CrossMark

ORIGINAL PAPER

Habitat, spatial and temporal drivers of diversity patterns in a wild bee assemblage

Orianne Rollin · Vincent Bretagnolle · Laura Fortel · Laurent Guilbaud · Mickaël Henry

Abstract Across Europe conservation actions have been implemented to mitigate the decline of pollinators in agricultural landscapes. However, recent concerns have appeared about their efficiency to promote pollinator diversity. To increase the efficiency of these interventions, one must acquire a better knowledge of the target species diversity patterns and its sources of variations at different spatial and temporal scales. This study sets out to identify the main sources of variation in wild bee assemblages at a regional scale (450 km^2) in mass-flowering crops and semi-natural habitats. During three consecutive sampling years, we monitored bee diversity and its temporal and spatial turnovers. We show that an intensive agricultural landscape in western France can hold nearly 200 wild

---

O. Rollin (✉)
ITSAP-Institut de l'abeille - UMT PrADE, 228 route de l'Aérodrome, Domaine Saint Paul, Site Agroparc, CS 40509, 84914 Avignon Cedex 9, France
e-mail: orianne.rollin@itsap.asso.fr; orianne.rollin@gmail.com

O. Rollin · L. Guilbaud · M. Henry
UMT Protection des Abeilles dans l'Environnement, 228 route de l'Aérodrome, Domaine Saint Paul, Site Agroparc, CS 40509, 84914 Avignon Cedex 9, France

V. Bretagnolle
Centre d'Etudes Biologiques de Chizé, CNRS & Université de la Rochelle, UMR 7372, 79360 Beauvoir-Sur-Niort, France

V. Bretagnolle
LTER « Zone Atelier Plaine & Val de Sèvre », Centre d'Etudes Biologiques de Chizé, CNRS, 79360 Villiers-En-Bois, France

L. Fortel · L. Guilbaud · M. Henry
INRA, UR 406 Abeilles et Environnement, Domaine Saint Paul, Site Agroparc, CS 40509, 84914 Avignon, France

bee species at a regional scale, i.e. 20 % of the whole bee fauna known in mainland France. Wild bee diversity was 3–4 times lower in oleaginous crops than in semi-natural habitats, with a substantial number of these being social and gregarious species. Spatial and seasonal species turnover in semi-natural habitats explained 28.6 and 34.3 %, respectively, of regional species richness. Given the importance of the spatial component of the bee diversity turnover, we suggest wild bee conservation efforts should be carried out at relevant spatial scales. The spatial turnover was estimated to be steeper within 50 km^2 scales. This provides an order of magnitude for the spatial extent of *relevant conservation units* within which one may concentrate conservation efforts in order to optimise the number of species promoted per surface area.

Introduction

Entomophilous pollination service could be at risk due to a global decline in pollinator populations, particularly in agricultural landscapes (Biesmeijer et al. 2006; VanEngelsdorp et al. 2008; Potts et al. 2010a, 2010b, Cameron et al. 2011). Thus, conservation actions specific to agrosystems have been proposed to mitigate the effects of agricultural intensification on pollinators, especially bees (Dicks et al. 2010), but results are equivocal (Kleijn et al. 2001; Kleijn and Sutherland 2003; Knop et al. 2006). One reason for this uncertainty may lie in our poor knowledge of diversity patterns of the target species, and their sources of variation at a landscape scale. In this study we qualify the spatial and temporal variations in species richness as "diversity patterns" (Tylianakis et al. 2005). Species richness is likely to vary with available foraging habitats due to species' specific ecological requirements (i.e., the ecological niche theory: Chase 2011). Species richness may alternatively change along temporal or spatial axes due to natural species turnover, which can lead to different perceptions of diversity depending on the scale of focus (Palmer 1995; New 1999). For instance, spatial turnover may arise from limiting the dispersal of species, as constraining their spatial distribution will lead to heterogeneity of species richness in space (Hubbell 2001). The balance between deterministic and stochastic processes in shaping community assemblages is currently hotly debated (Chave 2004; Leibold and McPeek 2006).

There is empirical evidence that bee species richness displays high levels of spatial and temporal turnover due to specific seasonal or habitat requirements (Roubik 2001; Oertli et al. 2005; Tylianakis et al. 2005; Munyuli et al. 2013). In agricultural landscapes, semi-natural habitats provide continuous and more diversified floral resources and nesting sites than mass-flowering crops (Steffan-Dewenter and Tscharntke 2001; Potts et al. 2003). They also harbour a greater abundance and possibly greater diversity of wild bees (Rollin et al. 2013). In particular, functional traits, such as sociality, nesting behaviour or differing pollen collection apparatus (Westrich 1989; Michener 2007) may to a large extent influence whether a species chooses to forage, or not, on particular monospecific mass-flowering crops.

Beyond species-specific habitat requirements, bee communities are subject to strong temporal changes in their composition, both within and among years (Roubik 2001; Oertli et al. 2005; Tylianakis et al. 2005; Munyuli et al. 2013). In Oertli et al. (2005), of the 247

recorded bee species, 22.3 and 25.5 % were found during a single month and single year, respectively. The same trends were observed by Tylianakis et al. (2005), with temporal and spatial turnovers accounting for 23.1 and 38.6 % of the total diversity, respectively. Wild bees have evolved different phenologies, scaled on climatic preferences and/or on the availability of specific floral resources (Pouvreau 2004). For example, in temperate regions, some bee species are maturing early and are active in spring (e.g. in April–May for *Andrena bucephala* and *Nomada fabriciana*), while others emerge later in the season (e.g. in June or later for *Hylaeus brevicornis* or in late August for *Colletes hederae*) (Westrich 1989).

Regardless of habitat- and season-driven variations in bee diversity, a substantial part of total species turnover may be explained by the geographic distance between patches. Two areas located further apart from each other might have less species in common than two neighbouring areas (Gering et al. 2003; Tylianakis et al. 2005; Müller and Goßner 2010). As a universal rule, species richness increases with the size of the sampled area (Scheiner 2003; Dengler 2009) because new species are always encountered (Magurran 2004) due to biotic or abiotic environmental changes such as feeding and nesting resources, temperature, hygrometry, predation, etc. The additive partitioning method provides a straightforward way to statistically quantify such changes in species diversity over different spatial and temporal scales. Lande (1996) has formalized a specific terminology to describe additive partitioning patterns, with the among-community diversity changes (β diversity) being defined as the difference between total species diversity of a region (γ diversity) and the average within-community diversity (α diversities), leading to the general equation $\beta = \gamma - \alpha$ (Crist et al. 2003). The statistical significance of β is usually assessed through random permutations of samples to simulate the hypothesis of no spatial turnover of species occurrence (Crist et al. 2003). β diversity may be further subdivided into a broader range of intermediate spatial scales, and even assigned to temporal changes in diversity (Tylianakis et al. 2005).

This study sets out to provide a general and functional description of the wild bee diversity and to identify its main sources of variation at a range of spatial scales in an intensive farming system, from the very local scale (c. 100 m^2) to the regional scale (450 km^2). Three general questions were addressed and investigated using a spatially extensive survey: (i) at the regional scale, how does species richness vary between the main foraging habitats, namely mass flowering crops and herbaceous semi-natural habitats?, (ii) how can variation in bee species richness be explained by species functional traits related to dietary specialisation, nesting and social behaviour?, (iii) beside habitat, can those species variations be associated with significant turnover throughout seasons ($\beta_{seasonal}$) and spatial scales ($\beta_{spatial}$). We further argue that if the bee community shows evidence of substantial species turnover below the regional scale, it is critical for conservation biologists to identify at which scale this turnover is steepest. We finally discuss the implications of these diversity patterns for optimising the spatial allocation of bee conservation efforts in intensive farming systems.

