Organic farming positively affects honeybee colonies in a flower-poor period in agricultural landscapes

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Abstract

1. Conventional farming has been implicated in global biodiversity and pollinator declines and organic farming is often regarded as a more ecological alternative. However, the effects of organic farming on honeybees remain elusive, despite honeybees' importance as pollinators of crops and wild plants.
2. Using six years of data from a large-scale study with fortnightly measurements of honeybee colony performance traits (10 apiaries per year distributed across a 435 km^2-large research site in France), we related worker brood area, number of adult bees and honey reserves to the proportions of organic farmland in the surroundings of the hives at two spatial scales (300 m & 1500 m).

3. We found evidence that, at the local scale, organic farming increased both worker brood production and number of adult bees in the period of flower scarcity between the blooms of oilseed rape and sunflower (hereafter ‘dearth period’). At the landscape scale, organic farming increased honey reserves during the dearth period and at the beginning of the sunflower bloom.
4. The results suggest that worker brood development benefitted from organic farming mostly through a more diverse diet due to an increase in the availability of diverse pollen sources in close proximity of their hives. Reduced pesticide drift may have additionally improved bee survival. Honey reserves were possibly mostly affected by increased availability of melliferous flowers in foraging distance.
5. *Synthesis and applications.* Organic farming increases honeybee colony performance in a period of resource scarcity, likely through a continuous supply of floral resources including weeds, cover crops and semi-natural elements. We demonstrate how worker brood area increases in the critical dearth period (between the blooms of oilseed rape and sunflower). This has previously been linked to winter colony survival, suggesting that organic farmland may mitigate repercussions of intensive farming on colony vitality. We conclude that organic farming benefits a crucial crop pollinator with potential positive implications for agriculture in the wider landscape.

Résumé français

1. L’agriculture conventionnelle a des conséquences avérées sur la biodiversité globale, incluant le déclin des pollinisateurs. L’agriculture biologique apparaît comme une alternative à l’agriculture intensive, mais son influence sur les abeilles domestiques

reste très mal connue, malgré l’importance de celles-ci en tant que pollinisateurs des cultures et des plantes sauvages.

2. Six années d’étude à grande échelle avec des mesures bimensuelles de traits de performance des colonies d’abeilles (10 ruchers par an répartis sur une zone d’étude de 435 km^2 en France), ont permis d’établir une relation entre la surface de couvain d’ouvrières, le nombre d’abeilles adultes ou les réserves de miel, avec la proportion de terres agricoles conduites en pratique biologique aux alentours des ruches à deux échelles spatiales, locale et paysagère (300 m et 1500 m).
3. Nous montrons, à une échelle locale, que l’agriculture biologique augmente à la fois la production de couvain et le nombre d’ouvrières en période de pénurie de fleurs, entre les floraisons du colza et du tournesol (ci-après dénommée « période de disette »). À l’échelle du paysage, l’agriculture biologique augmente aussi les réserves de miel pendant la période de disette ainsi qu’au début de la floraison du tournesol.
4. Nos résultats suggèrent que le développement du couvain d’ouvrières bénéficie de l’agriculture biologique principalement grâce à un régime alimentaire plus diversifié lié à une augmentation des ressources de pollen à proximité immédiate des ruches. La réduction de la pression pesticide semble également améliorer la survie des abeilles, alors que l’augmentation des réserves en miel résulterait d’une disponibilité accrue des fleurs mellifères à proximité de la ruche.
5. Synthèse et applications. Nous décrivons ici comment la surface de couvain d’ouvrières peut augmenter, même au cours de la période critique de disette entre les floraisons du colza et du tournesol. L'agriculture biologique peut ainsi augmenter la

performance des colonies d'abeilles en période de pénurie de ressources, notamment grâce à un approvisionnement continu en ressources florales, comme les adventices des cultures, des couverts prairiaux ou la présence de composantes paysagères semi-naturelles (haies). La période de disette a été montrée comme une période critique pour la survie hivernale des colonies d’abeilles ; nous suggérons ici que l’agriculture biologique peut atténuer les conséquences de l'agriculture intensive sur la vitalité des colonies d’abeilles. Ainsi, l’agriculture biologique profite à un pollinisateur majeur des cultures, avec des implications favorables potentielles pour l’ensemble des activités agricoles.

