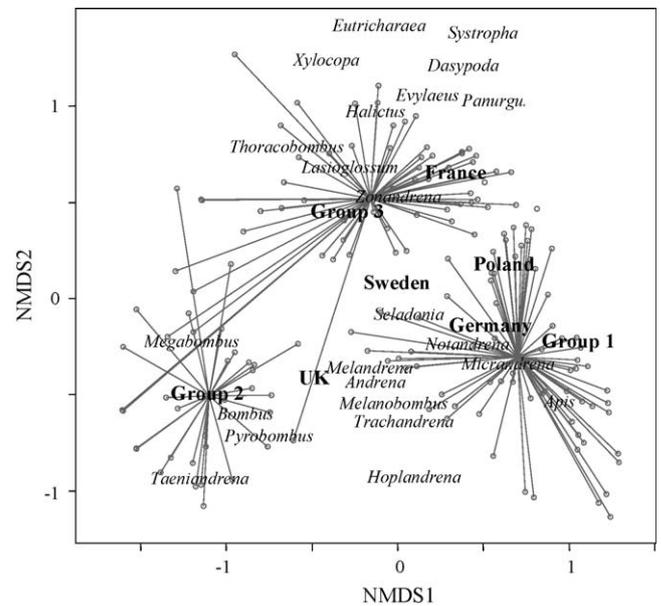
### 3. Results

#### 3.1. Bee fauna composition and structure across Europe

A total of 10,026 bees were collected in the five country-crop combinations, of which 8510 were captured by net in transects and 1516 in pan traps. In Germany, Poland and Sweden, bee abundance was explained primarily by the presence of honeybees, which represented 80–92% of the total bee specimens collected in these countries, while honeybees represented only 32% of the specimens in the UK and 29% in France. We recorded 59 sub-genera of wild bees over all countries, with 43 sub-genera from transects, 17 from pan traps and 27 from both methods. The highest sub-generic richness was found in France (37) and the lowest in Sweden (6), while other countries had intermediate values (UK 24, Germany 21, and Poland 18).

There were 23 sub-genera with less than 10 specimens caught over all countries and these were excluded from subsequent analyses (Annexe 1). The NMDS conditions of use were satisfied and variation in sub-generic bee assemblages among sites was adequately summarized by an NMDS ordination with three-dimensions (stress based  $R^2 = 0.98$ ). The clustering analysis identified three main groups of sub-genera corresponding to three country-crop groups. Group 1 characterized the bee fauna in Germany-strawberry, Poland-buckwheat and Sweden-spring oil-seed rape and comprised an average of 94% of the individuals from these countries. Group 2 was UK-field bean comprising 53% of the bees captured in this system, and group 3 consisted of France-cantaloupe comprising 65% of the bees captured.

Each group was characterized by a distinct sub-generic pattern (Fig. 2). Group 1 was defined by nine sub-genera which represented 72% of the total number of specimens over all samples, and it was strongly dominated by honeybees (92% of the specimens). Group 2 was defined by four sub-genera that represented only 13% of the total number of specimens, with



**Fig. 2.** Distribution of bee sub-genera for the three groups of European country-crop on the first NMDS plane. Each field site  $\times$  date is indicated by a small grey circle. The country names and sub-genera were placed in their centroid. The grey 'spider web' indicates each group, as determined by clustering analysis based on Ward criteria. The centre of the 'spider web' indicates the centroid of the group and each related line the site  $\times$  date belonging to the group.

*Bombus* as the main sub-genus accounting for 93% of the group, and three other sub-genera representing 7% (79% of which were *Megabombus* and *Pyrobombus*, two sub-genera closely related to *Bombus*). Group 3 was defined by 10 sub-genera that accounted for 15% of the total specimens. Two sub-genera (*Dasyptoda* and *Evylaeus*) dominated this group and accounted for 59% of the specimens in the group.