Material and method

Sampling design

The field data are those used in Rollin et al. (2013), detailed thereafter, supplemented by two additional sampling periods each year. The spatial and seasonal turnover of bee communities was investigated using surveys of flower-visiting bees in spring and summer

of 2010, 2011 and 2012 in the LTER "*Zone Atelier Plaine et Val de Sèvre*", a 450 km^2 intensive agricultural territory in western France (Fig. 1). Each year, surveys encompassed four distinct periods within the bee seasonal activity: (i) the oilseed rape *Brassica napus* flowering period, (ii) a period during which floral resources are quantitatively much reduced, i.e. without any mass-flowering crops, hereafter called the *food restriction* period, (iii) the sunflower *Helianthus annuus* flowering period and (iv) the *stubble field* period, with few flowering crops (mainly alfalfa *Medicago sativa*). Sampling was exclusively carried out in foraging habitats (i.e., with flowers), including mass-flowering crops (oilseed rape, sunflower and alfalfa), conspicuous patches of spontaneous wild flowers in semi-natural habitats (permanent grasslands, hedgerows, trees, external field margins) and spontaneous weed plant patches in crops or stubble fields.

We favoured an extensive sampling strategy to cover a wide variety of ecological contexts in the study area. The sampling design detailed below led to the selection of 1,286 sampling sites evenly distributed across sampling periods and habitat types. Sampling sites were located in 30 grid cells (10 cells per year) randomly drawn without replacement from a 3.3 × 3.3 km spacing grid covering the whole study area (Fig. 1). The ten grid cells to be investigated during a given year and period were processed within 12–15 days. Oilseed rape sampling periods were from April 16th to May 1st in 2010, from April 1st to 13th in 2011, and from April 6th to May 5th in 2012. Food restriction sampling periods were from June 3rd to 14th in 2010, from May 23th to June 8th in 2011, and from June 5th to 28th in 2012. Sunflower sampling periods were from July 16th to 23rd in 2010, from June 28th to July 12th in 2011, and from July 17th to August 7th in 2012. Stubble field sampling periods were from September 9th to 21st in 2010 and from August 21th to 28th in 2011. The 2012 stubble field period (from September 13th to 21th) survey yielded very few bee samples due to poor weather conditions, and therefore was not included in the analyses.
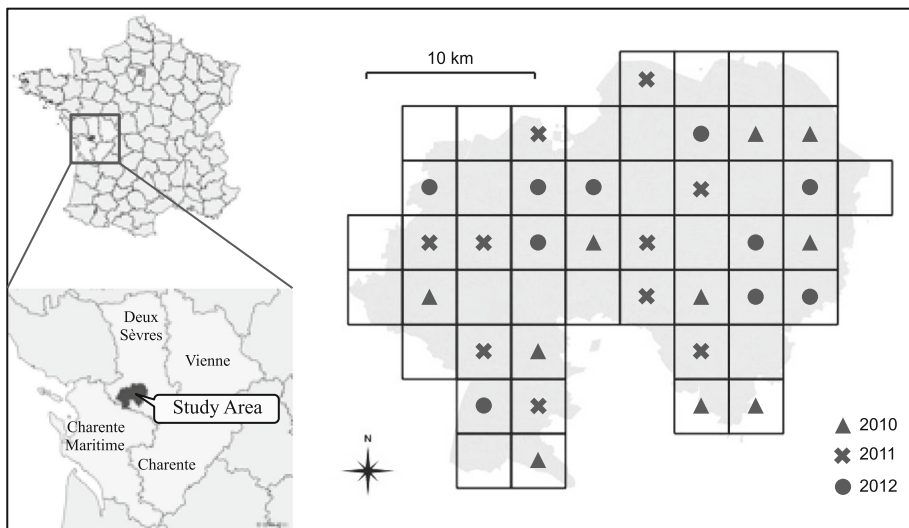
Fig. 1 Situation and map of the study area, an intensive agricultural territory in western France (Zone Atelier "Plaines et Val de Sèvres"). *Dark lines* delineate the 3.3 × 3.3-km spacing grid from which 30 grid cells were randomly drawn without replacement for bee sampling. *Dark triangles*, *crosses* and *circles* indicate the grid cells randomly selected in 2010, 2011 and 2012, respectively. All relevant flowering habitats (mass-flowering crops and semi-natural habitats) were sampled within each grid cell, though the numbers of sampling sites varied among periods and grid cells due to phenological of plant species

Because the location of wild flower patches could not be determined a priori, like mass-flowering crops and grasslands which are recorded on a local GIS database (Rollin et al. 2013), purely random sampling site selection was precluded. Instead, we developed a pseudo-random sampling strategy to study a large number of flowering crop fields and wild flower patches, located at various distances from each other, and with a preserved homogeneity between habitat types in terms of spatial and temporal distribution. Firstly, a series of itineraries transversal to each grid cell were predetermined on road maps. All mass-flowering crops and grasslands (with wild flowers patches) located close to (<500 m) those sampling itineraries were systematically visited and sampled. While traveling within fields, all accessible wild flower patches were sampled in semi-natural habitats other than grasslands (e.g. field margins), respecting a minimal 50 m distance between samples. Secondly, where time permitted, nearby flowering crops and wild flower patches were additionally sampled within the selected grid cells. In flowering crops, transects were set transversely to the most accessible field margin, toward the field centre. A buffer distance of 10 m from the field margin was kept to reduce any edge effects. In grassland, field and road margins, transects were centred on the conspicuous flower patches of at least 50 m in width.

Each site was surveyed once by capturing flower-visiting bees with a net whilst walking transects 50 m long and 2 m wide (for a duration of 15 min), between 10:00 and 19:00, under clement weather conditions (Westphal et al. 2008; Hoehn et al. 2010; Rollin et al. 2013).

Functional description of the bee community

All captured specimens were identified to the species level by respective authority for each genus (see Acknowledgements). Specimens were temporarily stored in a standard freezer until pinned and dried for identification. Only 1.75 % of the specimens could not be identified to species level, either due to damage or a difficulty to distinguish some closely related species. Species names follow the nomenclature of Kuhlmann et al. (2013) (see Appendix 1 for the entire species list). All voucher specimens were deposited in the bee collection of INRA (Institut National de la Recherche Agronomique) in Avignon (France).

The most relevant behavioural information on identified species was collected from the current literature on wild bee ecology to provide a broad picture of the functional characteristics of the whole community at the regional scale (Westrich 1989; Amiet et al. 1999, 2001, 2004, 2007, 2010). Functional traits cover diet, nesting behaviour, and social behaviour. Diet may be either *polylectic* or *oligolectic*. *Polylectic* bees forage on various unrelated kinds of flowers for pollen, whereas *oligolectic* bees are specialized on a particular pollen taxon (Michener 2007). Nesting behaviour may be either *Endogeic* or *hypergeic* (Oertli et al. 2005). *Endogeic* bees nest in the ground whereas *hypergeic* bees nest in a variety of structures above ground, e.g. in natural cavities (branches and twigs of trees and bushes, spaces under rocks, etc.; (Michener 2007). Social behaviour may be either *solitary*, *gregarious*, *primitively eusocial* or *parasitic*. *Solitary* bees construct their own nest and provide offspring with food without any help from conspecifics. *Gregarious* bees breed individually like solitary bees but nest close to conspecifics, sometimes at high densities over a limited area (mostly observed in ground nesting species). *Primitively eusocial* bees live in small colonies composed of a queen, the only egg-laying female which also initializes the nest, and of worker females which perform current tasks including foraging, cell provisioning, and nursing. *Parasitic* bees are mostly kleptoparasitic bees (cuckoo bees), which enter the nest of a host and lay eggs in existing cells (Michener 2007).

Characterization of bee γ diversity at the regional scale

Data were pooled among sampling years (2010–12) and habitat types (oilseed rape, sun-flower, alfalfa, herbaceous and woody semi-natural habitats) for computing total regional (γ) diversity. *Observed* species richness was plotted as a function of the number of sampled sites under the form of a species accumulation curve smoothed by 1,000 random rear-rangements of sampling order which also provided confidence intervals (program Esti-mateS version 9.1; Colwell 2013). Additionally, total *expected* species richness was assessed using the non-parametric estimators Chao2 and Jackknife 1 (Jack1), known to be the most accurate estimators for species-rich communities (Walther and Morand 1998). Finally, the relative difference between *expected* and *observed* species richness was computed to assess the *completeness* of the field survey, i.e. the proportion of total γ diversity that was effectively covered by our survey.

Relative difference of diversity between mass-flowering crops and semi-natural habitats at the regional scale

To compare diversity patterns between the two main foraging habitat types (mass-flow-ering crops and herbaceous semi-natural habitats) at the regional scale, the above-detailed species diversity analyses were repeated separately for each habitat type. For these anal-yses, mass-flowering crops were only represented by oilseed rape and sunflower, and semi-natural habitats refer only to herbaceous habitats. Woody floral resources and flowering alfalfa were not considered in this analysis as they were too scarce in the database for meaningful comparisons (3.8 and 5.6 % of the total samples respectively).

