Research

Ecography 40: 85–97, 2017
doi: 10.1111/ecog.02632

Subject Editor: Nick Haddad. Editor-in-Chief: Miguel Araújo. Accepted 25 October 2016

Relationships among ecological traits of wild bee communities along gradients of habitat amount and fragmentation

Romain Carrié, Emilie Andrieu, Saul A. Cunningham, Pia E. Lentini, Michel Loreau and Annie Ouin

R. Carrié (http://orcid.org/0000-0003-3016-0702) (carrieromain@gmail.com), E. Andrieu and A. Ouin, Dynafor, Univ. de Toulouse, INRA, INPT, INP-EI Purpan, Castanet Tolosan, France. – S. A. Cunningham, Fenner School of Environment and Society, Australian National Univ., Canberra, ACT 2601, Australia. – P. E. Lentini, School of BioSciences, Univ. of Melbourne, Parkville, Victoria 3010, Australia. – M. Loreau, Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, CNRS and Paul Sabatier Univ., Moulis, France.

Amount of semi-natural habitats (permanent grasslands, woodlands and hedgerows) and their level of fragmentation are among the main determinants of wild bee diversity in agricultural landscapes. However, their impact on the distribution of bee ecological traits has received little attention. In this study, we aimed to explore whether changes in the distribution of bee ecological traits along gradients of habitat amount and fragmentation were due to a direct effect of landscape context on multiple traits ('response traits') or to a correlation of response traits with other ecological traits not involved in the response of bee species to landscape context. In two study regions in southwest France and southeast Australia, we used a RLQ analysis (three-table ordination method) to link bee traits with habitat amount and fragment isolation measured at the landscape scale. We found that bee ecological traits shifted at the community-level in association with landscape gradients, whereas species-level associations among bee traits and phylogenetic clustering in bee communities were of only minor importance in determining such shifts. We found that traits such as body size and nest location were closely linked to habitat amount and fragmentation. We also observed regionally-specific relationships among ecological traits, suggesting that the regional species pool can play an important role in determining the response of bee communities to habitat amount and fragmentation. Our findings suggest that improved knowledge about how trait-based responses mediate the impact of landscapes on wild bee communities will allow better prediction and understanding of subsequent effects on ecosystem functioning.

Human activities shape biodiversity at all scales, affecting ecosystem processes via changes in climate and alteration of habitat availability and quality (Pimm et al. 1995, Parry 2007). Agricultural intensification has led to simplification of landscapes and changes in farming practices, and has been identified as the main cause of biodiversity decline in temperate agricultural landscapes (Krebs et al. 1999, Tilman 1999, Robinson and Sutherland 2002, Potts et al. 2010). These environmental changes can lead to biotic homogenization (Chapin et al. 1997, Gámez-Virués et al. 2015) and alteration of ecosystem processes through changes in functional community structure (i.e. distribution of ecological traits in communities) (Loreau et al. 2001, Lavorel and Garnier 2002, Suding et al. 2008).

In agricultural landscapes, highly frequent disturbances in annual crops constrain components of biodiversity which influence pivotal ecosystem processes such as pollination (Tscharntke et al. 2005). In such landscapes, wild bees play a pivotal role in the maintenance of biodiversity and ecosystem processes, by their contribution to crop and wild plant pollination (Memmott et al. 2004, Klein et al. 2007, Garibaldi et al. 2013). Both wild bee species richness and pollination are affected by the loss and fragmentation of natural or semi-natural habitats (Kremen et al. 2007, Winfree et al. 2009, Garibaldi et al. 2011), but the functional mechanisms that link wild bee community structure and pollination provision at the community level are poorly understood (Kremen et al. 2007, Wood et al. 2015). Farmland bee species differ in their responses to the amount and fragmentation of semi-natural habitats ('habitat amount and fragmentation' herein) depending on their traits: for example, the proportion of semi-natural habitats in the landscape correlates with an increase in the abundance of social bee species compared to solitary ones (Williams et al. 2010, Hopfenmüller et al. 2014).

The relationship between the response of a community to environmental factors and subsequent impacts on ecosystem processes has been formalized in the response-and-effect framework (Lavorel and Garnier 2002, Suding et al. 2008). In this trait-based framework, response traits are associated with the response of species to environmental factors and effect traits determine their contribution to ecosystem function (Lavorel and Garnier 2002, Suding et al. 2008). Communities may vary in the combinations of response and effect traits along landscape gradients, thus shaping the effect of landscape structure on ecosystem function. For example, if functionally important species respond negatively to habitat loss and fragmentation, this would drive an overall decrease in function. This was observed in wild bee communities, where large-bodied species were the most efficient crop pollinators but also the most sensitive to habitat amount (Larsen et al. 2005). Response and effect traits could be related in wild bee communities because 1) some response traits also act as effect traits, reinforcing the effect of habitat amount and fragmentation on pollination delivery (Larsen et al. 2005, Suding et al. 2008); 2) many traits are correlated among species, such that effect trait distributions may not be biologically or statistically independent of response traits (Williams et al. 2010, Ekroos et al. 2013); 3) some closely-related species with similar traits could co-occur in given environments, therefore traits that are phylogenetically linked to response traits might also shift along environmental gradients (Hoiss et al. 2012, Sydenham et al. 2015). Alternatively, if the response and effect traits are not related, then landscape changes affecting wild bee communities should not alter pollination delivery on short timescales. The absence of a link between response and effect traits could be caused if the community is randomly assembled in terms of sensitivity to habitat amount/fragmentation and functional importance (Suding et al. 2008). However, it should be noted that the relationship between response and effect traits in this framework does not take into account species interactions such as resource partitioning or competition, and these could change the prediction of pollination delivery in relation to changes in functional community structure (Kremen 2005, Larsen et al. 2005, Blüthgen and Klein 2011).

In this study, we explored the effects of habitat amount and fragmentation on the functional structure of wild bee communities (distribution of bee ecological traits), and whether the covariations among ecological traits revealed by landscape gradients were consistent between two regions with different species pools and different agricultural contexts. We explored the joint effects of habitat amount and fragmentation on bee communities as these two landscape changes are often correlated in real-world landscapes and have contrasting effects on biodiversity (Fahrig 2003, Haddad et al. 2017). For example, an increase in the total amount of semi-natural habitat can be associated with increased species richness due to a sample area effect (Fahrig 2013). The fragmentation of semi-natural habitats, through an increase in isolation, edge density and/or size of habitat fragments can decrease species richness via a reduction in movement among fragments, decreased population sizes and higher exposure to neighboring matrix (Haddad et al. 2015, Resasco et al. 2017). We also examined the phylogenetic structure of wild bee communities along the landscape gradients (phylogenetic clustering), to detect if changes in some trait distributions were due to a direct effect of landscape variables or to a phylogenetic association among species, leading to similar shifts of true response traits and other functional traits (Webb et al. 2002). We studied shifts in body size, sociality, diet breadth, nest location, the duration and beginning of foraging season along gradients of habitat amount and isolation. We selected these bee traits because they affect resource use in landscapes. Indeed, body size is correlated with bee foraging ranges (Greenleaf et al. 2007) which determine habitat patches bee species can visit within these ranges (Bommarco et al. 2010). Nest location, diet breadth and sociality can determine the type and range of resources a bee depends on (Potts et al. 2005, Williams et al. 2010, Kremen and M'Gonigle 2015). Temporal range of foraging activity influences the correspondence of foraging periods of bees with the flowering periods of plants (Woodcock et al. 2014, Mallinger et al. 2016). We predicted that the distribution of these traits would shift along the gradient of habitat amount and fragmentation (e.g. reduced body size, occurrence of oligolectic bees and above-ground nesters in landscapes with low amounts and high fragmentation of semi-natural habitats). We hypothesized that such correlated shifts in traits would be due to either 1) an effect of landscape variables on one or more response traits that in turn influence the shift in other ecological traits, and could be caused by a) a correlation among traits at the species level, or b) a clustered phylogenetic structure in the community (closely related and functionally similar species respond similarly to landscape variables) leading to the phylogenetic association of several traits at the community level (co-occurrence of the values of different traits along the landscape gradients) or; 2) a direct effect of landscape variables on multiple traits. Due to differences in the regional species pools and traits between the two regions, we applied the same statistical tests to both regions and then tested for consistency of the detected patterns.