#### 3.2. Bee community in relation to landscape context

The proportion of semi-natural habitat over a 3 km radius, ranged from 0 to 91% (Table 2). Crops were the most represented habitat in the landscape (mean 63%), except for Sweden which was dominated by semi-natural habitats. Urban habitat was the least common with a mean of 8% of landscape context. The landscape range of 3 km radius explained the highest proportion of variance for bee abundance and diversity as determined by the PLS1 analyses. We therefore used this range for the following analyses.

At the country scale, only in the UK did bee abundance increase significantly with the proportion of semi-natural habitats, and only in Poland did bee diversity increase significantly with the

**Table 2**

Crop species and main landscape context for the five country-crop pairs in which our study was conducted. Values are means with range given in parentheses.

Pairs		Corine level 1 habitat type (over 3 km radius)		
Country	Crop model	Urban (%)	Crop (%)	Natural (%)
France	Cantaloupe, <i>Cucumis melo</i>	5 (0–15)	67 (17–88)	28 (11–83)
Germany	Strawberry, <i>Fragaria <math>\times</math> ananassa</i>	14 (3–27)	70 (39–91)	16 (2–53)
Poland	Buckwheat, <i>Fagopyrum esculentum</i>	9 (1–41)	69 (19–96)	22 (2–80)
Sweden	Spring rape, <i>Brassica napus</i>	0	44 (9–99)	56 (1–91)
United Kingdom	Field bean, <i>Vicia faba</i>	12 (0–34)	67 (9–97)	21 (0–91)

**Table 3**  
Significance of the linear regression between the proportion of semi-natural habitats defined as the level 1 CORINE classification in a 3 km radius around each site and the abundance and diversity of wild bees.

Category	Country/crop	Number of sites	$r^2$	$P$ value	Slope coefficient (for $P \leq 0.05$ )
Wild bee abundance	France/cantaloupe	9	0.09	0.81	–
	Germany/strawberry	10	0.17	0.64	–
	Poland/buckwheat	6	0.59	0.22	–
	Sweden/spring rape	10	0.32	0.34	–
	UK/field bean	10	0.83	0.003	21.7
Wild bee diversity (number of sub-genera)	France/cantaloupe	9	0.32	0.39	–
	Germany/strawberry	10	0.32	0.37	–
	Poland/buckwheat	7	0.90	0.01	12.9
	Sweden/spring rape	10	0.30	0.39	–
	UK/field bean	10	0.48	0.16	–

proportion of semi-natural habitats (Table 3). At the European scale, considering all country-crops together, neither wild bee abundance and nor sub-generic diversity were affected by the proportion of semi-natural habitats. Therefore a more detailed approach was necessary to understand the possible links between specific landscape features and wild bee communities, and we used the more detailed CORINE level 3 classification.

The CORINE level 3 landscape parameters explained  $\geq 17\%$  of the variance in bee abundance and diversity (minimum  $r^2$  value in Table 4), and all the models were significant ( $P < 0.05$ , Table 4). Seventeen of the 160 initial landscape parameters significantly affected the patterns of bee sub-genera (Table 4). We did not find any effect of the number of different habitats in the landscape on bee abundance or diversity in any of the three crop-country groups.