To understand how species richness varies between the main foraging habitats we computed and compared the 95 % confidence intervals of both *observed* and *expected* species richness values. Non-overlapping confidence intervals would indicate that the two compared richness values are significantly different. If a significant difference in species richness was detected between mass-flowering crops and semi-natural habitats, the underlying ecological processes were investigated by analysing species occurrence in relation to the functional traits of bee species. Pearson's Chi squared tests were used to determine whether particular functional traits would make some species more likely to occur in mass-flowering crops (0–1 binary data) compared to the pool of species found in semi-natural habitats during the same period. We specifically focused on social behaviour (*solitary* versus *no-solitary*), diet (*oligolectic* versus *polylectic*) and nesting behaviour (*endogeic* versus *hypergeic*). Chi squared tests were performed using the R software version 2.12.0 (R Development Core Team 2010).

Spatial and seasonal partitioning of bee diversity

The analysis of change in spatial and seasonal bee diversity focused on foraging in her-baceous semi-natural habitats as this was the only habitat type consistently sampled during the whole season. Furthermore, species richness in mass-flowering crops was too scarce to sustain partitioning analyses (see Results). Species accumulation curves and species richness were recomputed on a per-period basis (the oilseed rape flowering period, the food restriction period, the sunflower flowering period and the stubble field period) to document seasonal variations of bee diversity in herbaceous semi-natural habitats.

To determine the statistical significance of species turnover throughout spatial and sea-sonal scales, an additive diversity partitioning analysis was performed (Lande 1996; Crist and
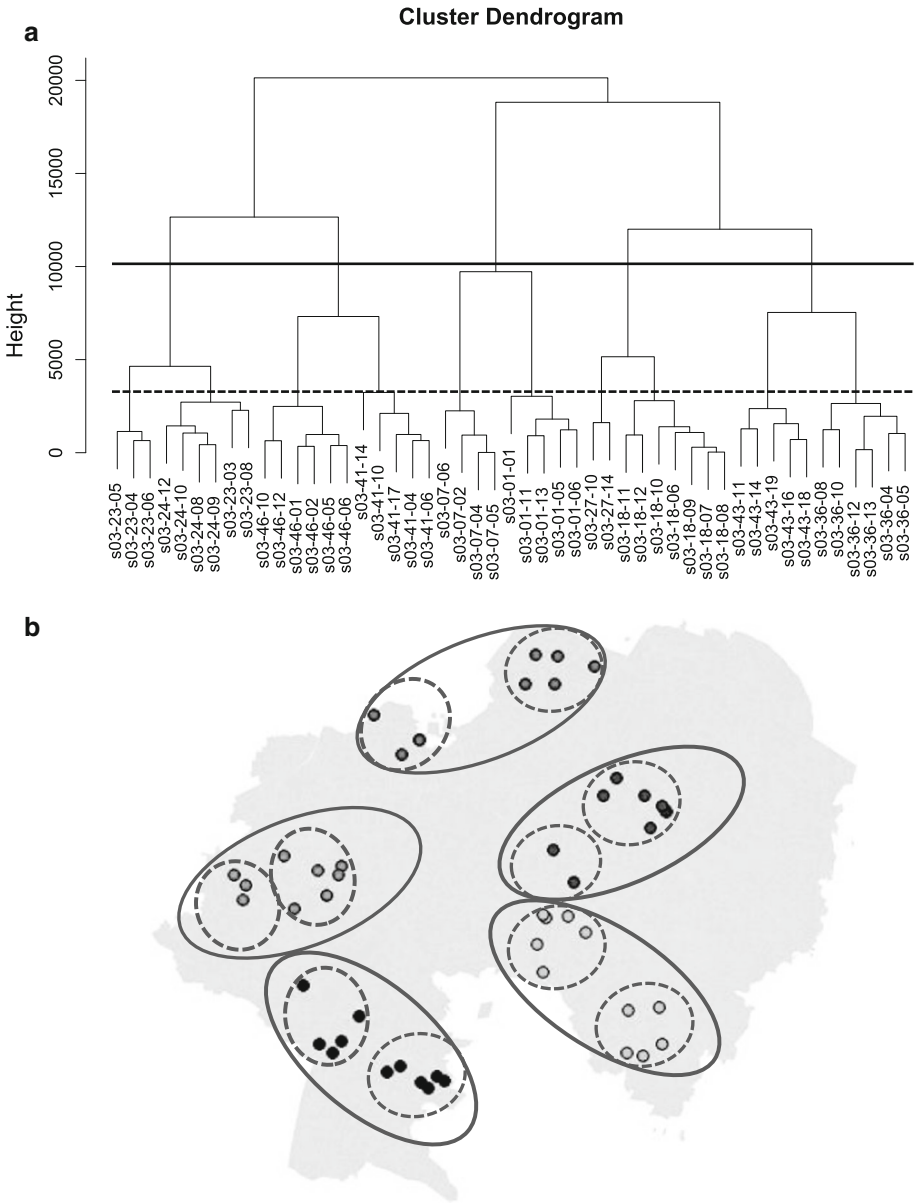
Fig. 2 Graphical representation of the hierarchical cluster analysis used for grouping sites throughout a suit of hierarchically nested spatial scales. **a** Hierarchical clustering of the 49 sites sampled in semi-natural herbaceous habitats during the sunflower flowering period in 2011 (for the example), based on Euclidian distance. The *horizontal solid* and *dashed line* shows an example of cut heights (10,000 and 3,000 m respectively) to define two nested subsets of sites. **b** Spatial representation of the corresponding site clusters obtained by cutting the cluster tree at the *solid* and *dashed line* levels (outer and inner boundaries, respectively). The analysis was repeated separately for each sampling period within each year, so that two sites processed at different sampling periods will not fall within the same cluster

Veech [2006]). Bee samples were first grouped following a series of hierarchically nested temporal and spatial scales (Fig. 2). Temporal scales were the study period (4 periods per year), nested within each study year. Likewise, the hierarchical grouping of sites across spatial scales was achieved by a hierarchical clustering of sampling sites using complete Euclidian distance linkage (hierarchical cluster analysis). Sites were then classified into a series of hierarchically nested groups by cutting the cluster tree at different neighbouring distances (250, 500, 750, 1000, 1500, 2000, 3000, 5000, 10000, 15000 m). To further disentangle spatial from seasonal species turnover, the spatial grouping of sampling sites was performed separately for each period and year (Fig. 2). In other words, spatially neighbouring sites were classified into different spatial groups if they were not sampled during the same period of the same year. Then, following the additive diversity partitioning algorithm (Oksanen et al. [2011]), mean values of local (α) diversity observed at a given spatial or temporal scale were compared to the total diversity in the entire data set (γ). To determine the species turnover across spatial and temporal scales, we compared the observed α diversity to its expected random value under the hypothesis of absence of turnover, i.e. the theoretical α returned by 1,000 simulations of random distribution of species among samples at the considered spatial and temporal scales (Oksanen et al. [2011]). Likewise, the change in β from one given scale to the next can be computed as $\beta_i = \alpha_{i+1} - \alpha_i$ (Crist et al. [2003]), and may be tested against the random expectations between successive spatial and temporal scales. Additive diversity partitioning can simultaneously handle spatial (β_S) and temporal (β_T) turnover, with $\gamma = \alpha + \beta_S + \beta_T$ (Tylianakis et al. [2005]).

In our study, spatial turnover (β_S) corresponds to spatial changes within a given period in a given year. The temporal turnover (β_T) corresponds to seasonal changes (between periods) within a given year. The suit of sampled grid cells changed from one year to the other (Fig. 1). We thus cannot fully disentangle the inter-annual variations per se from the spatial variations inherent to the change in sampling allocation at this temporal scale. Thereby, another component of the additive partitioning appeared, specific to our study, the mixed diversity turnover (β_{mixed}) which corresponds to inter-annual changes (between years) combined with sampling grid cell changes.