Material and methods

Study site and sampling design

Southwest France

Our study location was in southwestern France (Fig. 1a), in the Vallées et Coteaux de Gascogne, which is part of the Long Term Ecological Research Network (LTER_EU_FR_003). This hilly region (250–400 m a.s.l.) covers 220 km² (43°17′N, 0°54′E) and is characterized by a mosaic of small woodlands, grasslands and crop fields. The region is dominated by mixed crop-livestock farming systems where permanent grasslands tend to be located on steep slopes and annual crop fields (winter cereals, rapeseed, corn and sunflower) in the valleys (Choisis et al. 2010). The climate is sub-Atlantic with slight Mediterranean influences (mean annual temperature, 12.5°C; mean annual precipitation, 750 mm).

Within the studied region, we selected 80 cereal fields (40 different winter wheat and barley fields in each of 2013 and 2014 years) differing in the surrounding proportion of semi-natural habitats within a 500 m buffer, to cover independent gradients of woodland and grassland proportions. Preselection of sampling sites was based on French agricultural land cover data (for permanent grasslands, Registre Parcellaire Graphique, RPG) and woodland cover data (BD TOPO®, IGN). In each field (hereafter sampling site), the sampling points were located near a field border that had a grassy margin, at least 100 m from a non-cropped area (woodland or built area). In each crop field, we established four sampling points: two 50 cm inside the field and 25 m apart from each other (field border transect), and two 25 m inside the field and parallel to the first two points (field interior transect). We sampled bees with six pan traps

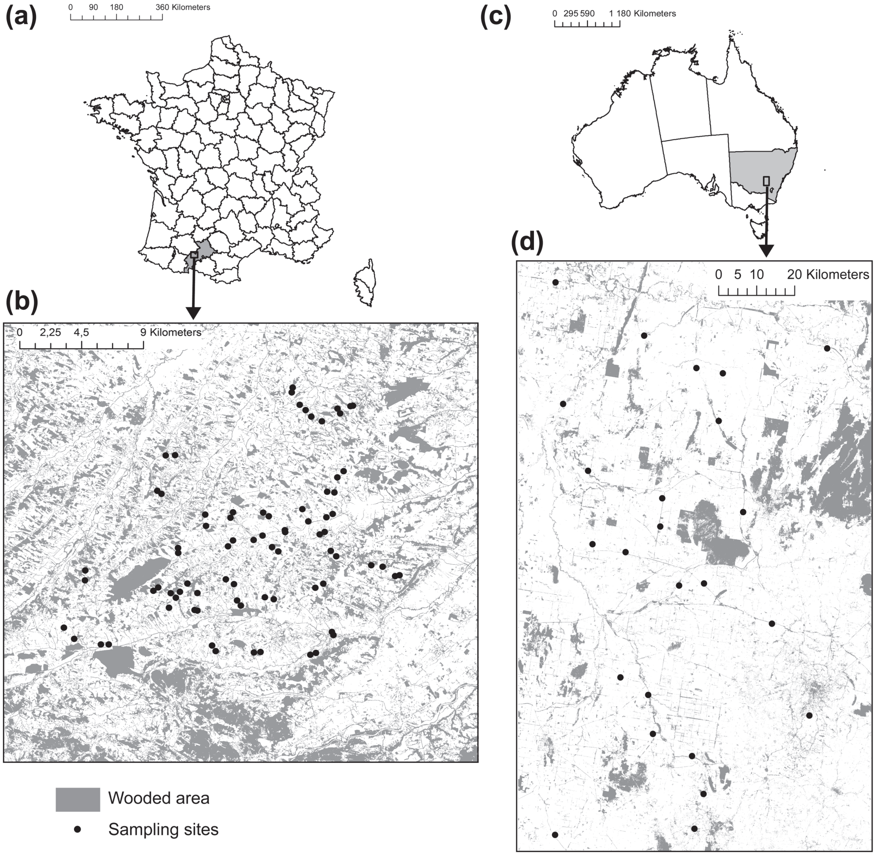

Figure 1. Maps showing (a), (c) the French and Australian study areas, (b) the 78 sampled crop fields in southwest France and (d) the 24 sampled crop fields in NSW Australia.

per sampling site (colored plastic cups, 15 cm diameter, 7 cm height) placed at the top of four poles (one pole per sampling point), one or two traps per pole. We used three colors of pan traps (white, yellow and blue UV color paint) and each pole had two different colors. The location of the trap colors was the same for each sampling site. Traps were 2/3 filled with water, with a small amount of soap to break surface tension. The poles were designed such that the height of the traps was adjustable to the crop canopy (10 to 120 cm). The traps were placed during two periods of 3 or 4 days per sampling site. The two sampling periods were from 22 April to 24 May and from 27 May to 21 June in 2013, and from 17 April to 12 May and from 22 May to 16 June in 2014. The number of individuals and the number of species determined for each sampling site represented the sum of all traps from the two sampling periods conducted in that site. Wild bee individuals (solitary and social species) were identified to species level. We excluded honeybees *Apis mellifera* from the analyses because the abundance of this managed species is likely to be related to beekeeping rather than a direct effect of landscape structure. We also excluded cleptoparasitic bees because they are less efficient pollinators than other bee species.

NSW, Australia

Wild bee communities were surveyed in the wheat–sheep belt of New South Wales, Australia (33–34°S, 147–148°E, Fig. 1c). This region is dominated by cereal and livestock production, with crop fields interspersed with linear remnants of native grassy box woodlands dominated by yellow box *Eucalyptus melliodora*, grey box *E. microcarpa*, white box *E. albens*, Blakely's red gum *E. blakelyi* and some white cypress pine *Callitris columellaris* (Lentini et al. 2012). Large scattered *Eucalyptus* can also be found throughout the fields.

Bees were sampled in 24 different annual crop fields (hereafter sampling sites) across the region, consisting of five native pastures, five agriculturally-improved pastures dominated by exotic grasses, five fields sown with lucerne *Medicago sativa* and/or clover *Trifolium* spp., six fields of wheat *Triticum* spp., and three fields of canola *Brassica* spp. Sampling points were located in isolated trees at 100, 200 and 400 m from an adjacent woodland remnant. Bees were surveyed using blue vane traps (64 oz capacity, collecting jar: 15 cm in diameter × 15 cm high, two blue vanes: 24 × 13 cm), which were hung in trees (a single trap per sampling point) located within the fields for a week-long period during two survey periods in spring/summer approximately two months apart (12 Nov–8 Dec 2009 and 14 Jan–9 Feb 2010). Wild bees were identified to species level and honey bees were excluded from the analysis for the same reason as in southwest France. As in southwest France, cleptoparasitic bees were excluded from the dataset. The number of individuals and the number of species determined for each site represented the sum of all traps (located at 100, 200 and 400 m from woodland remnants) from the two sampling periods conducted on that site. More detailed information about the sampling method can be found in Lentini et al. (2012).

Landscape variables

Southwest France

Landscape variables were calculated within a radius of 500 m centered on the field border transect in each site. The radius was chosen according to the results of previous studies on the functional scale of wild bees (Gathmann and Tscharntke 2002, Zurbuchen et al. 2010, Holzschuh et al. 2010). Using aerial photographs (IGN 2013) the different land covers (woodlands, hedgerows, permanent grasslands, crop fields and isolated trees) were mapped using ArcGIS 10.2 (ESRI). Crop field and grassland boundaries were validated by ground surveys in July 2013, May 2014 and April 2015.

Three habitats were considered semi-natural: woodland edges, hedgerows and permanent grasslands. In each 500 m buffer (hereafter landscape), we calculated the proportion of permanent grasslands and the length of woodland edges and hedgerows as a measure of habitat amount and we computed, for each habitat type, a proximity index as a measure of isolation or fragmentation of habitat patches. This proximity index was derived from the 'patch proximity index' (proximity index calculated at the patch scale, McGarigal et al. 2002, Bender et al. 2003), which was adapted to take into account the proximity of habitat fragments at the landscape scale. To calculate this proximity index, we created buffers around each habitat patch as an approximation of the maximum foraging distance (100 m) of the least mobile species that we captured (Greenleaf et al. 2007). We then calculated the proximity index, which was the proportion of overlapping zones amongst all the landscapes (proximity index = area of buffer overlap/total buffer area) to measure the zones in the landscapes where foraging movements between habitat patches, in the crop mosaic, were possible even for the least mobile species (Fig. 2).

As some of the sampling sites were surveyed for a different study, sites were paired in such a way that they were at least 200 m apart. As a consequence, spatial autocorrelation of wild bee species richness and abundance was analyzed in the data. After a random resampling process, two buffers were finally removed from the analysis to minimize spatial autocorrelation (Moran index = 0.07, p = 0.19). Statistical analyses were then performed on the 78 remaining landscapes (Fig. 1b).