Keywords: honeybee, agricultural intensification, landscape composition, spatial scale, honey production, worker brood, floral resources, rapeseed, organic farming

Introduction

Modern farming has been questioned because of its effect on public health (O'Kane, 2012), climate change (Conway, 2012) and biodiversity (Stoate et al., 2009). Biodiversity decline causes losses of ecosystem functions, such as biological pest control and insect pollination (Thompson et al., 2014). A radical alternative to conventional agriculture is organic farming that bans the use of synthetic inputs. Organic farming aims at providing healthy food (Forman & Silverstein, 2012), conserving species richness and maintaining ecosystem functioning (Sandhu, Wratten, & Cullen, 2010). Indeed, organic farming increases biodiversity on-site (Hole et al., 2005; Tuck et al., 2014) and in adjacent fields (Henckel, Borger, Meiss, Gaba, & Bretagnolle, 2015). This holds particularly true for pollinators, which show a greater increase in diversity than other functional groups (Tuck et al., 2014). Organic farming enhances bee species richness (Holzschuh, Steffan-Dewenter, & Tscharntke, 2008; Kennedy et al., 2013), the abundance of solitary bees and bumblebees (Holzschuh et al., 2008; Kennedy et al., 2013; Morandin & Winston, 2005) and pollination rates (Morandin & Winston, 2005; Smith, Andersson, Rundlo, Rundlöf, & Smith, 2012). Wild bees benefit from organic farming on both the local (Kennedy et al., 2013) and the landscape scale (Holzschuh et al., 2008).

The reasons why wild bees benefit from organic farming are less clear, however. Positive effects may result from lower pesticide exposure and a consequently reduced intoxication risk. Numerous laboratory and field studies showing toxic effects of single pesticides, particularly the neonicotinoids, suggest that bees may profit from the ban of synthetic pesticides in organic farming, but the extent to which this would occur remains unclear (Mallinger, Werts, & Gratton, 2015). Indeed, studies assessing the impact of pesticide use along a continuous toxicity index showed varying results. Mineau et al. (2008) could link reported honeybee mortality incidents at hives to pesticide use intensity, while Kremen et al. (2004) failed to relate pollination services to insecticide use. Intensive pesticide use reduces the abundance and species richness of wild bees, but impacts vary across seasons and taxa (Mallinger et al., 2015; Park, Blitzer, Gibbs, Losey, & Danforth, 2015; Tuell, 2010). Varying impacts may result from differing landscape composition (Carvalheiro, Seymour, Nicolson, & Veldtman, 2012; Mallinger et al., 2015; Park et al., 2015) or from differences between species in life-history traits (Tuell, 2010) or the sensitivity to pesticides (Arena & Sgolastra, 2014). Honeybees may be less impacted by pesticides than wild bees, as their large colonies can compensate for individual forager losses (Henry et al., 2015; Osterman et al., 2019; Rundlöf et al., 2015). Boosted bee populations in organic farms are not necessarily due to reduced pesticide exposure. In fact, the risk of intoxication can in some instances be higher in organic than in conventional agricultural land (Mallinger et al., 2015).

Alternatively, organic farming may outperform conventional agriculture in maintaining large diverse pollinator communities by provisioning floral resources continuously across the landscape and throughout the season (Brittain, Bommarco, Vighi, Settele, & Potts, 2010; Winfree, Williams, Gaines, Ascher, & Kremen, 2008). The ban on synthetic herbicides and mineral fertilizers increases the diversity (Ekroos, Hyvönen, Tiainen, & Tiira, 2010; Gabriel & Tscharntke, 2007) and density (Bengtsson, Ahnström, & Weibull, 2005; Ponce, Bravo, de León, Magaña, & Alonso, 2011) of weeds in organic farms. In addition, organic farmland is often sown with a greater variety of crops than conventional farmland (Barbieri, Pellerin, & Nesme, 2017; Hole et al., 2005) and comprises larger areas of semi-natural elements (Gibson, Pearce, Morris, Symondson, & Memmott, 2007), such as hedgerows, which provide forage and nesting opportunities to bees (Hannon & Sisk, 2009).