This procedure was performed from species richness values, amenable to additive partitioning (Gering et al. [2003]; Crist et al. [2003]; Summerville and Crist [2005]; Tylianakis et al. [2005]; Müller and Goßner [2010]; Munyuli et al. [2013]). The additive diversity partitioning analysis was performed using the *vegan* package (Oksanen et al. [2011]) in R version 2.12.0 (R Development Core Team [2010]).

To further assess at which spatial scales species turnover was steepest, we coined a measurement of spatial turnover effect size, defined as the relative deviation of observed species richness from random expectations at each spatial scale:

Spatial turnover effect size (%) = $(\alpha_{i[random]} - \alpha_{i[observed]})/\alpha_{i[random]}$ where $\alpha_{i[observed]}$ is the mean observed species richness of bee samples pooled at spatial scale i and $\alpha_{i[random]}$ the corresponding random expectation for no spatial partitioning, as returned by the random rearrangement of species among samples at spatial scale i.

Results

Characterization and functional description of bee diversity at the regional scale

A total of 12,629 foraging wild bees were collected in 794 of the 1,286 sampling sites, the remaining 492 sites having returned nil samples. The species richness accumulation curve

over the entire study area showed no evidence of approaching a ceiling (Fig. 3a), even though the survey was extensive and covered many sites during four flowering periods over three consecutive years. The survey completeness was estimated to 76.1–80.2 % only, with 191 species actually identified out of a total expectation of 238–251 species for the study site (Jack-1 and Chao-2 estimators, respectively; Table 1). Wild bees belonged to 6 families and 25 genera (Appendix 1). At the sampling site level, species richness ranged from 0 to 25 species, with 0–149 individuals.

Bee community at the regional scale was characterized by a high proportion of rare species. Of the 191 species, 43 (22.5 %) were represented by a single individual (singletons). Conversely, the five most dominant species accounted for c. 50 % of the total number of collected individuals, including 2,477 *Bombus lapidarius* (19.6 % of the total), 1,250 *Bombus terrestris* (9.9 %), 1,112 *Lasioglossum malachurum* (8.8 %), 750 *Lasioglossum pauxillum* (5.9 %) and 688 *Lasioglossum subhirtum* (5.5 %). All those five species have generalist dietary habits (polylectic) and are primitively eusocial or gregarious species, which could partly explain their fairly high abundance in the survey.
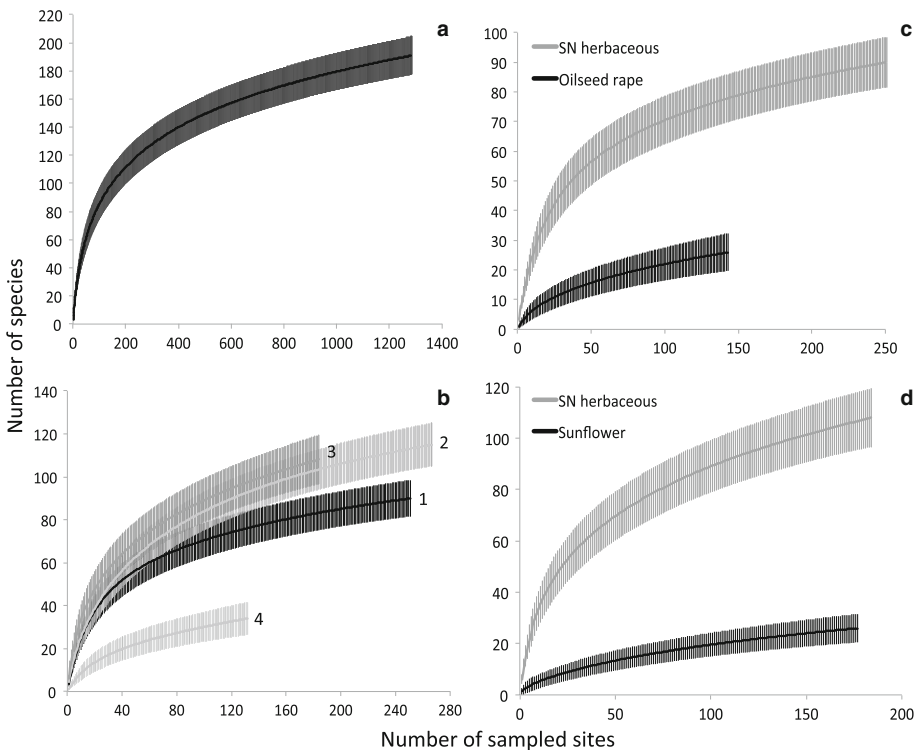
Fig. 3 Mean species accumulation curve for bee samples **a** pooled among all habitats, periods and years, **b** in semi-natural herbaceous habitats during each sampling period for all years, **c** in semi-natural herbaceous habitats and oilseed rape during the oilseed rape flowering period for all years, and **d** in semi-natural herbaceous habitats and sunflower during the sunflower flowering period for all years. *Lines* show the mean species richness, assessed by 1,000 random rearrangement of sampling order, and the shaded areas define the 95 % confidence intervals. *SN herbaceous* semi-natural herbaceous habitats, *1* period 1 = oilseed rape flowering period, *2* period 2 = food reduction period, *3* period 3 = sunflower flowering period, *4* period 4 = stubble field period

Only 12 species (6.3 %) were primitively eusocial, all of which were bumble bees (*Bombus muscorum*, *B. hortorum*, *B. lapidarius*, *B. lucorum*, *B. pascuorum*, *B. pratorum*, *B. ruderatus*, *B. sylvarum* and *B. terrestris*) or halictid bees (*Halictus rubicundus*, *L. malachurum* and *L. pauxillum*). Of the 191 recorded species, 35 (18.3 %) were parasitic (cuckoo bees). Among non-parasitic species for which information about their sociality, diet and nesting preferences were available (see Appendix 1), 21.2 % are known to aggregate for nesting, and 43.2 % to nest above the ground in different types of structure, especially wood, stems or any kinds of natural cavity. Of the 159 species with known foraging habits, 28 (17.6 %) were oligolectic with a preference for Asteraceae (13 of the 28 oligolectic bee species), Fabaceae (4), Brassicaceae (3), Apiaceae (2) and genera *Allium* (1), *Bryonia* (1), *Echium* (1), *Ranunculus* (1), *Reseda* (1), and *Veronica* (1).

Relative difference of diversity between mass-flowering crops and semi-natural habitats at the regional scale

The bee species accumulation curves for oilseed rape, sunflower and semi-natural habitats during the two mass-flowering periods (Fig. 3c, d) suggested that more sites were needed to complete the survey (completeness = 66.5–73.4 % and 71.1–81.1 % for mass-flowering crops and semi-natural herbaceous habitats, respectively). Nevertheless, overall less species were recorded in mass flowering crops than in semi-natural habitats. Both observed and expected richness in semi-natural herbaceous habitats were approximately three times and four times greater than the species richness in oilseed rape and sunflower, respectively (Table 1). These differences can be taken as statistically significant given the non-overlapping confidence intervals of estimates.

Most of the species found in mass-flowering crops (22 out of 26 found in oilseed rape and 23 out of 26 found in sunflower) were also found in semi-natural herbaceous habitats. Exceptions were uncommon species (singleton): *Andrena fulva, Halictus rubicundus,*

Table 1 Observed and expected richness of bee communities

Habitat	Period	Observed Richness	95 % Confidence Interval	Chao2 ± SD (completeness)	Jack1 ± SD (completeness)	N (range per grid cell)
All	All	191	177.4–204.6	251 ± 23.7 (76.1 %)	238 ± 7.3 (80.2 %)	1,286 (16–73)
Herbaceous semi-natural	P1	90	81.4–98.5	110.9 ± 11.8 (81.1 %)	111.9 ± 5.3 (80.4 %)	251 (0–23)
Herbaceous semi-natural	P2	115	104.9–125.1	145.9 ± 14.7 (78.8 %)	145.9 ± 6.1 (78.8 %)	267 (1–16)
Herbaceous semi-natural	P3	108	96.6–119.4	151.8 ± 20.7 (71.1 %)	140.8 ± 6.4 (76.7 %)	184 (2–13)
Herbaceous semi-natural	P4	34	26.3–41.7	54.8 ± 14.6 (62 %)	48.9 ± 5.4 (69.5 %)	132 (0–17)
Oilseed rape	P1	26	19.6–32.4	39.1 ± 10.2 (66.5 %)	37.9 ± 3.9 (68.6 %)	143 (2–10)
Sunflower	P3	26	20.4–31.6	35.4 ± 7.2 (73.4 %)	37.9 ± 5.6 (68.6 %)	177 (2–11)

P1 oilseed rape flowering period, *P2* food restriction period, *P3* sunflower flowering period, *P4* stubble field period, *N* number of sampled sites, *SD* Standard deviation

Osmia cornuta, Sphecodes gibbus found only in oilseed rape and *Hoplitis adunca* found only in sunflower.