NSW, Australia

Landscape variables were calculated within a 500 m radius centered between the 200 and 400 m trapping points in each sampled field. Using the 'Land Use: New South Wales' spatial data set, dated 8 Apr 2011 and supplied by the NSW Dept of Environment, Climate Change and Water, we calculated four landscape variables as a measure of semi-natural habitat amount and fragmentation using ArcGIS 10.2 (ESRI). We calculated the proportion of native pasture and the edge length of woody vegetation as a measure of habitat amount, and using the same method as for southwest France and for each habitat type we computed a proximity index to quantify habitat fragmentation (Fig. 2).

Bee traits

Six ecological and life-history traits were chosen based on knowledge in the literature regarding their potential to influence the response of wild bees to variation in habitat amount and fragmentation (body size, diet breadth, nest location, sociality and timing of foraging season). For bees in southwest France, we sourced trait information from the ALARM project database (Settele et al. 2005), and from Michener (2000), Gathmann and Tscharntke (2002), Bommarco et al. (2010), Fortel et al. (2014) and Forrest et al. (2015). Diet specialization was defined by the number of plant families bees collect pollen from (polylectic species = several plant families, oligolectic species = one plant family). Body size was estimated using the inter-tegular distance (ITD), which is the distance between the nearest

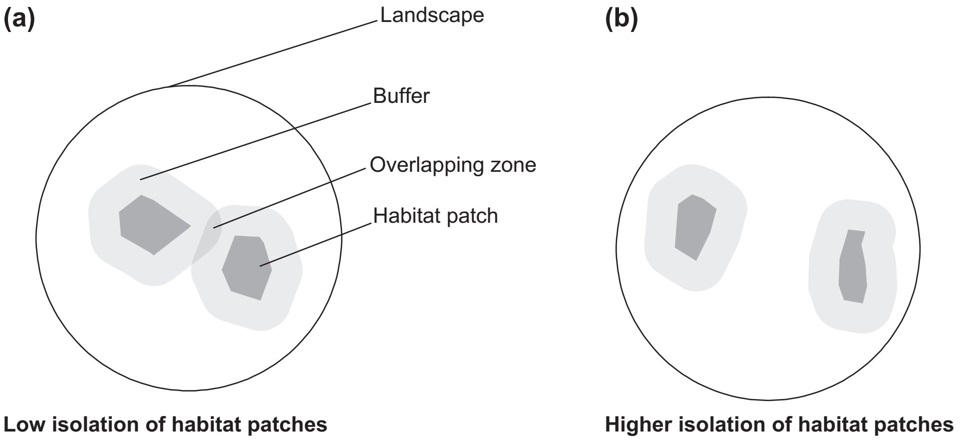

Figure 2. Calculation of the proximity index, showing examples of low habitat isolation (a) and high habitat isolation (b). A buffer zone was created around each habitat patch per habitat type which corresponded to the estimated maximum foraging distance of the least mobile species captured in the traps (100 m), based on its body size (Greenleaf et al. 2007, Zurbuchen et al. 2010). The proximity index was the ratio of the area of buffer overlap/total buffer area. In this example the proximity index would be 4% for (a) and 0% for (b).

edges of the tegulae (plates covering the wing bases). The beginning and duration of the foraging season in southwest France was based on expert knowledge (David Genoud, pers. comm.). For body size values in France, when no data were available on a particular taxon, ITD was measured on at least five female individuals per taxon, and queens were used for eusocial species. In NSW Australia, ITD was measured on one to ten female individuals per taxon. For both regions, social bees included species that live in a colony characterized by cooperative brood care, therefore including eusocial and primitively social species. Solitary bees included species that care only for their own offspring. If trait values compiled from the literature varied for a given taxon, the mean value was retained in our trait database. We were able to obtain traits for 60 of 111 species in southwest France and for 29 of 30 species in NSW Australia (representing 97 and 99% of the sampled individuals respectively) (Supplementary material Appendix 1, Table A1; Appendix 2, Table A2). Species lacking trait values were excluded from the analyses. In southwest France, we were able to include six traits in the analysis, whereas only two traits (body size and nest location) were used in NSW Australia. Indeed, the foraging period was unknown for every Australian species and we excluded diet breadth and sociality as only one sub-dominant species was oligolectic (*Hylaeus albocuneatus*) and all the species were solitary in the Australian dataset (Supplementary material Appendix 2, Table A2).

Statistical analyses

We conducted two analyses with the same method, separating the French and Australian regions, due to the differences in the number of available traits. The objective was to explore the landscape–trait relationship in each region, and then to test for the consistency of the detected patterns for the traits available for both regions.

We used an RLQ analysis (Dolédec et al. 1996) to test the covariance between the amount and isolation of semi-natural habitats (table R) and species trait values (table Q), constrained by their relative abundance (table L). Because it allows the exploration of the joint structure of the three tables, RLQ analysis is particularly useful for exploring the link between environmental variables and multiple species traits (Barbaro and Van Halder 2009, Trichard et al. 2013, Duflot et al. 2014, Gámez-Virués et al. 2015). As RLQ is an ordination analysis, this method reduces the number of environmental variables that influence community structure and is therefore useful when exploring the combined effect of correlated variables in real-world landscapes such as habitat amount and fragmentation (Fahrig 2003). Indeed, in our study, habitat amount and inter-patch proximity were positively correlated in both southwest France and NSW Australia (Supplementary material Appendix 3, Table A3).

RLQ analysis involves the selection of axes that maximize the covariance between linear combinations of the columns of R- and Q-tables (Dolédec et al. 1996). The R-table (p environmental variables recorded at m sites) comprised the amount and proximity index of permanent grasslands, woodlands and hedgerows in each landscape for southwest France and of permanent grasslands and woody vegetation in each landscape for NSW Australia. In NSW, Australia, bees were surveyed in different crop types, so crop type was added in the R-table to account for a local effect of crop type on bee functional structure. The Q-trait table (n ecological traits characterizing k species) comprised body size, nest location, the beginning and duration of foraging season, diet breadth and sociality for each bee species of southwest France, and only body size and nest location for each bee species of NSW Australia. The three tables were analyzed separately first using ordination methods. The L-species table (k species abundances noted at m sites) was analyzed using Correspondence Analysis (CA), and the R-environmental variables table using Principal Component Analysis (PCA), with the CA site scores (coordinates of the sites – i.e. row weights – on the axis of the CA of the L-species table) being used as row weighting to couple R and L. The Q-trait table was analyzed by a Hill Smith PCA, which combines quantitative and qualitative variables, using CA species scores (coordinates of bee species – i.e. column weights – on the axis of the CA of the L-species table) as a column weighting to couple Q and L. Second, the RLQ analysis was used to combine the three independent analyses in a single ordination, using the L ordination to link the R-environmental table and the Q-trait table (Barbaro and Van Halder 2009, Trichard et al. 2013, Gámez-Virués et al. 2015). New coordinates (or scores) of species and sites on the RLQ axes were then obtained. Finally, to test the significance of the link between traits and landscape variables, we used a two-step analysis (Gámez-Virués et al. 2015). First, we tested the link between site scores on the RLQ axes and landscape descriptors using Spearman correlations for continuous variables and Kruskal–Wallis tests for categorical variables (Trichard et al. 2013, Gámez-Virués et al. 2015). Second, we tested the link between species scores on the RLQ axes and corresponding trait values using Spearman correlations for continuous traits and Kruskal–Wallis tests for nominal traits (Trichard et al. 2013). Independently of the RLQ analysis, we used Spearman rank correlations to quantify the association between traits among species, because the effect of one trait on the response to environmental change or on ecological function may not be biologically independent of others (Williams et al. 2010, Ekroos et al. 2013, Forrest et al. 2015).

