

Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape

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Summary

1. Land-use change frequently reduces local species diversity. Species losses will often result in loss of trait diversity, with likely consequences for community functioning. However, the converse need not be generally true: management approaches that succeed in retaining species richness could nevertheless fail to maintain trait diversity. We evaluated this possibility using bee communities in a California agroecosystem.

2. We examined among site patterns in bee species diversity and functional-trait diversity in a landscape composed of a mosaic of semi-natural habitat, organic farms and conventional farms. We sampled bees from all three habitat types and compiled a data base of life-history ('functional') traits for each species.

3. Although species richness was higher on organic farms than conventional farms, functional diversity was lower in both farm types than in natural habitat. Nesting location (below-ground vs. above-ground) was the primary trait contributing to differences in functional diversity between farms and natural habitat, reflecting observed differences in availability of nesting substrates among habitat types. Other traits, including phenology and sociality, were also associated with species' occurrences or dominance in particular site types. These patterns suggest that management practices common to all farms act as environmental filters that cause similarly low functional diversity in their bee communities.

4. *Synthesis and applications.* Although our results support the value of organic farming in maintaining abundant and species-rich bee communities, components of bee functional diversity are not well supported in farmed landscapes, regardless of farming practice. Maintenance of natural habitat, and/or the addition of natural habitat elements to farms, is therefore important for the retention of functionally diverse bee assemblages in agroecosystems.

Key-words: agroecosystems, Apoidea, biodiversity, ecosystem function, environmental filtering, functional traits, life history, organic farms, pollinators, species composition

Introduction

Biodiversity losses, such as those resulting from land-use intensification, can impair ecological functioning (e.g. Balvanera, Kremen & Martínez-Ramos 2005; Hooper *et al.* 2012). However, ecological functioning is determined not by species richness *per se*, but by the diversity and composition of functional traits represented in the community (Cadotte, Carscadden & Mirotnick 2011). It is frequently assumed that species and functional-trait diversity will decline simultaneously with land-use intensification. However, more complex relationships are possible if land-

use change disproportionately affects certain functional groups (Flynn *et al.* 2009; Mayfield *et al.* 2010; Luck, Carter & Smallbone 2013). Indeed, functional groups defined by such traits as diet specialization or body size often respond differently to land-use change (Williams *et al.* 2010; Newbold *et al.* 2012; Senior *et al.* 2013; Rader *et al.* 2014). If the functional traits that determine sensitivity to environmental change (response traits) are also those that affect ecosystem processes (effect traits), then understanding how functional-trait diversity is affected by land-use change is critical for predicting changes in community functioning (Lavelle & Garnier 2002).

Conversion of natural habitat to agriculture is among the most widespread human impacts on the planet. Agricultural intensification reduces species diversity in many groups, including pollinators (Dobson *et al.* 1997; Kerr &

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Cihlar 2004; Kennedy *et al.* 2013). However, despite the potential for agricultural land use to harm wild pollinator populations, bee responses to agriculture are not uniformly negative (Tscharrntke *et al.* 2005; Winfree *et al.* 2009; Williams *et al.* 2010). In all but the most intensive landscapes, agriculture includes mosaics of semi-natural and cultivated habitats that differ in vegetation, edaphic characteristics and inputs of water and chemicals – all factors that may affect different species in different ways, depending on their response traits. Cultivation itself changes plant composition, flowering phenology and structural aspects of the environment in ways that may favour some bee species (Cane 2008; Julier & Roulston 2009). Thus, agricultural land use is likely to change not only the species richness and abundance of pollinator communities, but also their species and trait compositions.

Cultivated habitats (especially those dominated by annual crops) share certain attributes, such as tillage, loss of native plant diversity and scarcity of dead wood, but they also vary in aspects of management that may affect both species diversity and the representation of different functional groups. Diversity usually declines as management intensity increases (e.g. Hole *et al.* 2005; Clough *et al.* 2007; Rundlöf, Nilsson & Smith 2008; Batáry *et al.* 2011; though see Brittain *et al.* 2010; Kehinde & Samways 2012), and aspects of organic farming, such as flowering weed abundance, lack of insecticides and local habitat diversity, should favour many bee populations. Whether organic farming should also maintain trait diversity is unclear, since many of the structural elements of organic farms are the same as those of conventional agriculture. Retention of functional diversity in bee communities is important because species with different traits can provide complementary pollination services (Hoehn *et al.* 2008; Albrecht *et al.* 2012) and are likely to vary in sensitivity to different disturbances, making service provision more stable at the community level (Mori, Furukawa & Sasaki 2013). Unfortunately, most studies assessing the biodiversity benefits of organic farming compare organic farms only with conventionally managed farms, not with natural habitat (e.g. Hole *et al.* 2005; Clough *et al.* 2007; Rundlöf, Nilsson & Smith 2008; Batáry *et al.* 2011; Tuck *et al.* 2014; but see Hodgson *et al.* 2010; Kehinde & Samways 2012). Without comparisons to natural habitats, we cannot know how well the communities of organic farms retain the structure and functional diversity of those in the surrounding natural environment.