A total of 46.2 and 57.7 % bee species were primitively eusocial or gregarious in oilseed rape and sunflower, respectively (Appendix 1). These species accounted for 65.7 and 93.5 % of the total number of collected individuals in oilseed rape and sunflower, respectively. Nearly all bee species in oilseed rape and sunflower had a polylectic diet (24 species in each crop; 92.3 %), representing 81.6 and 99.6 % of the total number of collected individuals, respectively.

None of the tested functional traits apparently made bee species more prone to occur in oilseed rape out of to the pool of species found in semi-natural herbaceous habitats (diet specialization: $\chi^2 = 0.6339$, df = 1, p value = 0.42; nesting behaviour: $\chi^2 = 0.0956$, df = 1, p value = 0.76; social behaviour: $\chi^2 = 0.333$, df = 1, p value = 0.56). Conversely, social or gregarious bee species were found in greater proportion in sunflower samples (68.18 %) than expected from semi-natural habitats (32.09 %) ($\chi^2 = 7.9554$, df = 1, p value = 0.0048), while neither diet specialization or nesting behaviour appeared to be statistically significant traits for occurrence in sunflower (diet specialization: $\chi^2 = 0.9267$, df = 1, p value = 0.34; nesting behaviour: $\chi^2 = 0.0189$, df = 1, p value = 0.89).

Spatial and seasonal partitioning of bee diversity

The bee species accumulation curves for semi-natural habitats during each sampling period (Fig. 3b) suggested that more sites were needed to complete the survey (completeness = 62.0–81.1 %). Judging from the non-overlapping 95 % confidence intervals (Table 1), bee species richness in semi-natural habitats was significantly lower during the stubble field period compared to all other periods. Species richness values during sunflower and food restriction periods did not differ, but were both significantly greater than during the oilseed rape period.

Of the total bee community in semi-natural herbaceous habitats ($\gamma = 184$ species for all periods and years), 30 % was accounted for by spatial changes within- and among-sites (α_1 and $\beta_{Spatial}$) during a given period (Fig. 4). The seasonal turnover ($\beta_{seasonal}$) accounted for an overall 34.3 % of the regional species richness.

Fig. 4 Percentage of total bee species richness accounted for by α and β components for the whole diversity in semi-natural herbaceous habitats (184 species) on three spatial and temporal scales: $\beta_{spatial}$ (among sites), $\beta_{seasonal}$ (among sampling periods of the season), β_{mixed} (among sampling years). The relative contribution of each scale was calculated by an additive diversity partitioning method using the *vegan* package in R
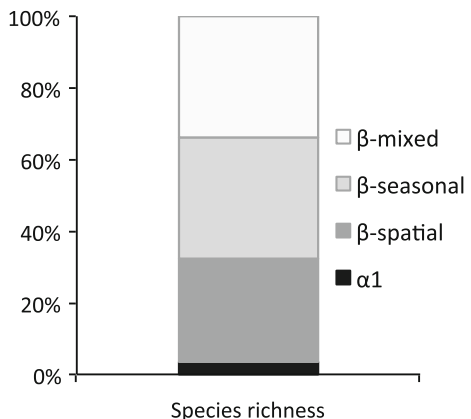
Table 2 Spatial and seasonal additive diversity partitioning for bee community in semi-natural herbaceous habitats

Spatial scale	Observed richness	Random expectation (95 % CI range)	Z	p value
α_1 (within sites)	6.24	11.74 (11.65;11.83)	−122.54164	<0.001
α_2 (within groups of 250 m)	6.98	13.14 (13.04;13.24)	−118.29424	<0.001
α_3 (within groups of 500 m)	7.83	14.65 (14.53;14.76)	−112.48987	<0.001
α_4 (within groups of 750 m)	8.46	15.91 (15.77;16.04)	−108.46117	<0.001
α_5 (within groups of 1000 m)	9.29	17.11 (16.97;17.27)	−99.61675	<0.001
α_6 (within groups of 1500 m)	10.89	19.81 (19.62;19.99)	−92.59884	<0.001
α_7 (within groups of 2000 m)	12.66	22.73 (22.52;22.95)	−87.96288	<0.001
α_8 (within groups of 3000 m)	16.26	28.64 (28.32;28.92)	−81.25652	<0.001
α_9 (within groups of 5000 m)	19.59	33.14 (32.76;33.5)	−68.91236	<0.001
α_{10} (within groups of 10,000 m)	26.25	42.69 (42.07;43.25)	−53.83416	<0.001
α_{11} (within groups of 15,000 m)	35.91	55.31 (54.41;56.16)	−43.22438	<0.001
$\alpha_{seasonal}$ (within periods)	58.91	88.27 (86.54;89.91)	−32.86783	<0.001
α_{mixed} (within sampling years)	122	138.33 (135.33;141)	−11.34099	<0.001
γ (total diversity)	184	184	0	1
β_1 (among sites)	0.73	1.39 (1.35;1.44)	−26.44007	<0.001
β_2 (among groups of 250 m)	0.85	1.51 (1.46;1.56)	−24.61825	<0.001
β_3 (among groups of 500 m)	0.64	1.26 (1.21;1.31)	−23.26793	<0.001
β_4 (among groups of 750 m)	0.83	1.21 (1.14;1.28)	−10.89673	<0.001
β_5 (among groups of 1,000 m)	1.59	2.69 (2.59;2.79)	−21.28401	<0.001
β_6 (among groups of 1,500 m)	1.77	2.93 (2.82;3.03)	−21.31591	<0.001
β_7 (among groups of 2,000 m)	3.61	5.91 (5.72;6.07)	−25.3971	<0.001
β_8 (among groups of 3,000 m)	3.33	4.51 (4.27;4.75)	−9.59182	<0.001
β_9 (among groups of 5,000 m)	6.67	9.54 (9.12;9.94)	−13.50644	<0.001
β_{10} (among groups of 10,000 m)	9.65	12.61 (;13.22)	−9.38366	<0.001
β_{11} (among groups of 15,000 m)	23.01	32.96 (31.52;34.46)	−13.22758	<0.001
$\beta_{seasonal}$ (among periods)	63.09	50.03 (47.27;52.64)	9.44275	<0.001
β_{mixed} (among sampling years)	62	45.67 (43;48.67)	11.34099	<0.001

P values stands for the null hypothesis that observed richness falls within the range of random expectations (95 % CI), based on the z statistic. All observed richness values are significantly lower than random expectations, regardless the considered spatial scale ($P < 0.001$)

The mixed diversity turnover (β_{mixed}), combining inter-annual variations per se and spatial variations inherent to the change in sampling allocation at this temporal scale, accounts for 33.7 % of the species richness in our dataset (Fig. 4).

The additive diversity partitioning analysis returned an average richness of 59 species per sampling period for a given year ($\alpha_{Seasonal}$ in Table 2). Partitioning this value at different nested spatial scales, found that there is a decreasing effect in the size of α diversity turnover with an increasing spatial scale (Fig. 5). The decreasing rate was maximal within a 50 km^2 area. Beyond that scale threshold, the spatial turnover effect size stabilized at a rather constant, but still high value (>30 %). This pattern was best depicted by a negative power function of area (Fig. 5).

Discussion

This study examined patterns of spatial and temporal variations in bee diversity across an intensive farming system, with contrasting forage types. During the seasonal survey, which covered three consecutive years, 191 wild bee species were recorded, which represented approximately 80 % of the total expected richness at the scale of the study site, and up to 20 % of the total French bee diversity (in only 0.08 % of the national territory area), currently estimated at 960 species (Kuhlmann et al. 2013). The seasonal species turnover ($\beta_{Seasonal}$) accounted for 34.3 % of the species richness overall and 30 % of the spatial changes within- and among-sites (α_1 and $\beta_{Spatial}$) during a given period. The relationship between effect size of α spatial turnover and sampling spatial scale was curvilinear, with the highest spatial turnover observed at about 50 km^2.