We used a three-step analysis to check for a phylogenetic signal in wild bee communities along landscape gradients (Sydenham et al. 2015). First, we built a polytomous, ultrametric tree based on bee taxonomy for the two regions (Supplementary material Appendix 4, Fig. A4) using the R package ape. Branch lengths were calculated setting the p-parameter to 1 (Hoiss et al. 2012, Sydenham et al. 2015). Second, we checked for evidence of niche conservatism (i.e. that closely related species are ecologically similar and thus share similar trait values; Webb et al. 2002, Wiens et al. 2010). We used the phylogenetic independent contrasts (PIC, R package picante) and Blomberg's K for each trait to test if ecological traits displayed phylogenetic signals in the species pool. The observed PIC for each trait was compared to a null distribution generated by randomly shuffling taxa names across the phylogeny while leaving the ecological trait in place (Sydenham et al. 2015). We ran 10 000 iterations to obtain the null distribution. If the p-values of observed vs random variance of PICs were lower than 0.05, we interpreted them as an evidence of non-random phylogenetic signal for the given trait. Blomberg's K was used to quantify phylogenetical clustering for each trait: high values of K indicate a strong similarity in trait values among closely related species (Münkemüller et al. 2012). Third, we calculated the net relatedness index (NRI) to quantify phylogenetic clustering at the community level (Webb et al. 2002). The null model for the NRI was generated by calculating for each site the mean and standard deviation of the phylogenetic distances expected for the number of taxa found on the site, based on a random selection of species from the regional species pool found in our study (10 000 iterations per site) (Hoiss et al. 2012). As we assumed that the ability of a species to colonize a sampling site would be proportional to its frequency in the species pool, the random draws were weighted by the relative abundance of each species in the pool (Hoiss et al. 2012). Positive values of NRI indicate phylogenetic clustering and negative values phylogenetic over-dispersion. To test whether NRI significantly changed along landscape gradients, we performed linear regressions for the two regions with site scores from the RLQ as predictors and NRIs per site as response variables.

Results

Landscape gradients affecting the functional structure of bee communities

Southwest France

Even though the first two axes of the RLQ explained only 26% of the total joint inertia of the three tables, they accounted for most of the variability explained by the separate analyses of landscape variables and trait data (65% for landscape and trait data). Therefore the covariance between the R-landscape variables and Q-trait table was well described in the RLQ analysis.

For each type of semi-natural habitat, habitat amount and isolation were correlated to the same axes of the RLQ analysis (Table 1). The first RLQ axis separated landscapes according to the amount and isolation of hedgerows and permanent grasslands (Table 1), with a positive correlation between the first axis of the RLQ and the amount and proximity of grasslands and hedgerows. The second axis of the RLQ was positively associated with the amount and proximity of woodland edges (Table 1).

Body size, sociality and nest location were significantly associated with the first RLQ axis, describing the amount and proximity of grasslands and hedgerows (Table 1). Small-bodied, solitary and below-ground nesting species were associated with the highest levels of amount and proximity of grasslands and hedgerows, whereas large-bodied, social and above-ground nesting species were associated with reduced amounts and proximity of grasslands and hedgerows (Table 1, Fig. 3).

Body size, the beginning of foraging period, sociality, diet breadth and nest location were significantly associated with the second RLQ axis, describing the amount and proximity of woodland edges (Table 1). Indeed, the small-bodied, late foraging, social, polylectic and below-ground nesting species were associated with greater amounts and proximity of woodland edges. In contrast, the large-bodied, early foragers, solitary, oligolectic and above-ground nesting species were associated with reduced amounts and proximity of woodland edges (Table 1, Fig. 3). The duration of foraging season was not correlated with either of the two RLQ axes (Table 1).

Table 1. Correlation coefficients between the environmental variables and traits with the first and second axis of the RLQ for the southwest France and NSW Australia regions. Spearman correlation coefficients are for continuous variables and Kruskal–Wallis chi-squared statistics are for the categorical variables (marked with an a). The highest correlations are in bold. ($p < 0.05$*; $p < 0.01$**; $p < 0.001$***).

		RLQ axis 1	RLQ axis 2
Southwest France			
Environmental variables	hedge	**0.69*** **	–0.26*
	prox_hedge	**0.73*** **	–0.12
	woodland_edge	0.16	**0.93*** **
	prox_woodland_edge	0.29**	**0.78*** **
	grassland	**0.65*** **	0.09
	prox_grassland	**0.74*** **	0
Traits	ITD	**–0.65*** **	**–0.54*** **
	Sociality[a]	**15.14*** **	**21.96*** **
	Diet breadth[a]	2.83	**23.62*** **
	Foraging duration	–0.14	0.15
	Foraging beginning	0.26*	**0.45*** **
	Nest location[a]	**14.59*** **	**10.1** **
NSW Australia			
Environmental variables	crop[a]	**17.07** **	**15.71** **
	woodland_edge	0.43*	**–0.85*** **
	prox_woodland_edge	0.13	**–0.81*** **
	grassland	0.45*	**–0.66*** **
	prox_grassland	0.46*	**–0.52** **
Traits	ITD	**0.95*** **	0.17
	Nest location[a]	**11.61*** **	**16.55*** **

NSW Australia

The first two axes of the RLQ explained 57% of the total joint inertia of the three tables. The variability explained by the separate analyses of landscape variables and trait data was conserved in the RLQ analysis (77% and 100% respectively). Therefore the RLQ analysis gave a good description of the covariance between the R-landscape variables and Q-trait table.

The first RLQ axis separated crop fields according to their identity (Table 1, Fig. 4), with sampling sites in canola fields having the lowest scores (left-hand site on the RLQ axis) and the sites in lucerne having the highest scores on this axis (right-hand site on the RLQ axis). Wheat fields, mixed and exotic pastures were located at intermediate positions. The second axis of the RLQ was negatively associated with the amount and proximity of woody and grassy habitats (Table 1).

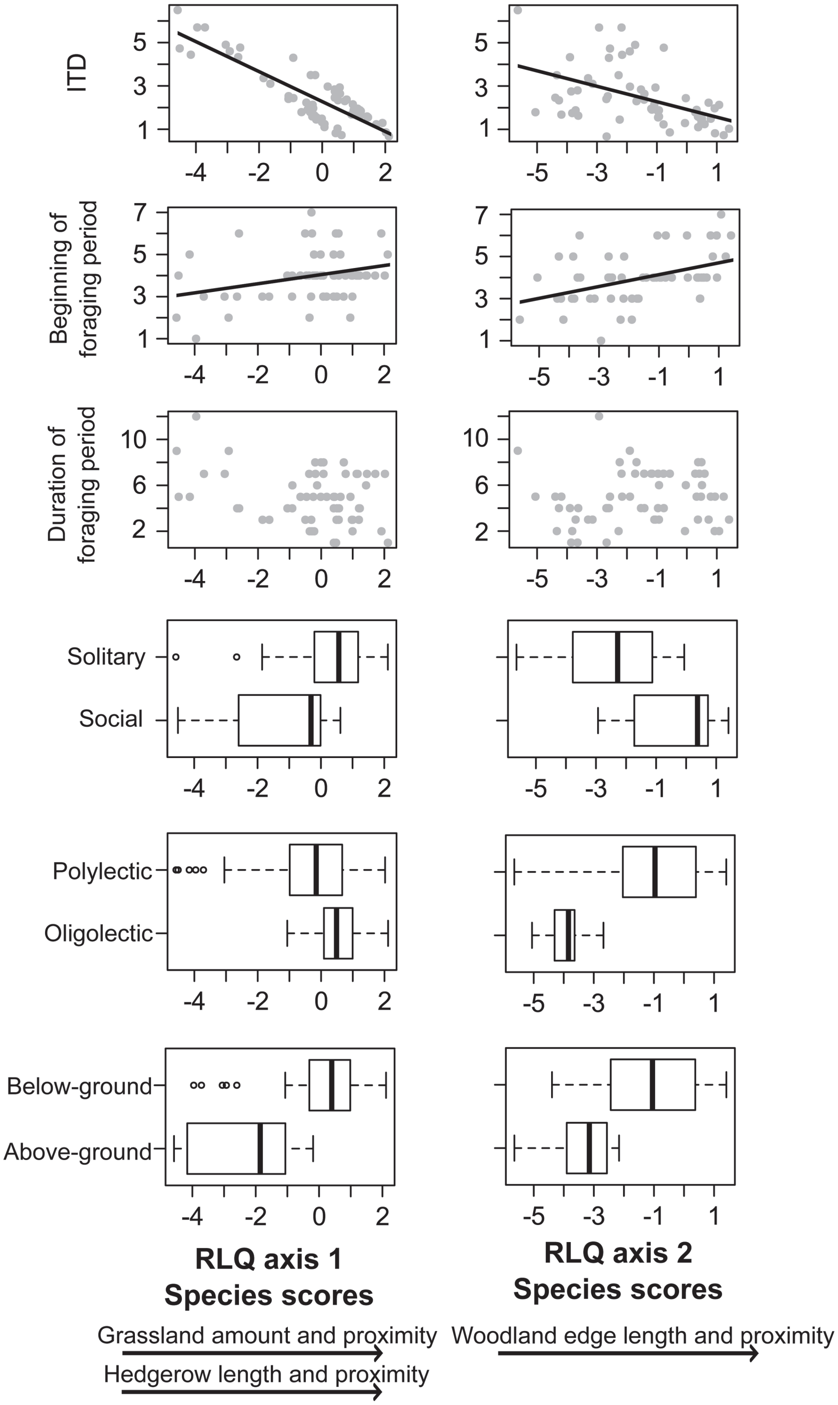

Figure 3. Correlation between trait values and species scores along the first and second axes of the RLQ for the southwest France region. Regression lines for significant correlations are shown for illustrative purposes. Description of RLQ axes in terms of environmental gradients was added for interpretation purposes.