We sampled bee communities on organic farms, conventional farms and adjacent natural habitat within a mosaic agricultural landscape in northern California. We also compiled a data base of life-history ('functional') traits for the sampled species. We used these data to ask, first, whether agricultural land use exerts similar effects on species and functional diversity. Secondly, we tested whether organic farms support bee communities that are more functionally diverse than conventional farms and better retain species and trait compositions similar to

those of natural habitat. Finally, we investigated which bee traits contributed most to the observed differences in functional diversity, and why these traits differed between farms and natural habitat. Differences in trait diversity among habitat types did not parallel differences in species richness: although organic farms supported more species than conventional farms, their functional-trait diversity was similarly impoverished compared to natural habitat. This effect was primarily due to the scarcity of above-ground nesting bees on farms, reflecting a lack of above-ground nesting structures in cultivated habitat.

Materials and methods

STUDY SITES AND SAMPLING DESIGN

Data were collected at sixteen ~1.8-ha sites established at four conventional farms, five organic farms and seven semi-natural (henceforth 'natural') areas within a mixed agricultural–natural landscape on the western slope of the Sacramento Valley, California (see Appendix S1, Supporting Information). Native vegetation is mixed riparian scrub and gallery forest, and oak savanna with chaparral at higher elevations. Conventional farms were monocultures of sunflower or orchard crops; organic farms were diversified polycultures of vegetable and orchard crops. Sites fell along two drainages and were located so all sites were separated from each other by ≥ 1.5 km. Although separated from other study sites, farm sites were positioned so that they were within 350 m of natural habitat, and natural sites were positioned within 350 m of farmed land. This proximity allowed us to focus on the effects of local habitat type while maintaining a similar landscape context: all sites in our data set had $\geq 20\%$ natural habitat within a 1-km radius. We sampled each site on eight dates at 3–4 week intervals from March to August 2002. On each occasion, we netted all bees observed visiting flowers of all flowering plants, including crops, during a 2-h period (1 h each in the morning and early afternoon), while moving systematically throughout the site. Total time netting was equal among all sites. Sites were positioned to capture the representative microhabitats for that site type; thus, within natural habitat, they included mixtures of vegetation types, and on farms, they included cultivated fields, field margins and farm roads. Sites were approximately rectangular, although dimensions varied to fit land configuration (e.g. avoiding water bodies) and property boundaries. We sampled on sunny days above 16 °C with wind speed < 2.6 m s⁻¹.

On the same day that we sampled bees, we quantified flower resources by counting flowers of all non-graminoid species within 54 1 m² quadrats spaced along two 100 m transects arranged in a cross over the midpoint of the site. To quantify nesting substrates, which change little between years, we returned to each location in a subsequent growing season and recorded nesting variables following a protocol modified from Potts *et al.* (2005). At each site, we established three parallel 100 m transects ~20 m apart, with one centred on the midpoint of the site. Along each, we recorded the number of trees (>10 cm dbh) and shrubs of >1 m³ canopy. We also counted hollow or soft-pithed dead stems and recorded percentage cover of bare ground and dead wood in five 1 m² quadrats along each transect. For each site, we calculated a unitless index of availability of above-ground nesting structures (ranging from 0 to a theoretical maximum of 100) by equally weighting and summing total numbers of trees, shrubs and stems, and percentage cover of dead wood within quadrats.

THE DATA SET

Bees were identified to species if possible, following nomenclature of Ascher & Pickering (2012). Some specimens (797 out of 5555, primarily in the genera *Lasioglossum* and *Nomada*) could only be identified to genus or as unnamed, sex-specific morphospecies. For this reason, we used only female bees in analyses (4261 specimens). The data set excludes *Apis mellifera* L., which was abundant at all sites.

TRAIT ASSIGNMENTS

For all species in the data set (Appendix S2), we compiled information on eight life-history traits likely to affect a species' habitat associations: body size, dietary specialization (lecty), nesting location, nest construction behaviour, phenology (flight season midpoint and duration), sociality and landscape-wide abundance. Table 1 lists methods for characterizing these traits.

DATA ANALYSIS

Species and trait diversity

Samples were combined across all periods, and total abundance and species richness were calculated for the bee communities of each site. For each site, we plotted species-abundance histograms

to visualize abundance distributions. We calculated Fisher's α as a diversity metric and as a means of summarizing the species-abundance distribution; it represents, roughly, the expected number of rare species in a sample of a given number of species and individuals (Magurran 2004). Species richness and Fisher's α were compared among site types with ANOVA. Total abundance data were overdispersed and were therefore analysed with a negative binomial GLM using the package MASS (Venables & Ripley 2002) of R v. 2.14.1 (R Core Team 2012). Although sampling effort was consistent among sites, the number of collected bees varied. To compare species richness for an equal number of sampled individuals, we generated rarefaction curves for all sites using the *vegan* package (Oksanen *et al.* 2011).