However, how organic farming affects honeybees (*Apis mellifera* L.) cannot necessarily be inferred from positive effects on wild bees. Evidence for preferential honeybee foraging on organic farmland is lacking (Couvillon, Schürch, & Ratnieks, 2014) and honeybees differ from wild bees in many respects such as nesting requirements, foraging behaviour and the extent of human management. Honeybees forage particularly intensively on mass-flowering oilseed crops (Rollin et al., 2013) and may therefore be disadvantaged by the low amount of oilseed rape in organic land in Europe (Barbieri et al., 2017). In addition, naturally larger food reserves and greater foraging distances (Gathmann & Tscharntke, 2012; Steffan-Dewenter & Kuhn, 2003) allow honeybees to better compensate for local or temporary food shortages as compared to wild bees. Nevertheless, honeybees may benefit from a more continuous provision of flowers in organic farmland. Compared to conventional farmland, organic farmland contains more grassland and weeds in annual crops (European Commission, 2018), which honeybees rely on in periods of low resource availability, e.g. between the blooms of oilseed rape and sunflower (Odoux et al., 2012; Requier et al., 2015). To sum up, potential benefits of reduced pesticide exposure may be offset in spring by less forage due to a lower availability of oilseed rape in organic than in conventional agriculture, but over the course of the season honeybees should profit from a more continuous supply of wild flowers in organic agriculture.

Here, we use empirical data collected during six years from 60 apiaries located in landscapes varying in the proportion of organic farmland to quantify how organic farming affects honeybee colony performance. We predict that during the oilseed rape bloom, organic farming benefits particularly adult bees through reduced pesticide exposure, but potentially harms honey or brood production through reduced availability of oilseed rape. However, afterwards organic farming should mitigate the dearth between the blooms of oilseed rape and sunflower through a more continuous supply of resources. Despite potential trade-offs with worker brood area, we predict that organic farming will increase honey reserves towards the end of the dearth period due to enhanced availability of melliferous weeds or a prior positive effect on number of adults and therefore the number of available foragers. We test these hypotheses and assess more generally (i) how honeybee colonies respond to organic farming (ii) at what spatial scale responses are the largest and (iii) what proportion of organic farmland in the landscape is required to observe an effect on honeybee colony performance. Finally, we aim at gaining insight into the characteristics of organic farming (crop choice, weeds, insecticide risk) that affect honeybee colonies the most.

Materials and methods

THE STUDY SITE

The study was conducted in the *'Zone Atelier Plaine & Val de Sèvre',* a 435 km^2-large Long-Term Social-Ecological Research (LTSER) site in central western France (46°23'N, 0°41'W; Fig. 1). The region is characterized by a warm temperate climate with c. 820 mm of annual precipitation and a mean annual temperature of 12.0°C. Since 1994, the land use within the LTSER site has been recorded and mapped on vector-based shapefiles

(Bretagnolle et al., 2018). Within the study period (2012-2017), the area was covered on average by 40.4% with cereals (mainly winter wheat: 33.8%), 9.9% maize, 9.7% sunflower, 7.9% grassland, 7.7% oilseed rape, 3.5% alfalfa and 7.5% other crops. The site contains also 9.8% of urban areas and 3.1% of fragmented woodlands and is bordered in the north by the town Niort and in the south by a large forest (Fig. 1). Half of the LTSER site is designated as a Natura 2000 site under the Birds Directive.

Farmers receive payments for both the conversion to and the maintenance of organic farming practices. Here, we merged organic farmland in the conversion (three years) and the maintenance period. Within the study period, the organic farmland in the study site was covered on average by 34.7% with cereals (mainly winter wheat: 22.7%), 13.7% grassland, 17.7% legumes (mostly alfalfa: 9.5%), 9.1% sunflower, 6.0% maize, 1.3% oilseed rape.