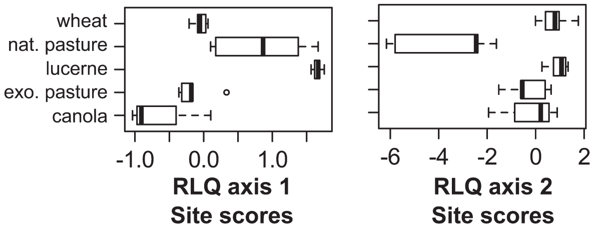

Figure 4. Correlation between crop type and site scores along the first (a) and second (b) axes of the RLQ for the NSW Australia region. These boxplots allow interpreting the directionality of the correlation between crop type (categorical variable) and RLQ axes. Correlation between continuous environmental variables and RLQ axes can be found in Table 1.

The first axis of the RLQ, describing local crop type, separated wild bee species according to their body size and nest location (Table 1). Small-bodied and below-ground nesting species were associated with sampling sites located in canola fields, whereas large-bodied and above-ground nesting species were associated with sampling points located in lucerne (Fig. 5).

Only nest location was correlated with the second axis of the RLQ, describing the amount and proximity of woody and grassy habitats (Table 1). Above-ground nesters were associated with landscapes that had a greater amount and proximity of semi-natural habitats, whereas below-ground nesters were dominant in crop-dominated landscapes (Fig. 5).

Association among ecological traits at the species level

In both regions, above-ground nesters were significantly larger than below-ground nesters (Table 2). In the southwest France region, body size was negatively correlated with the beginning of the foraging period (Table 2). Late-emerging species tended to forager for shorter periods than early-emerging species. Oligolectic species foraged for shorter periods and were mostly solitary compared to polylectic species.

Phylogenetic signal in species traits and bee communities

The majority of the traits showed significant phylogenetic signals in both regions (Table 3). In southwest France, the largest bees were from the genus *Bombus*. Sociality was exclusive to the *Bombus*, *Halictus* and *Lasioglossum* (subgenus *Evylaeus*) genera. Oligolectic species were all from the *Andrena* and *Eucera* genera. Above-ground nesters were found in *Xylocopa*, *Osmia* and *Bombus* genera (*B. sylvarum* and *B. ruderarius*). In NSW Australia, nest location showed a greater phylogenetic signal than body size (Table 3). Above-ground nesters were exclusive to the genera *Megachile* and *Hylaeus*, and species from the *Amegilla* and *Megachile* genera were the largest bees.

There was no significant association between relatedness in wild bee communities (NRI) and the RLQ axis neither for the French region (estimate RLQ axis 1: 0.03 ± 0.09 ns, RLQ axis 2: 0.08 ± 0.12 ns) nor the Australian one (estimate RLQ axis 1: –0.24 ± 0.26 ns, RLQ axis 2: –0.03 ± 0.11 ns).

Discussion

Changes in response to trait distributions along the gradients of habitat amount and fragmentation

We found that body size was strongly correlated with environmental gradients in both regions. In southwest

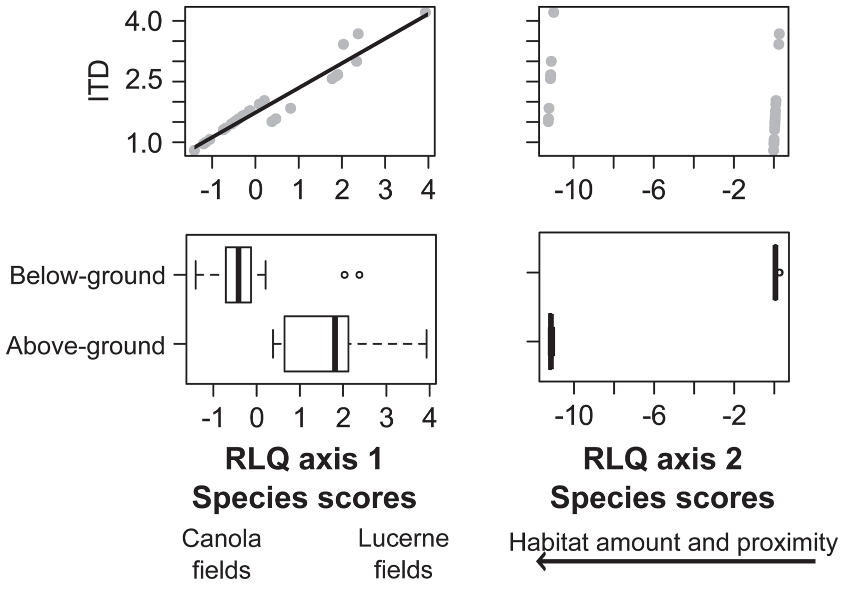

Figure 5. Correlation between trait values and species scores along the first and second axes of the RLQ for the NSW Australia region. Regression lines for significant correlations are displayed for illustration purposes. Description of RLQ axes in terms of environmental gradients was added for interpretation purposes.

Table 2. Spearman rank correlations among species traits for the southwest France (n = 60) and NSW Australia (n = 28). For nominal traits, trait values were coded as 0 or 1 to allow for correlation calculation. Sociality: social = 0, solitary = 1; diet breadth: polylectic = 0, oligolectic = 1; nest location: below-ground = 0, above-ground = 1 ($p < 0.05$*; $p < 0.01$**; $p < 0.001$***).

Southwest France

	Foraging duration	Beginning of foraging	Sociality	Diet breadth	Nest location
ITD	–0.07	–0.31*	0.08	–0.03	0.31*
Foraging duration		–0.41**	–0.25*	–0.39**	0.04
Beginning of foraging			–0.17	0.02	–0.16
Sociality				0.34**	0.17
Diet breadth					–0.09

NSW Australia

	Nest location
ITD	0.47*

France, body size negatively correlated with an increase in the amount and proximity of grasslands and hedgerows, and to a lesser extent with an increase in woodland edge length and proximity. This result was consistent with our expectation that small-bodied species that have limited dispersal abilities and therefore need to nest closer to floral resources (Greenleaf et al. 2007), would be more abundant in landscapes with high amount and low fragmentation of semi-natural habitats compared to large species. Indeed, wild bee species in agricultural landscapes can benefit from semi-natural habitats such as hedgerows, permanent grasslands and woodland edges as they can provide critical feeding resources and nesting sites for both above- and below-ground nesting species (Morandin et al. 2007, Bailey et al. 2014, Hopfenmüller et al. 2014, Forrest et al. 2015). Even though some crop fields can provide flowering resources for wild bees, such as mass-flowering crops or weeds (Garibaldi et al. 2013, Bretagnolle and Gaba 2015), farmed areas are likely to be less suitable habitats for bee species that depend on semi-natural habitats (Westrich 1996). Indeed, bees have been shown to move from semi-natural habitats into cropped areas to look for flowering resources, which explains the decrease in bee species richness and abundance with increasing isolation from semi-natural habitats (Steffan-Dewenter and Tscharntke 1999, Albrecht et al. 2007, Garibaldi et al. 2011, Bailey et al. 2014). Species with limited dispersal abilities in the farmed area in southwest France might therefore have benefitted from the large amount and the low isolation of semi-natural habitats, that might provide a high amount of available resources and opportunity for supplementation between habitats (Fahrig 2003, Ries et al. 2004). A decrease in the abundance of small-bodied species with decreasing habitat amount was also found in previous studies (Bommarco et al. 2010, Williams et al. 2010, Jauker et al. 2013). However, Larsen et al. (2005) found the opposite pattern as large-bodied species were more sensitive to habitat loss. Body size can be correlated with other traits such as diet breadth and sociality (Bommarco et al. 2010, Jauker et al. 2013), which also influence the response of bees to habitat amount and fragmentation. This may explain why studies not controlling for the correlation of body size with other traits, such as Larsen et al. (2005), found contrasting results when studying the effect of habitat amount or fragmentation.