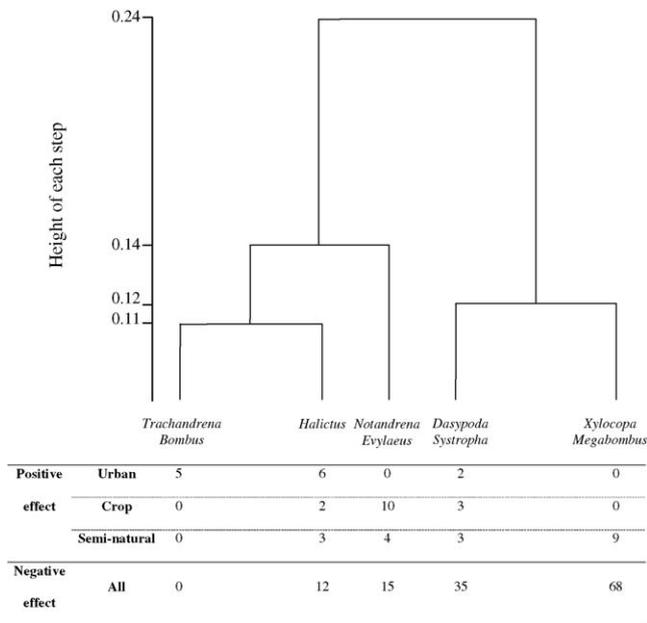
The abundance of honeybees in all countries was positively associated with urban habitats (Table 4), specifically with the interspersed and juxtaposition of discontinuous urban fabric and the area of continuous urban fabric and industrial or commercial units. In contrast, honeybee abundance was negatively affected by the interspersed and juxtaposition of non-irrigated arable land, and the Euclidian distance between complex cultivation patches. With honeybees removed, the abundance and diversity of wild bees were affected differently among the three crop-country groups (Table 4). For group 1 (Sweden, Poland, and Germany), wild

bee abundance increased with the aggregation of discontinuous urban fabric patches and decreased when the perimeter:area ratio of coniferous forest patches increased. Wild bee diversity increased with the mean area and perimeter of broad-leaved forest patches, the perimeter of non-irrigated arable land, and the perimeter:area ratio of sport and leisure facilities. For group 2 (UK-field bean), the abundance and diversity of wild bees increased with transitional woodland-shrubs habitats, and the area of these patches was correlated with wild bee abundance and their perimeter:area ratio was correlated with sub-generic diversity. For group 3 (France-cantaloupe), the abundance of wild bees increased with the area and aggregation of industrial or commercial units patches, while diversity decreased significantly with the interspersed and juxtaposition of discontinuous urban fabrics and semi-natural grassland.

The abundance of only nine of the original 23 sub-genera used in the previous analyses was significantly correlated with individual landscape parameters, and were therefore considered further. These sub-genera were also the most abundant overall and represented the most abundant taxa in each crop-country group (group 1–93% of the wild bees, group 2–96% and group 3–90%). The global  $\chi^2$  test of the correspondence analysis based on the array of the 12 significant landscape parameters of Table 4 by sub-genera abundance was significantly structured ( $P < 0.0001$ ), with the first five Eigenvalues explaining 81% of the total inertia.

**Table 4**  
Landscape parameters with significant positive and negative effects on bee sub-genera abundance and diversity among the groups of countries as defined by NMDS. The significance of parameter effect was first determined from the PLS analysis by bootstrapping ( $P \leq 0.05$ ). Habitat typology refers to the level 3 CORINE land cover and the parameters are those listed in Table 1.

Groups	Type	$r^2$	Effect	Habitat typology		Parameters $P$ value
				CORINE Level 1	CORINE Level 3	
<b>Honeybees</b>						
All countries	Abundance	0.30	Positive	Urban (1)	Discontinuous urban fabric (112) Continuous urban fabric (111)	IJI (<0.0001) AREA (0.010)
			Negative	Crops (2)	Industrial or commercial units (121) Non-irrigated arable land (211) Complex cultivation patterns (242)	AREA (0.007) IJI (0.004) ENN (0.026)
<b>Wild bees</b>						
Group 1 (Sweden, Germany, Poland)	Abundance	0.28	Positive	Urban (1)	Discontinuous urban fabric (112)	AI (<0.0001)
	Diversity		Negative	Semi-natural (3)	Coniferous forest (312)	PARA (0.03)
Group 2 (UK)	Abundance	0.17	Positive	Urban (1)	Sport and leisure facilities (142)	PARA (0.003)
	Diversity		Positive	Crops (2)	Non-irrigated arable land (211)	PERIM (0.005)
Group 3 (France)	Abundance	0.27	Positive	Semi-natural (3)	Broad-leaved forest (311)	AREA (<0.0001), PERIM (0.003)
	Diversity		Negative	Semi-natural (3)	Transitional woodland-shrub (324)	AREA (0.025) PERIM (0.005)
Group 3 (France)	Abundance	0.46	Positive	Urban (1)	Industrial or commercial units (121)	AREA (0.04), AI (0.01)
	Diversity		Negative	Urban (1)	Discontinuous urban fabric (112)	IJI (<0.0001)
				Semi-natural (3)	Natural grassland (321)	IJI (0.004)