Characterization and functional description of bee γ diversity at the regional scale

The high number of recorded bee species shows that wild bee faunas can reach unexpectedly high richness levels in intensive farming systems. For the sake of comparison, in a recent study by Le Féon et al. (2010), fourteen 16-km^2 sites were sampled over 7 weeks in the summer of 2001 and 5 weeks in the spring of 2002 (at the same location each year) in Belgium (four sites), France (three), the Netherlands (four) and Switzerland (three). Sites were predominantly agricultural areas with different mass-flowering crops (e.g. alfalfa, buckwheat *Fagopyrum esculentum*, oilseed rape and sunflower). Among the 1014 wild bee
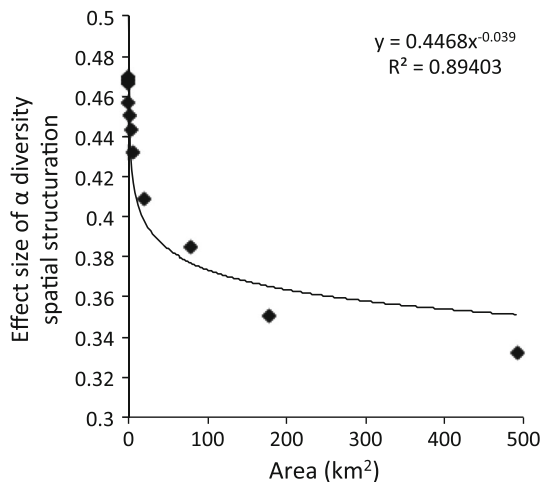
Fig. 5 Species spatial turnover effect size of *closed circle* diversity, from local to regional scale. Only bee diversity values from semi-natural herbaceous habitats were used, additively computed across spatial scales and averaged among study periods. Effect size was calculated as the relative difference between observed diversity and random expectations returned by the additive diversity partitioning analysis (Table 2). Area was calculated as the surface virtually covered by groups of sampling sites within which the hypothesis of species spatial partitioning was tested against random expectations (for instance, sampling sites grouped within a 1,500 m scale will cover *closed circle* × 0.750^2 = 1.77 km^2). For illustration purposes, the effect–area relationship was fitted by a power law [*solid line*, formula and R^2 coefficient displayed on the graph]. The species turnover is maximal within ∼50 km^2 areas (7–8 km in diameter), within which observed diversity is on average 38 % lower than what we would expect from random species distribution. Throughout larger focus areas, the species turnover decrease follows a more gentle slope

species expected from these four countries (Kuhlmann et al. 2013), only 125 (12.3 %) were actually sampled.

To our knowledge, no study has ever reported such a large number of bee specimens, at a scale equivalent to this study (the "*Zone Atelier—Plaine et Val de Sèvre*", 450 km^2) whilst covering a similar diversity of habitats and seasons (see Williams et al. 2001).

The overall community conforms to what is usually found in the literature, with few numerically dominant species and a long tail of rare species. In particular, the proportion of species represented by a single individual only (22.5 %) is similar to that of the four bee community studies reviewed by Williams et al. (2001) with a minimum of 4,000 recorded specimens (mean proportion of singletons = 23 %, range = 15–32 %).

The community was dominated by five super-abundant species (49.8 % of all recorded individuals), which are all characterized by a complex social behaviour (gregarious or eusocial). Their superabundance may be partly explained by their specific social behaviour, which results in high local abundances, generally close to nesting sites (Michener 2007). Gregarious bees construct numerous nests in limited areas and eusocial bees live in large colonies of many hundreds of individuals. However, the five dominant species were also found in a substantial proportion of the sampled localities (*Bombus terrestris*, found in 44 % of the sites with at least one recorded bee; *Bombus lapidarius*, 53 %; *Lasioglossum malachurum*, 28 %; *Lasioglossum pauxillum*, 26 %; *Lasioglossum subhirtum*, 23 %), indicating that their numerical dominance may not be solely explained by a sampling bias due to high local abundances. Sociality per se may also be well adapted to the studied agrosystem. Eusocial and gregarious (e.g. *B. terrestris*, *B. lapidarius*) bee species need food reserves to buffer the high spatial and temporal heterogeneity in resource availability and could favour mass-flowering crops which may help sustain locally dense populations (Rollin et al. 2013).

Relative difference of diversity between mass-flowering crops and semi-natural habitats at the regional scale

Diversity patterns varied greatly across habitat types. Bee communities in mass-flowering crops were three to four times less diversified than in semi-natural herbaceous habitats. Except for one and four species in oilseed rape and sunflower respectively, all bee species recorded in mass-flowering crops were also found in semi-natural habitats. Moreover, only one of the 43 species was represented by a single specimen in the data set and was observed in mass-flowering crops (*Hoplitis adunca* in sunflower). Previous studies have underlined the importance of semi-natural habitats for wild bees, particularly for abundance and diversity. Wild bees forage preferentially on wild floral resources in semi-natural habitats compared to on mass-flowering crops (Rollin et al. 2013). Pollinator density declines with the distance to natural habitats (Carvalheiro et al. 2010) and bee diversity increases with the proportion of natural and semi-natural habitats in the farming landscape (Duelli and Obrist 2003; Le Féon et al. 2010).

A substantial number of bee species found in mass-flowering crops (46.2 % in oilseed rape and 57.7 % in sunflower) were primitively eusocial or gregarious (such as *Bombus terrestris*, *B. lapidarius* and *Andrena cineraria*) and accounted for 65.7 and 93.5 % of the total number of collected individuals, in oilseed rape and sunflower respectively.

Sociality could partly explain the presence of bee species in sunflower crops. Because of their greater local abundance, eusocial and gregarious bees may need large amounts of floral resources to be easily exploitable in order to sustain the development of their colonies and to reduce intraspecific competition. These foraging conditions are fulfilled by

mass-flowering crops. Accordingly, previous studies have shown that bumble bees forage more frequently in mass-flowering crops (e.g. sunflower) than in semi-natural herbaceous habitats (Rollin et al. 2013) and that densities of bumblebees are not determined by the proportion of semi-natural habitats in agricultural landscapes but instead, are positively related to the availability of highly rewarding mass flowering crops (i.e. oilseed rape) (Westphal et al. 2003). As well as being primitively eusocial, bumble bees are large and more mobile, (Greenleaf et al. 2007; Zurbuchen et al. 2010a) and therefore can more easily take advantage of temporary mass flowering crops. Moreover, social bees are less affected by loss of semi-natural habitats than kleptoparasitic and solitary species (Jauker et al. 2013).

However, sociality could not explain the presence of bee species in oilseed rape. Instead, their presence could be explained by the growing stage of social bee colonies during each sampling period. For example, during the oilseed rape flowering period (in April–May), most of the bumble bee specimens were queens, whereas during sunflower flowering period, the majority of sampled bumble bees were workers. These observations are in agreement with bumble bee colony development. Colony founding of bumble bee species occurs in April–May, during the oilseed rape flowering period, which could explain the lower abundance of workers and possibly the lack of clear sociality effect on species occurrence probability as was found in sunflower fields.

In this study, mass-flowering crops do not seem to be essential habitats for wild bee species, whereas natural and semi-natural habitats are non-substitutable habitats for them, providing diversified foraging and nesting resources, as has been already highlighted in other studies (Rollin et al. 2013). Indeed, in our study, mass-flowering crops provide one flowering species at once while semi-natural sampling sites provide an average of six flowering wild plant species (range 1–24) with clovers and Asteraceae being the most common ones. Semi-natural habitats seem to act as "source habitats" for bee populations and provide a stronghold for wild bees in an impoverished landscape (Goulson et al. 2010).

However, this assertion may not apply to all bee species or to all mass flowering crop species. Some studies have shown that the availability and proximity of mass-flowering crops (e.g. oilseed rape) can strongly enhance the abundance of a solitary bee species nesting in nearby semi-natural habitats, especially for generalist bee species in heterogeneous landscapes (Holzschuh et al. 2013), and increase reproductive activity of some polylectic bee species (*Osmia rufa*) (Jauker et al. 2012). Consequently, it appears critical for conservation biologists to promote the amount and diversity of semi-natural habitats in farming systems, but also to establish a list of bee species that may benefit from local mass flowering crop species using standardized criteria.