Contrary to our expectations, the body size of bee species was not linked to the amount and proximity of semi-natural habitats in NSW Australia. The spatial extent of resource use by bees in this region therefore does not appear to influence community structure in response to habitat loss and fragmentation. However, there was a shift in body size at the community level along the first RLQ axis, which described the type of crop fields in which bees were captured (Table 1). Bee body size and proboscis length tend to be positively correlated (Cariveau et al. 2016), and our results suggest that short-tongued bees were more abundant in fields supporting crops with open and short corolla flowers (canola) whereas long-tongued species were associated with long and tubular flowering fields (lucerne, Fig. 5). This is consistent with other

Table 3. Phylogenetic signal in ecological traits of wild bee species for the southwest France and NSW Australia regions. For nominal traits, trait values were coded as 0 or 1 to allow for the phylogenetic independent contrasts (PIC) (Sociality: social = 0, solitary = 1; diet breadth: polylectic = 0, oligolectic = 1; nest location: below-ground = 0, above-ground = 1). The test of the significance of the phylogenetic independent contrasts (PIC) were based on the comparison between the variance of the observed contrasts (PIC.var.obs) and the mean variance in contrasts obtained by randomizing the relationship between the trait and the phylogeny (null expectation, PIC.var.rnd.mean). The relationship between the variance of the observed and randomized PIC provided a z-value (PIC.var.Z). A smaller p-value than 0.05 is a sign of phylogenetic signal in ecological traits.

	Blomberg's K	PIC.var.obs	PIC.var.rnd.mean	p-value	PIC.var.Z
Southwest France (n = 60)					
ITD	0.20	10.97	27.85	0.0001	–2.79
Foraging duration	0.15	44.67	81.89	0.0026	–2.22
Foraging beginning	0.16	12.06	21.30	0.0047	–2.07
Sociality	0.27	1.30	3.83	0.0001	–3.85
Diet breadth	0.20	0.99	2.51	0.0006	–2.87
Nest location	0.34	0.48	2.01	0.0003	–3.19
NSW Australia (n = 28)					
ITD	0.57	1.77	3.83	0.0523	–1.15
Nest location	4.39	0.07	1.16	0.0001	–2.56

studies that have found that proboscis length influences the flower choice of bee species (Goulson et al. 2008, Garibaldi et al. 2015, Cariveau et al. 2016). Therefore, the shift in bee body size observed along the first axis could have actually been due to the positive correlation between body size and tongue length. However, measurement of mouthpart length on bee individuals would be necessary to confirm the implication of tongue length relatively to body size in the response of bee communities to crop type in NSW Australia.

As with body size, shifts in nest location along the gradients of habitat amount and fragmentation differed between the two regions. Contrary to our expectations, above-ground nesters in southwest France were associated with landscapes with a low to intermediate levels of habitat amount and proximity (Fig. 3), whereas nesting sites for these species may be scarce in these crop-dominated landscapes (Potts et al. 2005, Williams et al. 2010). Therefore above-ground nesters did not seem to be strongly affected by the amount and proximity of semi-natural habitats. The shift in nest location along the landscape gradients that we detected in southwest France may have actually been due to the positive effects of the amount and proximity of semi-natural habitats on the occurrence of below-ground nesters. Indeed, permanent grasslands and woodland edges can provide zones of undisturbed bare soil and sparse vegetation that can benefit below-ground nesting species (Potts et al. 2005, Bailey et al. 2014, Hopfenmüller et al. 2014). However, the opposite pattern was found in NSW Australia (Table 1). Above-ground nesters were associated with landscapes that were dominated by permanent woody and grassy vegetation, whereas below-ground nesters were more abundant in crop-dominated landscapes. This pattern can be explained by the fact that above-ground nesters nest in stems or existing holes using plant materials, and native vegetation such as trees, shrubs and permanent grassy areas would have allowed them to fulfil their nesting requirements (Potts et al. 2005, Williams et al. 2010). Below-ground nesters might have found suitable nesting sites in crop-dominated landscape as they can also nest in crop borders (Svensson et al. 2000, Kim et al. 2006). Nest location also shifted depending on local crop type, but this trend was likely to be a correlated response driven by the shift in body size, rather than differences among crops in nesting opportunities. Indeed, below-ground nesters can nest in annual crop fields, contrary to above-ground nesters which need undisturbed vegetation to build their nests (Potts et al. 2005, Shuler et al. 2005, Kim et al. 2006).

Such differences in the response of wild bee species to habitat amount and fragmentation among the two regions were mainly due to the differences in the regional species pools. In southwest France, we captured species from five different families, with contrasting trait values such as sociality and diet breadth (Supplementary material Appendix 1, Table A1). In NSW Australia, the captured bees had less contrasting ecological requirements and were from only four families (Supplementary material Appendix 2, Table A2). Moreover, the lack of knowledge of ecological trait values of Australian bee species (Batley and Hogendoorn 2009) prevented us from testing all the associations among ecological traits that were tested in southwest France. These differences in the regional species pools can be explained by several factors that were impossible to disentangle in this study. First, the trapping method might have influenced the diversity of captured species. Indeed, blue vane traps are particularly appropriate for capturing bee individuals in the presence of abundant flowering resources but the use of only one color might have reduced the diversity of captured species (Toler et al. 2005, Westphal et al. 2008). Pan traps are less efficient in capturing the functional association between bee species and local flower resources, but they are efficient to assess bee community structure when using different colors (Westphal et al. 2008). Moreover, species pools presumably differed between the two regions because traps were placed in different habitats. Even though isolated trees in NSW Australia were located in crop fields, this location may have selected specific species due to the floral and nesting sites that isolated trees can provide (Tscharntke et al. 1998), whereas annual, non-entomophilous, crop fields sampled in southwest France were likely to provide fewer resources.

Second, the differences in the species pool might be due to biogeographic history. Indeed, the families Andrenidae and Mellitidae are not found in Australia, whereas species from the family Colletidae are over-represented compared to Europe. Further, *Bombus* are not part of the Australian fauna except as an introduced species on the island of Tasmania (Hines 2008, Batley and Hogendoorn 2009).

Third, differences in the species pools might be due to differences in the history and spatial extent of land-use change in the two regions. Indeed, in Australia the conversion of natural habitats to crop production took place within the last 200 years during European settlement and is thus recent compared to Europe (Benson 1991). However, in France, wood cover reached its minimum extent at the end of the 19th century and has increased since to reach currently 30% of the land (Andrieu et al. 2011). Conversely, hedgerow cover reached its maximum extent in the late 19th century, and suffered from further fragmentation during the second post-war period (Burel and Baudry 1990). As a result, southwestern France has relatively denser wood cover and smaller mean field size than the Australian region (~ 4 ha in southwest France, ~ 90 ha in NSW Australia). Therefore these relatively new and substantial land-use changes in NSW Australia compared to southwest France may explain the lower bee species richness and the absence of relatively mobile species responding to landscape changes in the Australian landscapes.

In southwest France, other traits such as sociality, diet breadth and the beginning of foraging season shifted along the gradients of habitat amount and fragmentation. We found that social bees were dominant in landscapes with low amounts and high fragmentation of grasslands and hedgerows (Fig. 3), which is in line with a previous study that found that solitary species were more sensitive to the local loss of grassy permanent vegetation than social species (Krauss et al. 2009, Jauker et al. 2013). However, we found the opposite relationship along the gradient of length and isolation of woodland edges, with social species being associated with highly forested landscapes. This is consistent with the meta-analysis of Williams et al. (2010), who found that social species in farmlands were more sensitive to the loss of natural habitats (mostly woody habitats) than solitary ones. The authors suggest that this was because social species need larger amount of floral resources to feed their numerous larvae. Our results therefore suggest that woodland edges provided critical resources for social bees, whereas solitary bees benefitted from grasslands and hedgerows. We also found that oligolectic species were associated with landscapes with low cover and high fragmentation of woodlands, which contradicted our expectations. This trend may be explained by the fact that the oligolectic species we captured in the southwest France sites were dominated by species from the *Andrena* and *Eucera* genera, foraging principally on plants in the Brassicaceae and Fabaceae respectively, which can be easily found in the crop mosaic, as mass-flowering crops (oilseed rape) or weed species (clover or mustard) (Le Féon et al. 2013, Bretagnolle and Gaba 2015, Rollin et al. 2016). As woodland and annual crop proportions were negatively correlated in the French landscapes ($r = -0.55$, $p < 0.0001$), oligolectic species were less abundant in wooded landscapes, presumably because they found fewer suitable floral resources than in less wooded landscapes.