**Fig. 3.** Groups of sub-genera with similar responses to landscape context. The correspondence and clustering analyses were based on the number of landscape parameters that significantly affected each taxon. The dendrogram of similarity illustrates the distance between taxon with respect to landscape. The height between step is based on similarity metrics from Ward criteria. The table under the dendrogram indicates the impact of habitat types on the abundance of the five groups of bee sub-genera. The figures refer to the numbers of landscape parameters among a total of 160 extracted from the level 3 CORINE land cover habitat types that positively or negatively affected bee abundance when pooled on the three level 1 CORINE habitat types ( $P \leq 0.05$  as determined by bootstraps in PLS1 analyses).

The consolidation of groups with the mobile barycentre method during the cluster analysis needed only three steps, which indicated group stability (Lebart et al., 1997). We found five groups of sub-genera with different responses to habitats (Fig. 3). In parallel, we identified a number of significant parameters when pooled at level 1 of CORINE classification for the five groups.

The density of *Trachandrena* and *Bombus* increased with urban habitats (Fig. 3), with five significant parameters of discontinuous urban fabric habitats (with  $P < 0.03$ ). The abundance of both *Xylocopa* and *Megabombus* increased significantly with some semi-natural habitats such as mixed, broad-leaved forest habitats (with several parameters and  $P < 0.02$ ), but was negatively impacted by a range of habitats including discontinuous or continuous urban fabrics, and dune or sand habitats (with  $P < 0.03$ ). These two sub-generic groupings were at the two extremes of the dendrogram. The abundance of *Notandrena* and *Evylaeus* was mostly affected by crops and their position was intermediate between the two previous extremes (Fig. 3).

The number of landscape parameters with a significant negative effect on the abundance of a sub-genus provides a 'vulnerability index', i.e. a range of resistance to landscape change for this sub-genus with regards to habitats. When sub-generic abundance is negatively correlated with a large number of landscape parameters, it will be more vulnerable than a sub-genus with its abundance affected negatively by none or only few parameters. Sub-genera that were positively affected only by semi-natural habitats were more vulnerable than those that were positively impacted only by urban habitats (Fig. 3). Between these extremes, the more a bee sub-genus was positively affected by disturbed habitats, such as urban habitats and crops, the less this sub-genus was vulnerable.

#### 4. Discussion

Our results indicate that agricultural intensification, defined by Kremen et al. (2007) as an increase of arable area combined with the loss and fragmentation of semi-natural habitats, may not lead to the extinction of all bees in agroecosystems, but instead may change its community composition with an increase in the most resilient bee sub-genera and loss of the more vulnerable species. Indeed, similar results have been found for wild plants in agroecosystems (Booth and Swanton, 2002; Fried et al., 2006). Our results also indicate that agricultural intensification leads to a decline of the more vulnerable sub-genera and thus in the overall bee diversity, an element of biodiversity which may be essential for the delivery of stable pollination services to crops and wild plants alike (Klein et al., 2002; Fontaine et al., 2006).

Over all samplings, the total diversity of 60 sub-genera we recorded was low compared to the total number of bee sub-genera in Europe (less than 20%; Michener, 2000) suggesting that only a small proportion of bees interact with annual crops. And, the proportion that contribute to the pollination service of these crops might be even less because pan traps might have attracted species that did not forage on the crop, but simply used the land for nesting. Furthermore, a crop may be effectively pollinated by a subset of its overall flower-visiting insect community. In view of the small number of taxa potentially involved in crop pollination, pollination services for entomophilous crops thus appear even more fragile when considering current bee decline (Chapin et al., 2000).