Seasonal partitioning of bee diversity

The seasonal species turnover ($\beta_{Seasonal}$) in bee diversity was highly significant and accounted for 30 % of the total observed diversity, similar to proportions reported from other bee communities in other types of agricultural systems (tropical crops such as rice, coffee, pasture, forest; Tylianakis et al. 2005). Bee communities were more diversified during the sunflower and food restriction periods than during the oilseed rape period. The oilseed rape period, in early spring, comprises highly diversified floral resources and early-maturing bee species with relatively short activity periods (e.g. *Andrena strohmella*, *A. fulva*). Conversely, the late stubble field period (August–September) is characterized by a lower availably of floral resources. Few bee species are active at this time of the year, as most wild bees have already completed their seasonal activity (Westrich

1989; Amiet et al. 1999, 2001, 2004, 2007, 2010). Moreover, a large number of species emerge and actively forage between May and July, corresponding to the food restriction period and the sunflower flowering period. These specific seasonal activities during these two intermediate sampling periods could explain the similar observations of species richness.

Spatial partitioning of bee diversity

Spatial variations ($\beta_{spatial}$ during a sampling period for a given year) are key components of the overall species diversity variations, as indicated by the significant deviations of $\beta_{spatial}$ from random expectations (Table 2). Spatial changes among sites accounted for approximately 35 % of the regional species richness. This spatial heterogeneity could be partly explained by the large proportion of rare species, which were usually found within small subsets of the study area. Dispersal limitation is another, not mutually exclusive, explanation for spatial diversity variations as organisms are intrinsically limited by their dispersal abilities. Dispersal limitation is therefore a form of resistance to spatial homogenisation of communities. One consequence is the emergence of spatially heterogeneous species assemblage patterns driven by the interplay of local extinctions and immigration events among local communities. These stochastic processes are at the root of the unified neutral theory of biodiversity (Hubbell 2001), mostly applied to plant communities. Although bees are highly mobile, flying animals, they are also subject to dispersal limitation at the scale of our study area. Wild bees cover relatively short foraging or commuting flights, most often one to several hundred meters long (Zurbuchen et al. 2010b, 2010a). The capability to cover long distances and to use resources on a large spatial scale mostly applies to larger bees (e.g. genera *Bombus* or *Xylocopa*; Greenleaf et al. 2007) whilst most of the sampled species in this study belong to the typically small-sized species, such as Halictid species (27.2 %; Appendix 1).

Flight capacities of bee species could also be an explanation of why the observed richness was always less than the expected richness. Indeed, some isolated patches could not be reached and foraged by small bees with small flight capacities (Zurbuchen et al. 2010b). Moreover, proximity to nesting sites is essential. The use of floral resource patches decreases with increasing distance to the nesting site, and availability of bare ground and potential nesting cavities are primary factors influencing the structure and composition of the bee community, and the relative abundance of the dominant species (Potts et al. 2005). Finally, morphological differences between the mouth parts of a given bee species and the corolla depth determine the range of plant species which can be foraged by this bee species. Bees forage more efficiently on flowers with corolla depth proportional to their tongue length (Ranta and Lundberg 1980; Michener 2007; Kirk and Howes 2012). Thus, the morphological characteristics of floral species which are locally available contribute to shape the local bee community.

Partitioning of bee diversity and sampling bias

The substantial mixed component of the diversity turnover ($\beta_{mixed} = 33.7$ % of the total bee species recorded) means that it could result from either temporal (inter-annual) or from spatial components (among sampling grid cells), making it difficult to disentangle causal factors. For the sake of comparison, Oertli et al. (2005) have obtained a rather high inter-annual diversity turnover, with 25.5 % of the recorded bee species actually collected during a single of the two sampling years. The inter-annual species turnover component of

β_{mixed} is therefore potentially not trivial in the present study. However, it may reveal phenological variations due to changes in climatic conditions between years which cannot be easily captured by discontinuous sampling schedules, rather than a species turnover per se, i.e. a succession of species extinction and colonization events at the regional scales.

Implications for the design and assessment of conservation actions

There was a non-constant effect of the size of species turnover throughout the focus spatial scales, with a maximal turnover within 50 km^2 areas (7–8 km in diameter). Consequently, it seems more efficient, in terms of mean number of species promoted per unit of area, to concentrate conservation efforts within such medium-scale areas, e.g. by maximizing the density of set-aside semi-natural habitats. Those *relevant conservation unit* areas might be replicated across the territory with a minimum buffer distance greater than the critical 7–8 km threshold to minimize the species composition overlap among conservation areas. However, a key issue remains as to where these conservation areas should be located. For example, it might be advisable to focus these areas where there are already high densities of semi-natural habitat remnants, but further studies should investigate whether the density of semi-natural habitats may actually be used to infer on the local bee diversity, and if so at which focus scale and/or beyond which density threshold.

Conclusion

This study has shown that semi-natural habitats are prevailing habitats for wild bee communities in intensive agricultural landscapes. Results are consistent with previous studies which have highlighted the importance of these habitats on the foraging activity of bees (Rollin et al. 2013) and the significant positive effect of the presence of these habitats in the landscape on the local bee species richness (Duelli and Obrist 2003), especially by serving as source habitats (Öckinger and Smith 2007). Therefore, semi-natural habitats are the most promising habitats for sustaining wild bee populations. Applied conservation measures on these habitats have been shown to have a positive effect on bee communities (Kleijn and Sutherland 2003; Knop et al. 2006). The additive partitioning analyses performed in this study (Gering et al. 2003) highlights the importance of spatial and seasonal components in the turnover of the bee diversity, and further underline the importance of increasing the extensiveness of surveys, i.e. giving priority to the number of sampling sites in space and time to cover a broad spectrum of the studied community. Moreover, we suggest that it might be more efficient to adopt a *relevant conservation unit* approach, i.e. to concentrate conservation efforts within medium-scale areas (herein ~ 50 km^2) to maximize the number of bee species promoted per unit of surface.

References

Amiet F, Müller A, Neumeyer R (1999) Apidae 2: *Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes,* Systropha. Centre Suisse de Cartographie de la Faune, Neuchâtel

Amiet F, Herrmann M, Müller A, Neumeyer R (2001) Apidae 3: *Halictus,* Lasioglossum. Centre Suisse de Cartographie de la Faune, Neuchâtel

Amiet F, Herrmann M, Müller A, Neumeyer R (2004) Apidae 4. Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia, Stelis. Centre Suisse de Cartographie de la Faune, Neuchâtel

Amiet F, Herrmann M, Müller A, Neumeyer R (2007) Apidae 5. *Ammobates, Ammobatoides, Anthophora, Biastes, Ceratina, Dasypoda, Epeoloides, Epeolus, Eucera, Macropis, Melecta, Melitta, Nomada, Pasites, Tetralonia, Thyreus,* Xylocopa. Centre Suisse de Cartographie de la Faune, Neuchâtel

Amiet F, Herrmann M, Müller A, Neumeyer R (2010) Apidae 6: *Andrena, Melitturga, Panurginus,* Panurgus. Centre Suisse de Cartographie de la Faune, Neuchâtel

Biesmeijer JC, Roberts SPM, Reemer M et al (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313:351–354. doi:10.1126/science.1127863

Cameron SA, Lozier JD, Strange JP et al (2011) Patterns of widespread decline in North American bumble bees. Proc Natl Acad Sci 108:662–667. doi:10.1073/pnas.1014743108

Carvalheiro LG, Seymour CL, Veldtman R, Nicolson SW (2010) Pollination services decline with distance from natural habitat even in biodiversity-rich areas. J Appl Ecol 47:810–820. doi:10.1111/j.1365-2664.2010.01829.x

Chase JM (2011) Ecological niche theory. the theory of ecology. University of Chicago Press, Chicago, p 416

Chave J (2004) Neutral theory and community ecology. Ecol Lett 7:241–253. doi:10.1111/j.1461-0248.2003.00566.x

Colwell RK (2013) Estimates: statistical estimation of species richness and shared species from samples. Divers Distrib 14:1–10

Crist TO, Veech JA (2006) Additive partitioning of rarefaction curves and species–area relationships: unifying α-, β- and γ-diversity with sample size and habitat area. Ecol Lett 9:923–932. doi:10.1111/j.1461-0248.2006.00941.x