We calculated trait diversity for the bee community at each site as the functional dispersion metric (FDis) of Laliberté & Legendre (2010). This metric quantifies the mean distance of each species from its community centroid in a multivariate space defined by all included traits. FDis is mathematically independent of species richness and can be calculated as an abundance-weighted (individual-level) or unweighted (species-level) metric (see also Hinnners, Kearns & Wessman 2012; Hoiss *et al.* 2012). To calculate FDis, we used the function *dbFD* in package *FD*, with the Cailliez correction for non-Euclidean distances generated by inclusion of categorical traits. We compared FDis among site types using ANOVA. To quantify the impact of single traits on functional-trait diversity, we recalculated trait diversity with each of the eight traits excluded in turn and re-analysed differences among site types.

Table 1. Traits used in analyses. Trait information was taken from the sources listed; when necessary (notably for lecty and sociality), we relied on educated guesses based on capture patterns in our data set (e.g. floral records) and the biology of related species. Species were excluded from analysis if we could not confidently assign a trait category. Cleptoparasites were excluded from quantitative analyses of lecty, nest construction and sociality; however, 'cleptoparasitic' was included as an additional level for each of these traits in the FDis analysis

Trait (units)	Trait type	Categories	Source
Abundance	Continuous	N/A	Number of female individuals in our data set, summed across all sites
Body size (mm)	Continuous	N/A	Mean intertegular distance of five haphazardly selected female individuals (or, if fewer than five, as many as possible) from our collection, supplemented by museum specimens when necessary. Worker bumble bees were measured
Flight season duration, rarefied (days)	Continuous	N/A	Difference between 90th and 10th percentile collection dates, calculated from 100 random draws of 30 specimens per species. Collection data from various independent Central Valley sources (Appendix S3)
Flight season median date (day of year)	Continuous	N/A	Collection data as above
Lecty (dietary specialization)	Categorical	Oligolectic (pollen specialist) Polylectic (pollen generalist) Cleptoparasitic	Krombein <i>et al.</i> (1979)
Nesting location	Categorical	Above-ground Below-ground Mixed*	Krombein (1967); Michener (2000); Cane, Griswold & Parker (2007); Sheffield <i>et al.</i> (2011)
Nest construction	Categorical	Excavate Rent Cleptoparasitic	Michener (2000)
Sociality	Categorical	Social (including multiple forms of sociality) Solitary Cleptoparasitic	Michener (2000)

*Species that nest both above-ground and below-ground were treated as 50% above-ground nesting for quantitative analyses.

Species and trait composition

We used non-metric multidimensional scaling (NMDS; metaMDS function in *vegan*, based on Bray–Curtis distances) to examine differences in species composition and relative abundances among site types. We selected a three-axis solution as the best portrayal of the data, because this lowered final stress below 0.1, and additional axes provided little improvement.

We tested for differences in the traits of bee communities among habitat types using one-way ANOVA followed by a Tukey test if ANOVA yielded a significant result. We analysed the proportional representation of each trait in both an abundance-weighted (individual-level) and unweighted (species level) fashion. Data transformations were unnecessary to meet assumptions of ANOVA. However, certain traits are correlated across species such that potential effects of one trait are not biologically or statistically independent of others (Williams *et al.* 2010). We therefore used Spearman rank correlations to quantify associations among traits. Cleptoparasites were omitted from this analysis, as certain traits (i.e. lecty and nest construction) are undefined for cleptoparasites, and the number of cleptoparasitic species was low (12 out of 140). The strongest correlations (Table 2) are between nest location and nest construction (species with below-ground nests tend to excavate rather than rent) and between flight season median date and duration (late-season species tend to have longer flight seasons). Many traits are correlated with sociality: social species tend to be smaller and more abundant than solitary species, and they also have long flight seasons, excavate below-ground nests and are polylectic (Table 2). We present habitat associations for each trait individually; however, in the Discussion, we note cases where correlated traits may cause these associations.

Habitat characteristics

To determine whether differences in bee communities among habitat types could be explained by differences in the seasonal timing of floral resource abundance, or in the availability of potential nesting habitat, we tested whether these attributes differed among site types. Specifically, we expected that farm sites would support more floral resources than natural sites late in the season, because of irrigation, while having fewer above-ground nesting structures. We used two repeated-measures ANOVAs to test how abundance and species richness of flowers varied among site types and through the season. We compared two different

metrics of nesting habitat availability among site types: percentage cover of bare soil (potential habitat for ground nesting bees) and our index of above-ground nesting structures (arcsine square root-transformed for normality and homogeneity of variances). Both were tested using ANOVA followed by Tukey tests.