THE STUDY DESIGN

In 2008, ECOBEE, a monitoring scheme of experimental apiaries was launched in the LTSER site. ECOBEE aims at correlating honeybee colony performance with landscape composition and farming practices. Therefore, the LTSER site was divided into 50 square plots, of which 10 are randomly selected without replacement each year for apiary installation. After all plots have once been occupied with an experimental apiary (i.e. after five years), a new random sampling cycle starts.

The apiaries, consisting of five colonies, are installed in semi-natural habitat near the centre of the 10 km^2-large plots, which encompass the mean foraging distance (c. 1.5

km) in such landscapes (Steffan-Dewenter & Kuhn, 2003). After each beekeeping season (March-September), colonies are assembled to overwinter outside the study site.

The colonies are managed using common practices of local beekeepers, including control treatments against the varroa mite and syrup supply in periods of resource scarcity. In the beginning of the season, hives consist of only a 10-frame-Dadant-Blatt brood box; as the colonies grow, honey supers are added (Odoux et al., 2014). Honey is harvested after the sunflower bloom, and from 2008 to 2012, also after the oilseed rape bloom. When needed, colonies are re-queened with queen cells of the same lineage.

Due to the colony placement scheme and the heterogeneous distribution of organic land, colonies were exposed to different amounts of organic land. In the LTSER site, the proportion of organic farmland increased gradually from 0.6% to 7.1% between 2008 and 2017, because several conventional farmers converted to organic farming, while no organic farmers switched to conventional agriculture.

In 2008-2011, the number of apiaries exposed to high amounts of organic farmland was too low to allow for meaningful inferences on how honeybee colony performance is affected by an organic farmland gradient and in 2008 honeybee data were only collected in June and July. Therefore, we restricted our analyses to 2012-2017, but presented results from analyses of the dataset for 2009-2017 as Supporting Information (Fig. S1 & S2).

MEASURED PARAMETERS

Monitoring of colonies in ECOBEE is described in detail in Odoux et al. (2014). We used three colony performance traits that are major components of a colony's temporal dynamic:

worker brood area, number of adults and honey reserves. These parameters were recorded in three colonies per apiary every two weeks during the beekeeping season (two additional colonies are used as controls or as substitutes in case of queen or colony failure (Odoux et al., 2014)). On both sides of the hive frames, the lengths and widths of the area covered by eggs, larvae or pupae were measured to estimate the elliptic brood area, which was then accumulated for each hive. Drone brood area was equally estimated and deducted from the total brood area to obtain worker brood area. Hive frames, honey supers and hive bottoms were weighed with and without adult bees. The difference was then divided by 0.1 g bee^{-1} to estimate number of adults. This estimate does not account for bees that were foraging during monitoring. To estimate honey reserves, the weights of honey supers and frames without bees were summed up; then, the estimated brood weight and the initial weight of empty supers and frames were deducted from this. The brood weight was derived from the brood area and an estimated brood surface density of 3.91 kg m^{-2} (Odoux et al., 2014). The weights of pollen and wax were neglected, as they are largely surpassed by the weights of nectar and honey.

STATISTICAL ANALYSES

Plant phenology varies between years due to differences in meteorological conditions, particularly the accumulation of heat (Miller, Lanier, & Brandt, 2001). To be able to compare years, Julian dates were, therefore, standardized through adjustment according to growing degree days (GDDs) for oilseed rape (Appendix S1).

In a first step, we examined how honeybee colony performance traits (i.e. worker brood area, number of adults and honey reserves) evolved over spring and summer, i.e.

from GDD-adjusted Julian day number (hereafter 'Julian day') 70 to 220. The colony performance traits were fitted by generalized additive mixed models (GAMMs) using the 'gamm' function of the 'mgcv' package in R with a 's' smooth-term (i.e. a penalized thin-plate regression spline) for Julian days. To obtain homoscedasticity and normally distributed residuals, honey reserves were fitted using GAMMs with a gamma distribution and a logarithmic link function, while for worker brood area and number of adults a Gaussian distribution was used. Smoothness selection was done via maximum likelihood for GAMMs with Gaussian distribution and via penalized quasi-likelihood for GAMMs with Gamma distribution. All GAMMs containing data of multiple years included colony identity nested in apiary identity nested in year as random factors, while GAMMs on individual years included colony identity nested in apiary identity as random factors. Confidence intervals of GAMM fits were calculated by non-parametric bootstraps with 1100 simulations, whereby apiaries were randomly selected.