Crist TO, Veech JA, Gering JC, Summerville KS (2003) Partitioning species diversity across landscapes and regions: A hierarchical analysis of α, β, and γ diversity. Am Nat 162:734–743

Dengler J (2009) Which function describes the species–area relationship best? A review and empirical evaluation. J Biogeogr 36:728–744. doi:10.1111/j.1365-2699.2008.02038.x

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Dicks LV, Showler DA, Sutherland WJ (2010) Bee conservation: Evidence for the effects of interventions, exeter. Pegasus Publishing, Cambridge

Duelli P, Obrist MK (2003) Regional biodiversity in an agricultural landscape: the contribution of semi-natural habitat islands. Basic Appl Ecol 4:129–138. doi:10.1078/1439-1791-00140

Gering JC, Crist TO, Veech JA (2003) Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. Conserv Biol 17:488–499. doi:10.1046/j.1523-1739.2003.01465.x

Goulson D, Lepais O, O'Connor S et al (2010) Effects of land use at a landscape scale on bumblebee nest density and survival. J Appl Ecol 47:1207–1215. doi:10.1111/j.1365-2664.2010.01872.x

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153:589–596. doi:10.1007/s00442-007-0752-9

Hoehn P, Steffan-Dewenter I, Tscharntke T (2010) Relative contribution of agroforestry, rainforest and openland to local and regional bee diversity. Biodivers Conserv 19:2189–2200. doi:10.1007/s10531-010-9831-z

Holzschuh A, Dormann CF, Tscharntke T, Steffan-Dewenter I (2013) Mass-flowering crops enhance wild bee abundance. Oecologia 172:477–484. doi:10.1007/s00442-012-2515-5

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton

Jauker F, Peter F, Wolters V, Diekötter T (2012) Early reproductive benefits of mass-flowering crops to the solitary bee *Osmia rufa* outbalance post-flowering disadvantages. Basic Appl Ecol 13:268–276. doi:10.1016/j.baae.2012.03.010

Jauker B, Krauss J, Jauker F, Steffan-Dewenter I (2013) Linking life history traits to pollinator loss in fragmented calcareous grasslands. Landscape Ecol 28:107–120. doi:10.1007/s10980-012-9820-6

Kirk WDJ, Howes FN (2012) Plants for bees: a guide to the plants that benefit the bees of the british isles. IBRA, p 280

Kleijn D, Sutherland WJ (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? J Appl Ecol 40:947–969. doi:10.1111/j.1365-2664.2003.00868.x

Kleijn D, Berendse F, Smit R, Gilissen N (2001) Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. Nature 413:723–725. doi:10.1038/35099540

Knop E, Kleijn D, Herzog F, Schmid B (2006) Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. J Appl Ecol 43:120–127. doi:10.1111/j.1365-2664.2005.01113.x

Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76:5–13. doi:10.2307/3545743

Le Féon V, Schermann-Legionnet A, Delettre Y et al (2010) Intensification of agriculture, landscape composition and wild bee communities: a large scale study in four European countries. Agric Ecosyst Environ 137:143–150. doi:10.1016/j.agee.2010.01.015

Leibold MA, McPeek MA (2006) Coexistence of the niche and neutral perspectives in community ecology. Ecology 87:1399–1410

Kuhlmann et al M (2013) Checklist of the western palaearctic bees (Hymenoptera: Apoidea: Anthophila). http://westpalbees.myspecies.info/. Accessed 10 Sep 2013

Magurran AE (2004) Measuring biological diversity. Blackwell Pub, Malden

Michener CD (2007) The Bees of the World, 2nd Revised Edition. Johns Hopkins University Press, Hopkins

Müller J, Goßner MM (2010) Three-dimensional partitioning of diversity informs state-wide strategies for the conservation of saproxylic beetles. Biol Conserv 143:625–633. doi:10.1016/j.biocon.2009.11.027

Munyuli MBT, Nyeko P, Potts S et al (2013) Patterns of bee diversity in mosaic agricultural landscapes of central Uganda: implication of pollination services conservation for food security. J Insect Conserv 17:79–93. doi:10.1007/s10841-012-9488-x

New TR (1999) Limits to species focusing in insect conservation. Ann Entomol Soc Am 92:853–860

Öckinger E, Smith HG (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. J Appl Ecol 44:50–59. doi:10.1111/j.1365-2664.2006.01250.x

Oertli S, Mueller A, Dorn S (2005) Ecological and seasonal patterns in the diversity of a species-rich bee assemblage (Hymenoptera: Apoidea: Apiformes). Euro J Entomol 102:53–63

Oksanen J, Blanchet FG, Kindt R et al (2011) Vegan: community ecology package. Blackwell Publishing, Oxford

Palmer MW (1995) How should one count species? Natural Areas Journal 15:124–135

Potts SG, Vulliamy B, Dafni A et al (2003) Linking bees and flowers: How do floral communities structure pollinator communities? Ecology 84:2628–2642

Potts SG, Vulliamy B, Roberts S et al (2005) Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecological Entomol 30:78–85. doi:10.1111/j.0307-6946.2005.00662.x

Potts S, Roberts S, Dean R et al (2010a) Declines of managed honey bees and beekeepers in Europe. J Apic Res 49:15. doi:10.3896/IBRA.1.49.1.02

Potts SG, Biesmeijer JC, Kremen C et al (2010b) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25:345–353. doi:10.1016/j.tree.2010.01.007

Pouvreau A (2004) Les insectes pollinisateurs. Delachaux et Niestlé, Paris

Ranta E, Lundberg H (1980) Resource partitioning in bumblebees: the significance of differences in pro- boscis length. Oikos 35:298–302. doi:10.2307/3544643

Rollin O, Bretagnolle V, Decourtye A et al (2013) Differences of floral resource use between honey bees and wild bees in an intensive farming system. Agric Ecosyst Environ 179:78–86. doi:10.1016/j.agee.2013.07.007

Roubik DW (2001) Ups and downs in pollinator populations: When is there a decline? Conserv Ecol 5. URL: http://www.ecologyandsociety.org/vol5/iss1/art2/

Scheiner SM (2003) Six types of species-area curves. Glob Ecol Biogeogr 12:441–447. doi:10.1046/j.1466-822X.2003.00061.x

Steffan-Dewenter I, Tscharntke T (2001) Succession of bee communities on fallows. Ecography 24:83–93. doi:10.1034/j.1600-0587.2001.240110.x

Summerville KS, Crist TO (2005) Temporal patterns of species accumulation in a survey of Lepidoptera in a beech-maple forest. Biodivers Conserv 14:3393–3406. doi:10.1007/s10531-004-0546-x

Tylianakis JM, Klein A-M, Tscharntke T (2005) Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. Ecology 86:3296–3302. doi:10.1890/05-0371

VanEngelsdorp D, Hayes J, Underwood RM, Pettis J (2008) A survey of honey bee colony losses in the U.S., fall 2007 to spring 2008. PLoS ONE 3:e4071. doi:10.1371/journal.pone.0004071

Walther BA, Morand S (1998) Comparative performance of species richness estimation methods. Parasi- tology 116:395–405

Westphal C, Steffan-Dewenter I, Tscharntke T (2003) Mass flowering crops enhance pollinator densities at a landscape scale. Ecol Lett 6:961–965. doi:10.1046/j.1461-0248.2003.00523.x

Westphal C, Bommarco R, Carré G et al (2008) Measuring bee diversity in different european habitats and biogeographical regions. Ecol Monogr 78:653–671. doi:10.1890/07-1292.1

Westrich P (1989) Die Wildbienen Baden-Württemburgs: Spezieller Teil—Die Gattungen und Arten. Eugen Ulmer, Stuttgart

Williams NM, Minckley RL, Silveira FA (2001) Variation in native bee faunas and its implications for detecting community changes. Conserv Ecol 5. URL: http://www.consecol.org/vol5/iss1/art7/

Zurbuchen A, Cheesman S, Klaiber J et al (2010a) Long foraging distances impose high costs on offspring production in solitary bees. J Anim Ecol 79:674–681. doi:10.1111/j.1365-2656.2010.01675.x

Zurbuchen A, Landert L, Klaiber J et al (2010b) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biol Conserv 143:669–676. doi:10.1016/j.biocon.2009.12.003