Results

SPECIES AND TRAIT DIVERSITY

Species richness and total abundance of bees varied among site types (species richness: ANOVA, $F_{2,13} = 4.15$, $P = 0.040$; total abundance: Analysis of deviance, $\chi^2 = 14.6$, d.f. = 2, $P = 0.0007$). Organic farms had the most species and individuals – more species than conventional farms and more individuals than conventional farms or natural sites (Figs 1 and 2). Organic farms and natural sites had similarly shaped rarefaction curves and similar diversity for a given number of sampled individuals (Fig. 1). Curves for conventional farms were generally positioned lower than those for other site types, suggesting that these communities were composed of fewer, more abundant taxa. Fisher's α was greater in natural sites than conventional farms (ANOVA, $F_{2,13} = 4.26$, $P = 0.038$; Fig. 2b), indicating that natural sites harboured more rare species. This interpretation is supported by the abundance–frequency plots (Appendix S4).

Trait diversity of bee communities (FDIs), whether based on abundance-weighted or unweighted data, was significantly reduced at farms compared to natural habitat (ANOVA, $F_{2,13} > 7.0$, $P < 0.01$; Fig. 2c,d) but did not differ between organic and conventional farms (Tukey's HSD, $P > 0.1$).

SPECIES AND TRAIT COMPOSITION

Non-metric multidimensional scaling showed that farms of both types hosted bee communities distinct from those of natural sites, while organic and conventional farms were less clearly distinguished (Fig. 3).

Table 2. Spearman correlations among traits. For categorical traits, the order in which character states are listed in row headers (column header for Sociality) is the same as that used for analysis

	Body size	Flight season duration	Flight season median date	Lecty	Nesting location	Nest construction	Sociality (social or solitary)
Abundance (continuous)	−0.22**	0.03	0.02	0.22*	−0.15	−0.23**	−0.38***
Body size (continuous)		−0.16	0.06	−0.01	0.00	0.23*	0.24**
Flight season duration, rarefied (continuous)			0.44**	0.30*	0.20	0.06	−0.32*
Flight season median date (continuous)				−0.10	0.24**	0.30**	−0.02
Lecty (oligolectic or polylectic)					0.08	0.06	−0.29**
Nesting location (below-ground, mixed, or above-ground)						0.76***	0.32***
Nest construction (excavate or rent)							0.19*

$N = 46$ – 140 , depending on the trait. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Bee body sizes were similar among site types [ANOVA; individual level (abundance-weighted) $F_{2,13} = 1.5$, $P = 0.25$; species level (unweighted) $F_{2,13} = 0.58$, $P = 0.58$; Fig. 4a, b]. Bees in natural sites had later flight seasons than bees on organic farms (weighted and unweighted $F_{2,13} > 4.0$, $P < 0.04$; Fig. 4c,d) and tended to fly later in the season than those at conventional farms (unweighted, Tukey's

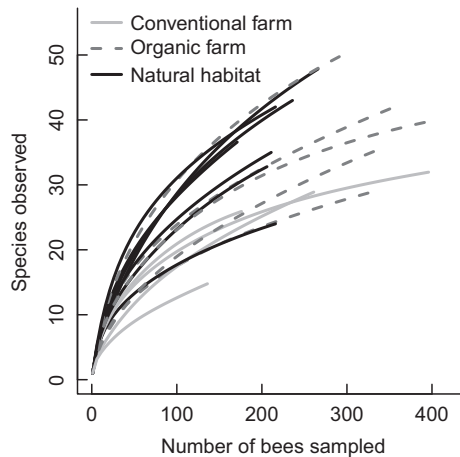


Fig. 1. Rarefaction curves for all three site types. Lines connect mean values of observed richness for each subsample size (in increments of five bees) for each site. Error bars are omitted for clarity. $N =$ four conventional farms, five organic farms and seven natural habitat sites.

HSD, $P = 0.089$). Natural sites also tended to be less dominated by bees with long flight seasons (abundance-weighted $F_{2,13} = 4.0$, $P = 0.045$; Tukey's HSD, $P = 0.07-0.09$; Fig. 4f). Differences in bee phenology among site types were not explained by floral resource phenology: floral density and species richness declined in parallel through the season in all site types (Appendix S5).

All site types supported similarly low proportions of oligolectic species (ANOVA, $F_{2,13} = 1.1$, $P = 0.37$; Fig. 5a), but numerically, oligolectes constituted a greater proportion of the community in natural sites than on either farm type ($F_{2,13} = 7.8$, $P = 0.0060$; Fig. 5b). Natural habitats also hosted greater proportions of solitary species than did conventional farms ($F_{2,13} = 8.4$, $P = 0.0046$; Fig. 5g) and greater proportions of solitary individuals than either farm type ($F_{2,13} = 9.9$, $P = 0.0024$; Fig. 5h).