In a second step, the relation between organic farming and honeybee colony performance was evaluated at two spatial scales (300 m & 1500 m). The smaller spatial scale (hereafter 'local scale') was chosen to cover the fields directly neighbouring the apiaries (mean field size = 5 ha), while the larger one (hereafter 'landscape scale') was chosen in regard to the average foraging distance of honeybees in farmland landscapes (mean=1300-1800 m, median=1100-1300 m (Steffan-Dewenter & Kuhn, 2003)). For this purpose, the proportion of organic farmland in 300 m and 1500 m circular buffers around the hives was obtained from shapefiles. GAMMs used to evaluate the effect of organic farming on colony performance, included a smooth-term for the main effects, and the interaction between Julian days and the proportion of organic farmland in the surroundings of the hives at either of the spatial scales (fixed-effect smooth-term: s(Julian days, proportion of organic farmland)). Finally, a third set of GAMMs was run, that included also two-way interactions between Julian days and the proportion of either oilseed rape, sunflower or grassland as predictor variables (fixed-effect smooth-terms: s(Julian days, proportion of organic farmland) + s(Julian days, proportion of a field cover type)). These were used to test whether differences between colonies with different extents of exposure to organic farming were simply due to differences in field cover rather than due to differences in farming practices. Unlike organic farmland, the three field cover types (oilseed rape, grassland, sunflower) were only mapped in the LTSER site; therefore, when calculating their proportion in the surroundings of apiaries at the edge of the study site, only the land area within the LTSER site and the neighbouring forest reserve was considered (Fig. 1). This is based on the assumption that the percentage of these field cover types in the LTSER site is largely the same as in the directly neighbouring area outside the LTSER site, except where the forest reserve is.

Before fitting GAMMs containing interaction-terms, all predictor variables were mean-centred and scaled to allow for isotropic smoothing. GAMMs on the whole study period (2012-2017) were fit to 162 colonies from 60 apiaries. A grand total of 2506 observations were used for worker brood area and number of adults. GAMMs on honey reserves were fit to fewer observations (1792), as we excluded data that were collected after the sunflower honey harvest. For colonies without honey harvest, we considered only data that were obtained before the date of the last honey harvest of the year in any apiary. We did not account for differences in honey harvest after the oilseed rape bloom, as within the study period, oilseed rape honey was only harvested in 2012.

Using the GAMMs, colony performance traits were estimated in 5% intervals within 0-15% organic farmland at 1500 m and 10% intervals within 0-30% at 300 m and in 5-day intervals of the timeframe between the beginning of the oilseed rape period, shortly after colonies were placed in the study site, to the end of the sunflower bloom, before the harvesting of honey. Estimation was done in smaller ranges of dates and organic farmland proportions than the ranges of the data used to fit the models to ensure high estimation accuracy at boundaries.

To estimate the effect of organic farming independently of field cover, estimation at different dates and organic farmland proportions was done using models incorporating the proportion of a field cover type, which was set to its mean.

Because the seasonal effect was very pronounced, the effect of organic farming (*OF effect*) was highlighted by expressing estimates at any proportion of organic farmland (*OF estimate)* as a percentage difference to the mean of the estimate itself and the estimate for no organic farmland at the same Julian day (*CONV estimate*):

$$\textit{OF effect} = 2 \times 100\% \times (\textit{OF estimate} - \textit{CONV estimate}) / (\textit{OF estimate} + \textit{CONV estimate})$$

(eqn. 1).