In southwest France, the beginning of the foraging period shifted along the gradient of woodland edge length and isolation: early emerging were more abundant in the least-forested landscapes. This trend is in accordance with previous studies on other taxa that found that early-active species were more abundant in open landscapes than in highly forested ones, presumably due to the fact that species may complete the majority of their life before the onset of agricultural disturbances in crop-dominated landscapes (Duflot et al. 2014). Therefore in the least-forested landscapes of our study, early-emerging species might have been favored due to their capacity to forage and reproduce before the main agricultural interventions that can impact bee survival, such as pesticide spraying, mowing or grazing in late spring (Le Féon et al. 2010, Gámez-Virués et al. 2015).

Relationships among ecological traits along the gradient of habitat amount and fragmentation in the landscapes

Our hypothesis, stating that correlated shifts of ecological traits along the landscape gradients would be due to a correlation between these traits at the species level, was not validated. Indeed, some traits that were associated at the species level also co-varied along the landscape gradients (body size and nest location in southwest France and NSW Australia, diet breadth and sociality in southwest France, body size and beginning of the foraging season in southwest France). However, this pattern was not detected for all the traits. Indeed, some trait values were associated at the species level but did not co-occur along the landscape gradients (sociality and diet breadth, beginning and duration of foraging season, Table 2, Fig. 3) and some other traits shifted along landscape gradients without being associated at the species level (body size and sociality, body size and diet breadth, Table 2, Fig. 3). Therefore species-level association among traits seemed to be of minor importance in determining co-occurrence of trait values along the gradient of habitat amount and fragmentation.

Even though there were phylogenetic associations in species traits, we did not find significant correlations between phylogenetic relatedness (NRI) and landscape drivers (RLQ axes) for either region. This result is consistent with Sydenham et al. (2015), who found that the response of wild bees to landscape habitat diversity did not involve a phylogenetic clustering of wild bee communities.

Our results therefore suggest that neither species-level nor phylogenetic association among ecological traits strongly influenced the shifts in multiple traits that were detected along the landscape gradients in both regions. The results thus suggest that such shifts were mainly due to a direct effect of landscape variables.

Potential influence of ecological trait shifts on pollination delivery

The majority of the ecological traits that we examined have been reported to affect pollination delivery in other studies. For example, body size can be an effect trait as large-bodied species have a greater chance of depositing pollen grains on flower stigmas (Larsen et al. 2005, Hoehn et al. 2008). However, the effect of body size on pollen deposition seems to depend on tongue length and on the plant species being considered (Garibaldi et al. 2015). Bee sociality might also influence pollination delivery, as Albrecht et al. (2012) found that social species visited *Raphanus sativus* L. more frequently than solitary ones and deposited more pollen grains. Conversely, Klein et al. (2003) found greater pollination efficiency of solitary bees in the case of coffee crops, therefore the pollination efficiency of social versus solitary bees may depend on the focal plant species or broader plant assemblages. Bee diet breadth might also determine pollination success as polylectic species are more likely to pollinate a variety of plant species (Williams et al. 2010). This could have important implications for pollination as plant–pollinator networks are asymmetric: specialist plants often rely on generalist pollinators and vice versa (Memmott et al. 2004, Potts et al. 2010). This could lead, in our case, to a depletion of pollen deposition on plants with specialized pollinator requirements at the plant community level in landscapes with few and highly fragmented woodlands, possibly causing a decrease in plant species richness. In southwest France, we also found that late-foragers were favored over early ones in forested landscapes, which could positively affect pollination success of late-flowering crop such as sunflower.

Conclusion

Our results show that there was a strong shift in distribution of traits along the gradient of semi-natural habitat amount and fragmentation across the two regions. We found that these shifts were more likely to be due to an effect of habitat amount and fragmentation on different response traits than a correlation among several traits due to morphological or phylogenetical constraints. We also observed regionally-specific trends in response traits along the gradients habitat amount and fragmentation, suggesting that the regional species pool can play an important role in the response of bee communities to landscape context. This study highlights the importance of multi-trait analyses to better understand the effect of habitat amount and fragmentation on communities of providers of ecosystem services in real-world landscapes.

Acknowledgements – RC received a PhD scholarship from the French Ministry of Higher Education and Research (Univ. de Toulouse). Field work in France was carried out as part of FarmLand, an ERA-Net BiodivERsA project funded by the French National Research Agency (ANR-11-EBID-0004). In Australia, financial support was provided by the Paddy Pallin Foundation in partnership with the Royal Zoological Society of NSW, the WildCountry Science Council, and an Australian Postgraduate Award and CSIRO scholarship to PL. ML was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41). We thank D. Genoud and M. Batley for their help on specimen identification and their expertise on bee species traits. We thank M. Kuhlmann and V. Le Feon for the provision of part of the French trait data. We also thank the farmers from France and Australia who allowed us to work in their fields, all the people involved in the field surveys and specimen identification, technical staff, colleagues and volunteers: L. Frontero, B. Dumora, A. Bourgeade, R. Rudelle and F. Calatayud, C. Singh, Z. Pujol, A-S. Larcebeau and R. Bertram (France) and M. Castles, M. Long, L. Lentini, A. Munro, B. Noel, K. Russell and J. Stanaway (Australia). We also thank the three anonymous reviewers for their helpful comments.

References

Albrecht, M. et al. 2007. The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. – J. Appl. Ecol. 44: 813–822.

Albrecht, M. et al. 2012. Diverse pollinator communities enhance plant reproductive success. – Proc. R. Soc. Lond. B 279: 4845–4852.

Andrieu, E. et al. 2011. History and spatial complexity of deforestation and logging in small private forests. – Landscape Urban Plan. 103: 109–117.

Bailey, S. et al. 2014. Distance from forest edge affects bee pollinators in oilseed rape fields. – Ecol. Evol. 4: 370–380.

Barbaro, L. and Van Halder, I. 2009. Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. – Ecography 32: 321–333.

Batley, M. and Hogendoorn, K. 2009. Diversity and conservation status of native Australian bees. – Apidologie 40: 347–354.

Bender, D. J. et al. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. – Landscape Ecol. 18: 17–39.

Benson, J. 1991. The effect of 200 years of European settlement on the vegetation and flora of New South Wales. – Cunninghamia 2: 343Á70.

Blüthgen, N. and Klein, A.-M. 2011. Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. – Basic Appl. Ecol. 12: 282–291.

Bommarco, R. et al. 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. – Proc. R. Soc. B 277: 2075–2082.

Bretagnolle, V. and Gaba, S. 2015. Weeds for bees? A review. – Agron. Sustain. Dev. 35: 891–909.

Burel, F. and Baudry, J. 1990. Structural dynamic of a hedgerow network landscape in Brittany France. – Landscape Ecol. 4: 197–210.

Cariveau, D. P. et al. 2016. The allometry of bee proboscis length and its uses in ecology. – PloS One 11: e0151482.

Chapin, F. S. et al. 1997. Biotic control over the functioning of ecosystems. – Science 277: 500–504.

Choisis, J.-P. et al. 2010. Understanding regional dynamics of mixed crop-livestock agricultural systems to support rural development in southwestern France uplands. – Cah. Agricult. 19: 97–103.

Dolédec, S. et al. 1996. Matching species traits to environmental variables: a new three-table ordination method. – Environ. Ecol. Stat. 3: 143–166.

Duflot, R. et al. 2014. Landscape heterogeneity as an ecological filter of species traits. – Acta Oecologica 56: 19–26.

Ekroos, J. et al. 2013. Trait-dependent responses of flower-visiting insects to distance to semi-natural grasslands and landscape heterogeneity. – Landscape Ecol. 28: 1283–1292.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. – Annu. Rev. Ecol. Evol. Syst. 34: 487–515.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. – J. Biogeogr. 40: 1649–1663.

Forrest, J. R. et al. 2015. Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. – J. Appl. Ecol. 52:706–715.

Fortel, L. et al. 2014. Decreasing abundance, increasing diversity and changing structure of the wild bee community (Hymenoptera: Anthophila) along an urbanization gradient. – http://dx.doi.org/10.1371/journal.pone.0104679

Gámez-Virués, S. et al. 2015. Landscape simplification filters species traits and drives biotic homogenization. – Nat. Comm. doi:10.1038/ncomms9568

Garibaldi, L. A. et al. 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits: habitat isolation and pollination stability. – Ecol. Lett. 14: 1062–1072.