Bee nesting habits differed markedly among site types. Above-ground nesting bees made up a smaller proportion of the community on farms than in natural habitat, both in number of species (ANOVA, $F_{2,13} = 18.0$, $P = 0.0002$; Fig. 5c) and individuals ($F_{2,13} = 18.8$, $P = 0.0001$; Fig. 5d). This difference was a consequence both of fewer above-ground nesting bees and more below-ground nesting bees on farms than in natural habitat (Appendix S6). Similarly, farms had a smaller proportion of nest-renting species than natural habitat ($F_{2,13} = 20.1$, $P = 0.0001$; Fig. 5e). These differences among site types reflect the availability of potential nesting habitat for above-ground

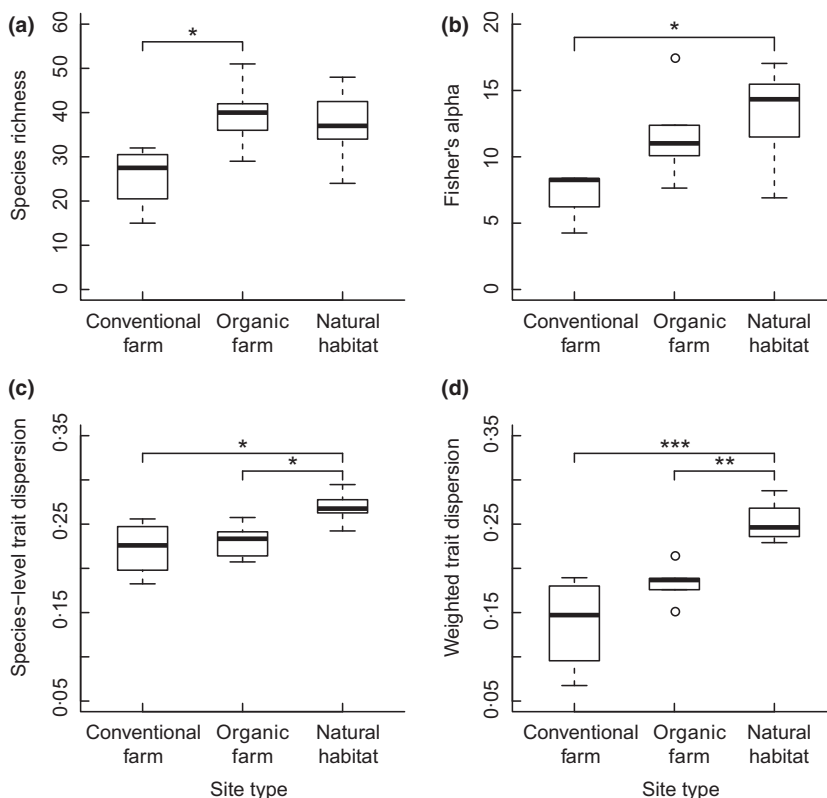


Fig. 2. Box plots of species and trait diversity for each site type. Boxes show medians and interquartile ranges; whiskers extend to values within 1.5 \times the interquartile range of the upper and lower quartiles. (a) Species richness. (b) Fisher's α . (c) Functional dispersion (FDis), calculated at the species level (unweighted by abundance). (d) Abundance-weighted FDis. Significant differences between site types, based on Tukey's HSD tests, are indicated by asterisks. $N =$ 4 conventional farms, 5 organic farms and 7 natural habitat sites. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

vs. below-ground nesting bees. Above-ground nesting substrates (trees, shrubs, stems and dead wood) were significantly more abundant at natural sites than either farm type ($F_{2,13} = 7.7$, $P = 0.0061$; Tukey's HSD, both $P < 0.05$), whereas percentage cover of bare soil tended to be greater on farms (though it was significantly greater

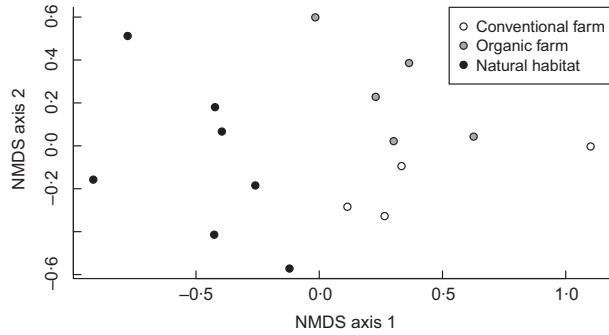


Fig. 3. Non-metric multidimensional scaling of the 16 study sites, based on species abundances (Bray–Curtis dissimilarities). Sites (circles) are shaded according to site type. For simplicity, only the two-first axes of the three-axis solution are shown. (Site types were not differentiated along axis 3). Stress of the three-axis solution is 0.098.

only on organic farms; $F_{2,13} = 4.7$, $P = 0.030$; Tukey's HSD, $P = 0.030$; Appendix S7).