Taking the mean across the OF and the CONV estimate ensured equal weighting. *P*-values were obtained from bootstraps with 1100 simulations, whereby apiaries were randomly selected. *P*-values under the null hypothesis that *OF effect* does not differ from zero were computed as the fraction of simulated mean-centred *OF effect* values that are greater than or equal to the estimate of *OF effect.*

The organic farming effect on honey harvest was evaluated using two different parameters. First, we tested how organic farming affected the probability that honey was harvested from a colony using generalized linear mixed-effects models (GLMM) with a logit-link; second, we analysed the effect on harvested amounts only in those colonies with honey harvest by linear mixed-effects models (LMM) with a Gaussian error distribution. Models on honey harvest after the oilseed rape bloom in 2012 contained apiary identity as a random factor and (G)LMMs on honey harvest after the sunflower bloom contained year and apiary identity as random factors. Amounts of honey harvest after the sunflower bloom were square-root transformed to obtain normally distributed model residuals. *P*-values of (G)LMMs were calculated by likelihood-ratio tests. Absence of considerable spatial autocorrelation was visually determined as exemplarily shown for honey harvest after the sunflower bloom (Fig. S3).

The 'lmer' and 'glmer' functions of the 'lme4' package were used to fit (G)LMMs. All analyses were done in R version 3.5.0.

Results

LANDSCAPE COMPOSITION AND SEASONAL VARIATION OF COLONY PERFORMANCE TRAITS

The amount of organic farmland varied strongly over space, which resulted in very different exposure levels between apiaries (Fig. 1 & S1). The proportions of organic land at the landscape and the local scale correlated strongly (r_s=0.67, P<0.001, N=60), but this was due to apiaries without any organic farmland at the local scale; when removed there was no correlation anymore (r_s=0.23, P=0.41, N=15). All apiaries were exposed to oilseed rape, grassland and sunflower at the landscape scale. Proportion of grassland correlated negatively with oilseed rape at both spatial scales and positively with sunflower at the local scale (Table S1). At neither scale, the proportions of these field cover types correlated with proportion of organic farmland (Table S1).

All three colony traits varied along the season, showing peaks in both spring and summer (Fig. 2, Fig. S5, Table S2). Worker brood production was highest in the second half of April, declined in May, and peaked again at the end of June. Number of adults exhibited a similar but less marked seasonal pattern, peaking approximately 10 days later than worker brood area in spring, whereas the summer peaks coincided. Honey reserves showed a first peak at the end of the oilseed rape flowering period and a much more pronounced one at the end of the sunflower bloom.

HONEYBEE COLONY RESPONSES TO ORGANIC FARMING

Honey reserves and worker brood area varied more strongly with organic farming and time than number of adults (Fig. 2, Table S2).

In the dearth period (between the blooms of oilseed rape and sunflower), colonies with organic farmland in their local environment had up to 37% more worker brood than colonies without organic farmland exposure at the same spatial scale. In fact, at the local scale (300 m), worker brood area tended to be positively related to organic farmland in almost all years (Fig. S6). The effect size varied, however, between years and was largest in 2012 and 2015, years in which all colonies exposed to organic farming at the local scale were exposed to at least 25% organic farmland. At the landscape scale, no effect of organic farming on worker brood area was detected (Fig. 2).

Number of adults followed generally a similar pattern as worker brood area, but effects tended to be weaker (Fig. 2) and statistically significant differences were detected in fewer years (Fig. S7). Largest positive differences between colonies with and without organic farmland in their surroundings were, as for worker brood area, detected at the local scale during the dearth period (~+20% at 10-25% organic farmland), which was particularly the case in 2014 when the estimated effect was even larger and occurred over a longer period than for worker brood area (Fig. 2 & S6). As for worker brood, no effect of organic farming on number of adults was observed at the landscape scale.

Contrary to worker brood area and number of adults, honey reserves was not related to organic farming at the local scale but at the landscape scale. Honey reserves were larger in colonies with organic farming exposure at the landscape scale throughout the dearth period until shortly before the peak of the sunflower bloom (Fig. 2; +53% at 5% organic farmland). This effect was only determined for colonies exposed to little amounts of organic farmland, as strong positive effects in colonies with high organic farmland exposure in 2013 and 2014 (Fig. S8) were partly offset by non-significant negative effects in 2016. Most consistent positive effects were observed at the landscape scale at the beginning of the sunflower bloom (Fig. 2 & Fig. S8). At the local scale, strong contrasting effects offset themselves (Fig. S8) so that no overall effect could be detected (Fig. 2).