Garibaldi, L. A. et al. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. – Science 339: 1608–1611.

Garibaldi, L. A. et al. 2015. Trait matching of flower visitors and crops predicts fruit set better than trait diversity. – J. Appl. Ecol. 52: 1436–1444.

Gathmann, A. and Tscharntke, T. 2002. Foraging ranges of solitary bees. – J. Anim. Ecol. 71: 757–764.

Goulson, D. et al. 2008. Diet breadth, coexistence and rarity in bumblebees. – Biodivers. Conserv. 17: 3269–3288.

Greenleaf, S. S. et al. 2007. Bee foraging ranges and their relationship to body size. – Oecologia 153: 589–596.

Haddad, N. M. et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. – Sci. Adv. 1: e1500052.

Haddad, N. M. et al. 2017. Experimental evidence does not support the Habitat Amount Hypothesis. – Ecography 40: 48–55.

Hines, H. M. 2008. Historical biogeography, divergence times, and diversification patterns of bumble bees (Hymenoptera: Apidae: *Bombus*). – Syst. Biol. 57: 58–75.

Hoehn, P. et al. 2008. Functional group diversity of bee pollinators increases crop yield. – Proc. R. Soc. B 275: 2283–2291.

Hoiss, B. et al. 2012. Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. – Proc. R. Soc. Lond. 279: 4447–4456.

Holzschuh, A. et al. 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? – J. Anim. Ecol. 79: 491–500.

Hopfenmüller, S. et al. 2014. Trait-specific responses of wild bee communities to landscape composition, configuration and local factors. – PloS One 9: e104439.

IGN 2013. – IGN Editions, Base de données orthophotographique BD Ortho®, survey 2013 FD 31 C 50 (numeric photographs).

Jauker, B. et al. 2013. Linking life history traits to pollinator loss in fragmented calcareous grasslands. – Landscape Ecol. 28: 107–120.

Kim, J. et al. 2006. Effects of cultivation and proximity to natural habitat on ground-nesting native bees in California sunflower fields. – J. Kans. Entomol. Soc. 79: 309–320.

Klein, A.-M. et al. 2003. Pollination of *Coffea canephora* in relation to local and regional agroforestry management. – J. Appl. Ecol. 40: 837–845.

Klein, A.-M. et al. 2007. Importance of pollinators in changing landscapes for world crops. – Proc. R. Soc. B 274: 303–313.

Krauss, J. et al. 2009. Habitat area but not habitat age determines wild bee richness in limestone quarries. – J. Appl. Ecol. 46: 194–202.

Krebs, J. R. et al. 1999. The second silent spring? – Nature 400: 611–612.

Kremen, C. 2005. Managing ecosystem services: what do we need to know about their ecology? – Ecol. Lett. 8: 468–479.

Kremen, C. and M'Gonigle, L. K. 2015. Small-scale restoration in intensive agricultural landscapes supports more specialized and less mobile pollinator species. – J. Appl. Ecol. doi: 10.1111/1365-2664.12418

Kremen, C. et al. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. – Ecol. Lett. 10: 299–314.

Larsen, T. H. et al. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. – Ecol. Lett. 8: 538–547.

Lavorel, S. and Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the holy grail. – Funct. Ecol. 16: 545–556.

Le Féon, V. et al. 2010. Intensification of agriculture, landscape composition and wild bee communities: a large scale study in four European countries. – Agricult. Ecosyst. Environ. 137: 143–150.

Le Féon, V. et al. 2013. Solitary bee abundance and species richness in dynamic agricultural landscapes. – Agricult. Ecosyst. Environ. 166: 94–101.

Lentini, P. E. et al. 2012. Supporting wild pollinators in a temperate agricultural landscape: Maintaining mosaics of natural features and production. – Biol. Conserv. 149: 84–92.

Loreau, M. et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. – Science 294: 804–808.

Mallinger, R. E. et al. 2016. Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. – Landscape Ecol. doi:10.1007/s10980-015-0332-z

McGarigal, K. et al. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. – McGarigal and Marks, Oregon State Univ., USA.

Memmott, J. et al. 2004. Tolerance of pollination networks to species extinctions. – Proc. R. Soc. Lond. B 271: 2605–2611.

Michener, C. D. 2000. The bees of the world. – JHU Press.

Morandin, L. A. et al. 2007. Can pastureland increase wild bee abundance in agriculturally intense areas? – Basic Appl. Ecol. 8: 117–124.

Münkemüller, T. et al. 2012. How to measure and test phylogenetic signal. – Methods Ecol. Evol. 3: 743–756.

Parry, M. L. 2007. Climate change 2007-impacts, adaptation and vulnerability: working group II contribution to the fourth assessment report of the IPCC. – Cambridge Univ. Press.

Pimm, S. L. et al. 1995. The future of biodiversity. – Science 269: 347.

Potts, S. G. et al. 2005. Role of nesting resources in organizing diverse bee communities in a Mediterranean landscape. – Ecol. Entomol. 30: 78–85.

Potts, S. G. et al. 2010. Global pollinator declines: trends, impacts and drivers. – Trends Ecol. Evol. 25: 345–353.

Resasco, J. et al. 2017. Theory, experiments, and the conservation of fragmented landscapes. – Ecography 40: 109–118.

Supplementary material (Appendix ecog-02632 at <www.ecography.org/appendix/ecog-02632>). Appendix 1–4.

Ries, L. et al. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. – Annu. Rev. Ecol. Evol. Syst. 35: 491–522.

Robinson, R. A. and Sutherland, W. J. 2002. Post-war changes in arable farming and biodiversity in Great Britain. – J. Appl. Ecol. 39: 157–176.

Rollin, O. et al. 2016. Weed–insect pollinator networks as bio-indicators of ecological sustainability in agriculture. A review. – Agron. Sustain. Dev. 36: 1–22.

Settele, J. et al. 2005. ALARM: Assessing LArge-scale environmental Risks for biodiversity with tested Methods. – Gaia-Ecol. Perspect. Sci. Soc. 14: 69–72.

Shuler, R. E. et al. 2005. Farming practices influence wild pollinator populations on squash and pumpkin. – J. Econ. Entomol. 98: 790–795.

Steffan-Dewenter, I. and Tscharntke, T. 1999. Effects of habitat isolation on pollinator communities and seed set. – Oecologia 121: 432–440.

Suding, K. N. et al. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. – Global Change Biol. 14: 1125–1140.

Svensson, B. et al. 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. – Agricult. Ecosyst. Environ. 77: 247–255.

Sydenham, M. A. K. et al. 2015. Does multi-level environmental filtering determine the functional and phylogenetic composition of wild bee species assemblages? – Ecography 38: 140–153.

Tilman, D. 1999. Global environmental impacts of agricultural expansion: the need for sustainable and efficient practices. – Proc. Natl Acad. Sci. USA 96: 5995–6000.

Toler, T. et al. 2005. Pan-trapping for bees (Hymenoptera: Apiformes) in Utah's West Desert: the importance of color diversity. – Pan-Pac. Entomol. 81: 103.

Trichard, A. et al. 2013. Identification of weed community traits response to conservation agriculture. – Agricult. Ecosyst. Environ. 179: 179–186.

Tscharntke, T. et al. 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. – J. Appl. Ecol. 35: 708–719.

Tscharntke, T. et al. 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. – Ecol. Lett. 8: 857–874.

Webb, C. O. et al. 2002. Phylogenies and community ecology. – Annu. Rev. Ecol. Syst. 33: 475–505.

Westphal, C. et al. 2008. Measuring bee diversity in different European habitats and biogeographical regions. – Ecol. Monogr. 78: 653–671.

Westrich, P. 1996. Habitat requirements of central European bees and the problems of partial habitats. – Linn. Soc. Symp. Ser. 18: 1–16.

Wiens, J. J. et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. – Ecol. Lett. 13: 1310–1324.

Williams, N. M. et al. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. – Biol. Conserv. 143: 2280–2291.

Winfree, R. et al. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. – Ecology 90: 2068–2076.

Wood, S. A. et al. 2015. Functional traits in agriculture: agrobiodiversity and ecosystem services. – Trends Ecol. Evol. 30: 531–539.

Woodcock, B. A. et al. 2014. National patterns of functional diversity and redundancy in predatory ground beetles and bees associated with key UK arable crops. – J. Appl. Ecol. 51: 142–151.

Zurbuchen, A. et al. 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. – Biol. Conserv. 143: 669–676.