The greater trait diversity of bee communities in natural habitat was most strongly influenced by inclusion of nesting location, without which FDis did not differ significantly among habitat types [unweighted (species level) FDis; ANOVA, $F_{2,13} = 0.82$, $P = 0.46$; Appendix S8]. Abundance-weighted FDis differed among site types even with nesting location excluded ($F_{2,13} = 8.8$, $P = 0.0039$). However, without nesting location, only conventional farms had lower trait diversity than natural sites (Tukey's HSD, $P = 0.0030$); organic farms were intermediate and did not differ significantly from other site types (Tukey's HSD, $P > 0.1$). The pattern of greater FDis in natural habitat than on farms was maintained when any trait other than nesting location was excluded (Appendix S8).

Discussion

The bee assemblages of farms in our study area were functionally depauperate compared to nearby natural communities. Although organic farms supported diverse

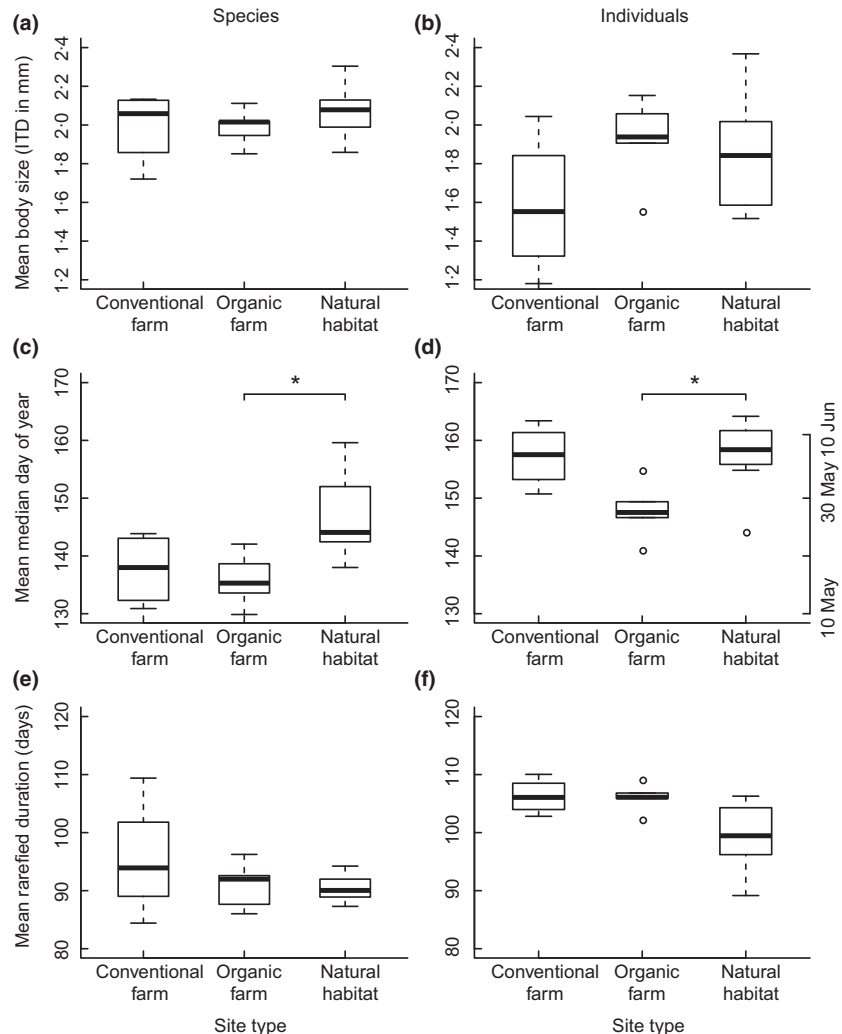


Fig. 4. Box plots showing distributions of community-wide mean body sizes (inter-tetragonal distances) (a, b) and phenologies (c–f), calculated at the species level (i.e. unweighted; left) and individual level (abundance-weighted; right), for each site type. Sample sizes as in Fig. 2. * $P < 0.05$.