In Germany-strawberry, Poland-buckwheat and Sweden-spring oilseed rape, we observed the lowest diversity of sub-genera (Appendix B) and the bees captured were mainly honeybees. Our results are consistent with the lower bee diversity in the nemoral and continental parts of Europe (Michener, 2000). In the UK, field beans had closed papilionaceous flowers that only pollinators with long and strong mouthparts can access (Free, 1993), an example in which trait complementarity of pollinators and exploitation barriers of the crop flower constrains the plant–pollinator network (Santamaria and Rodriguèz-Gironés, 2007). Thus, the majority of bees we collected on field bean were bumblebees. In France, cantaloupe had open-access flowers and the bee fauna was diverse with 37 sub-genera, many of which were unique to France. This probably reflects the geographical location since the sites were in south-eastern France, and the Mediterranean is a recognised hot spot of bee diversity (Michener, 2000; Vamosi et al., 2006).

At the European scale, honeybee abundance was favoured by the proximity of urban habitats and is probably a direct consequence of urban beekeeping practices. Steffan-Dewenter et al. (2002) found that honeybee abundance increased when the proportion of semi-natural habitats decreased and we did not find such an effect. We found that the distance between complex cultivation patches negatively affected honeybee abundance suggesting that beekeepers may choose to locate more honeybee colonies near aggregations of arable land.

Contrary to several previous studies (e.g., Steffan-Dewenter et al., 2002; Steffan-Dewenter, 2003), we found that wild bee abundance and diversity were not significantly affected by the proportion of semi-natural habitats. However, earlier studies did not sample field crops and we identified semi-natural habitat directly as defined at the level 1 of the coarse CORINE land cover classification ( $25 \times 25$  m), which differed from the direct mapping of semi-natural habitats used in other studies. Most studies to date considered only the influence of a few selected types of semi-natural habitats, such as forest or woodland (Roubik, 2000; Kremen et al., 2002, 2004; Klein et al., 2002) or aggregated landscape elements into few categories (Steffan-Dewenter, 2002, 2003; Steffan-Dewenter et al., 2002; Westphal et al., 2003;

Herrmann et al., 2007). We also defined wild bee diversity as the number of sub-genera which differs from other studies that considered species richness. The difference in results may thus reflect these differences in the definition of diversity and the landscape classification used.

In all systems with open flowers (buckwheat in Poland, cantaloupe in France, spring oilseed rape in Sweden, and strawberry in Germany), wild bee abundance was positively affected by urban habitats (Table 4) and these taxa could be locally very abundant. Urban habitats can provide suitable nesting habitat for some bees that nest in bare ground (Pouvreau and Loublier, 1995; Frankie et al., 2005; McFrederick and LeBuhn, 2006; Smith et al., 2006; Matteson et al., 2008; Wojcik et al., 2008). Our results also indicate that some semi-natural habitats can negatively affect wild bee abundance in nearby flowering fields. For example, the perimeter:area ratio of forests had a significant negative impact on wild bee abundance, suggesting that small forest patches can act as barriers isolating fields (Fagan et al., 1999). An alternate explanation could be that semi-natural patches act as sinks by drawing bees off the crops. If this were the case, semi-natural habitats might sustain bee populations but that does not show up in our surveys conducted in agricultural fields. This is unlikely at least in Provence, however, because our recordings were done in July when field plantations of cantaloupes are in bloom while the vegetation in semi-natural habitats is mostly all dried up with very few flowers available. In contrast, in the UK-field bean system, the papilionaceous crop flowers acted as a strong filter to the wild bee community in selecting for bumblebees, and wild bee abundance was positively linked to semi-natural habitats (e.g., pasture), which is consistent with other studies on bumblebees (Kremen et al., 2002; Steffan-Dewenter et al., 2002).