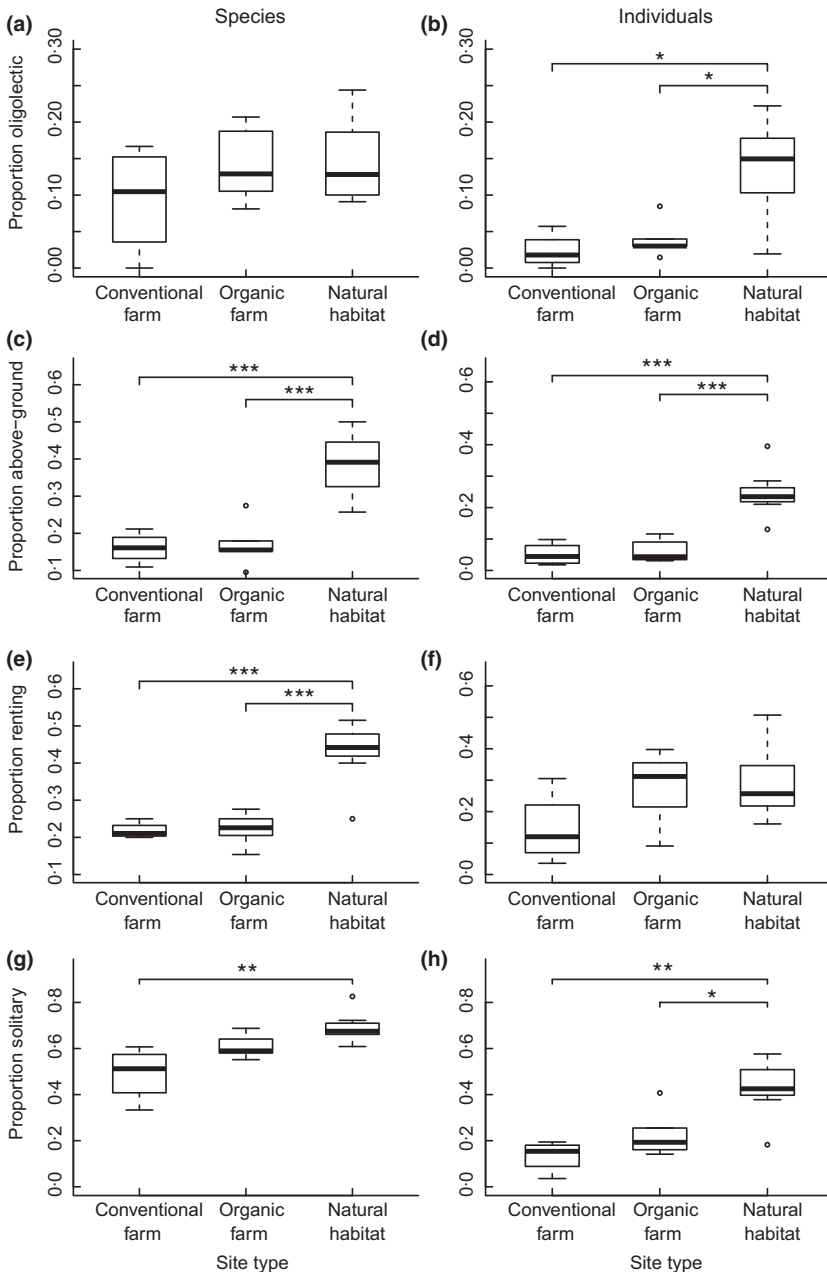


Fig. 5. Box plots showing proportions of oligolectic (a, b), above-ground nesting (c, d), nest-renting (e, f) and solitary (g, h) species (left) and individuals (right) for each site type. Cleptoparasites were scarce at all sites and are omitted here. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

and abundant bee faunas – suggesting some conservation advantage of organic farming over conventional management and consequently a possible pollination advantage (cf. Kremen, Williams & Thorp 2002) – trait diversity on farms was low regardless of management style. Studies of other taxa have also linked intensive agriculture with reduced functional-trait diversity (Schweiger *et al.* 2007; Flynn *et al.* 2009; Karp *et al.* 2012); our study shows not only that this pattern extends to bees, but also that even relatively benign management practices such as diversified organic farming can reduce bee functional diversity.

In our study system, organic and conventional farms were also more similar in species composition to each other than to natural habitat. Several of the most abundant species in our study [e.g. *Bombus vosnesenskii* Radoszkowski, *Halictus tripartitus* Cockerell, *Lasioglossum*

incompletum (Crawford)] were abundant in all site types, but a set of less abundant species clearly separated farms from natural habitat (Fig. 3). Organic farms supported several species that were rare on conventional farms [e.g. *Peponapis pruinosa* (Say), some *Andrena* species], but the dominant farm bees [e.g. *Halictus farinosus* Smith, *Lasioglossum (Evylaeus)* sp. F] were the same regardless of farm management.

Similarly, farms differed strongly from natural habitat in the trait composition of their bee communities. Most conspicuously, farms supported few above-ground nesting bees, regardless of management type. Conversely, organic farms supported more below-ground nesting species than were found in natural habitat (Appendix S6), indicating that some species may benefit from the irrigated bare soil on farms. Nest site availability does seem to limit some

bee populations (Steffan-Dewenter & Schiele 2008), and scarcity of above-ground nest sites in particular may act as a strong environmental filter on bee communities (e.g. Williams *et al.* 2010; Hoiss *et al.* 2012). The differences in traits we observed among habitat types (farms vs. semi-natural areas) are striking given the proximity of all habitat types in our study (within foraging range of many bee species; Greenleaf *et al.* 2007), emphasizing the role of local habitats as filters and determinants of bee community composition.