In our study, wild bee diversity was positively associated with some semi-natural habitats such as broad-leaved forest and woodland-shrub that can act as refuges for bees in agricultural landscapes (Kremen et al., 2002; Steffan-Dewenter et al., 2002; Tschardt et al., 2005). But some crop and urban habitats (e.g., pasture and sport and leisure facilities) were also found to have positive effects on bee diversity in group 1 (Germany, Poland and Sweden; Table 4), as found in other studies (Vaissière et al., 1985; Pouvreau and Loublier, 1995; Shuler et al., 2005). These mixed habitats often contain a diverse flora that may provide forage resources (Potts et al., 2003; Winfree et al., 2007). However, the total number of habitat types did not have a significant effect on bee diversity; while bee diversity was favoured by some habitats, it was not affected by the overall heterogeneity, contrary to the results of Tschardt et al. (2005), but consistent with those of Steffan-Dewenter (2003) who found no effect of overall landscape heterogeneity on species richness of wild bees.

The wild bee fauna in European crops was composed of sub-genera that were significantly affected by either (i) some urban habitats, (ii) some semi-natural habitats or (iii) a combination of urban, crop and semi-natural habitats. This variability may reflect the diversity of bee ecology and behavior (Michener, 2000). For example, *Xylocopa* spp. nest in wood and so may favour forest landscapes (Klein et al., 2002), whereas *Halictus* spp. nest in the soil under bare ground and may favour human-disturbed habitats. Some habitats, such as mass-flowering crops, may provide forage only while other habitats, such as semi-natural or urban habitats, can provide both nesting sites and foraging habitats. Mass-flowering crops can supplement foraging habitats, and, indeed, higher colony densities of common bumblebee species can be found in agricultural landscapes with large amounts of oilseed rape (Westphal et al., 2006; Herrmann et al., 2007). In our study, closely related sub-genera had strikingly different responses to different habitat types. For example, *Bombus* was positively impacted by urban areas, while *Megabombus* was positively impacted solely by

semi-natural habitats, and the closely related sub-genus *Thoracobombus* was not affected at all by the landscape context. This last finding was consistent with those of Herrmann et al. (2007) who found no effect of semi-natural habitats on the density of *Bombus* (*Thoracobombus*) *pascuorum* colonies.

Bee sub-genera for which abundance was positively correlated with urban or crop habitats were less vulnerable than others to disturbed habitats and they were also usually the most abundant recorded in our annual crops. This result explains why overall wild bee abundance was positively affected by some urban and crop habitats (Table 4). We conclude that, for our crop systems, some wild bee taxa may not be affected by semi-natural habitat in the surrounding landscape, as suggested by Ghazoul (2005), and some might even be favoured by land use intensification. However, our approach did not take into account other key measures of agricultural intensification such pesticide use that can negatively affect bee populations (Devilleers and Pham-Delègue, 2002; Mineau et al., 2008). In contrast, bee sub-genera whose density was positively affected by semi-natural habitats were more vulnerable to disturbed habitats in the landscape.

Our results provide evidence indicating which habitats in the landscape can affect the abundance and diversity of bees in flowering annual entomophilous crops. Management of wider landscapes could therefore be regarded as a tool for conservation managers to maintain or increase vulnerable species. One approach is to increase the coverage of ecological compensation areas, as this can be effective in enhancing bee abundance and diversity (Albrecht et al., 2007; Holzschuh et al., 2007). An alternative approach would be to protect or restore selected habitats in order to increase the prevalence of the more vulnerable bee taxa. From a wider perspective, it may be possible to manage bees to pollinate crops by assessing the functional needs of crop species and then matching bee taxa to these needs. However, before bee communities can be sustainably managed for pollination, more studies on the relationship between pollinators and their ability to deliver pollination services are needed.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.agee.2009.05.001](https://doi.org/10.1016/j.agee.2009.05.001).

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