Several traits that we expected to affect bee responses to agriculture did not differ between natural and farmed habitats. Large size is a correlate of extinction risk in many groups, including some bee assemblages (Larsen, Williams & Kremen 2005; Flynn *et al.* 2009; Hinners, Kearns & Wessman 2012), but we found no evidence that body size affected occurrence in agricultural habitat. In our study area, large-bodied apid bees were well represented on farms (see also Winfree, Griswold & Kremen 2007). Similarly, trophic specialization is frequently associated with sensitivity to land-use change (Lindell, Chomentowski & Zook 2004; Öckinger *et al.* 2010; Winfree, Bartomeus & Cariveau 2011), but it was relatively unimportant in our study sites. Oligolectic bees were less abundant on conventional farms than in natural habitat, but they were not less species rich (Appendix S6; see also Winfree, Griswold & Kremen 2007; Hinners, Kearns & Wessman 2012). Although some oligolectes were absent from farms (e.g. *Andrena suavis* Timberlake, a *Ranunculus* specialist; *Osmia montana* Cresson, an Asteraceae specialist), others were restricted to them [e.g. *P. pruinosa* (Say), the squash bee; *Andrena piperi* Viereck, a *Brassica* specialist]. Clearly, if the pollen host of an oligolectic bee is a crop or an agricultural weed, that bee may thrive on farms, provided nesting resources are available.

The summer drought of our Mediterranean-climate study area led us to expect bee communities with later flight seasons on farms, where irrigation supports late-season plant growth. Surprisingly, the opposite was true: late-season bees made up a larger proportion of the community in natural habitat. The correlation between phenology and nesting location may be responsible: above-ground nesters, such as *Megachile* spp., which were relatively rare on farms, tended to have later flight seasons (Table 2).

Overall, organic and conventional farms resembled each other in trait composition. Both were more dominated than natural habitat by social, polylectic ground-nesters with long flight seasons. This functional similarity between farm types reflects the structural elements common to all farms. Our results therefore support a view of bee communities from organic farms as more species rich, but functionally similar versions of those from conventional farms. Our findings parallel those of Rader *et al.* (2014), who found more species of pollinators in less intensively managed agricultural systems, but no differ-

ence among land-use types in pollinator functional dispersion. Like Schneider *et al.* (2014), we conclude that organic farming – which mainly bolsters numbers of regionally common taxa – is insufficient as a tool for biodiversity conservation and must be supplemented by conservation of natural habitat (see also Klein *et al.* 2012).

IMPLICATIONS

Results from other systems suggest that diversity in pollinator functional groups – defined by such traits as body size and sociality – increases pollination, because different functional groups use flowers in complementary ways (Chagnon, Gingras & de Oliveira 1993; Hoehn *et al.* 2008; Albrecht *et al.* 2012; Brittain, Kremen & Klein 2013). Nesting location, the trait that differed most strongly between farms and natural habitat in our data set, is not directly related to flower use and pollination. Many above-ground nesting bees are robust, long-tongued species (e.g. megachilids, *Xylocopa* spp.) that can effectively pollinate papilionaceous legumes (e.g. peas and beans) and contribute to pollination of spring orchard crops (Bosch, Kemp & Trostle 2006; Córdoba & Cocucci 2011). However, above-ground nesters are not listed as dominant pollinators of well-studied crops in our landscape (Kremen, Williams & Thorp 2002; Greenleaf & Kremen 2006a,b; Klein *et al.* 2012), and we know of no studies that actually link nesting biology to pollination function. Regardless, the most universal benefit of trait diversity is its insurance function (Yachi & Loreau 1999): Bee communities with a greater diversity of life-history traits should be more resilient to disturbance and provide more consistent pollination over time (Winfree & Kremen 2009; Garibaldi *et al.* 2011).

Our findings suggest that enhancement of above-ground nesting habitat on farms, perhaps as a component of hedgerow restoration, may benefit some pollinators that are currently under-represented on farms (cf. Morandin & Kremen 2013). Addition of artificial nesting structures to a random selection of farms would be a useful experimental test of whether nesting-habitat supplementation can increase populations of above-ground nesting bees and thereby boost the functional diversity of farm bee assemblages. More fundamentally, however, our results emphasize the limitations of organic agriculture and the crucial role of natural habitat in sustaining functionally diverse wild pollinator populations.

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Data accessibility

Study sites, species list and trait assignments: uploaded as online supporting information.

Bee specimen data and nesting habitat data: DRYAD entry <http://dx.doi.org/10.5061/dryad.dt7mh>

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Locations of study sites.

Appendix S2. Bee species list with traits.

Appendix S3. Methods for characterizing bee phenology.

Appendix S4. Abundance–frequency plots for each site.

Appendix S5. Phenology of floral resources by site type.

Appendix S6. Number of bees in each trait category by site type.

Appendix S7. Nesting habitat by site type.

Appendix S8. Sensitivity analysis for functional-diversity results.