We observed only relatively subtle effects on the estimated relation between organic farming and colony performance, when accounting for differences in field cover (Fig. S9, S10 & S11). Including the proportion of grassland reduced the positive effects of organic farming on worker brood area and number of adults (Fig. S9 & S10).

HONEY HARVEST

In 2012, honey was harvested from 62% of colonies after the oilseed rape bloom and the probability of harvest increased with the amount of organic farmland in a 300 m radius (Fig. 3; χ^2=4.39, P=0.036). Incorporating the proportion of oilseed rape in 300 m distance as a covariate into the model increased statistical significance (χ^2=6.74, P=0.009). At the landscape scale, no effect could be determined (χ^2=0.81, P=0.37), as confidence intervals were wider. Among colonies with harvest after the oilseed rape bloom, there was no relationship between organic farming and the amount of honey harvest in a 300 m (χ^2=0.47, P=0.49) or 1500 m radius (χ^2=0.78, P=0.46). In all years, honey was harvested after the sunflower bloom. The proportion of colonies with harvest varied, however, strongly between years from 6% in 2015 to 64% in 2012, but was unaffected by the proportion of organic farmland in 1500 m (χ^2=1.14, P=0.29) or 300 m distance (χ^2=0.31, P=0.58). Among colonies with harvest after the sunflower bloom, the amount of harvest was not affected by organic farming at the landscape scale (χ^2=1.14, P=0.29) or at the local scale (χ^2=2.69, P=0.10).

Discussion

Intensive agriculture has been blamed for low vitality and survival rates of honeybee colonies and organic farming is often regarded as a more bee-friendly alternative. However, how organic farming affects honeybee colony performance has, to our knowledge, not been studied yet.

We expected the effect of organic farming to vary with the period of the year and between colony traits, either in relation to reduced pesticide intoxication risk during mass-flowering of oilseed crops or in relation to increased availability of floral resources, such as weeds, meadows and semi-natural elements, during the dearth period (between the blooms of oilseed rape and sunflower). In the oilseed rape flowering period, we suspected, however, that honeybee colonies in landscapes rich in organic farmland may have fewer resources available, since oilseed rape, a crop that honeybees forage on extensively for nectar and moderately for pollen (Requier et al., 2015), is less commonly cultivated in organic agriculture.

We found, however, no negative relationship between honeybee colony performance and organic farming during the oilseed rape bloom. Oilseed rape was about seven times more common in conventional than in organic farmland in our study site, but due to dilution in the landscape, the correlation between the proportions of organic land and oilseed rape was not significant and barely negative (r_s ~ -0.13). Accounting for the proportion of oilseed rape in the surroundings of the bee hives did not affect the estimated organic farming effect, suggesting that differences in oilseed rape availability were not a major driver of colony performance, possibly because negative effects of reduced oilseed rape availability may have been offset by positive effects due to reduced pesticide exposure (Balfour et al., 2017), particularly since oilseed rape is typically the most heavily treated insect-pollinated crop in France (AGRESTE, 2013).

After the oilseed rape bloom, worker brood area declined less in colonies exposed to organic farming at the local scale compared to colonies without organic farming exposure, so that they had substantially more brood in the dearth period. Although effect sizes varied, this positive effect was fairly consistent across years. Worker brood production requires pollen supply and pollen resources are rare in the dearth period (Odoux et al., 2012; Requier et al., 2015; Requier, Odoux, Henry, & Bretagnolle, 2017). Organic farming may provide floral resources, including pollen sources, more continuously throughout the season and therefore prevent worker brood production from plummeting in periods of flower scarcity. Higher weed availability, resulting from the ban on synthetic herbicides in organic farming (Bengtsson et al., 2005; Henckel et al., 2015; Tuck et al., 2014) and more perennial or legume cover crops for nitrogen fixation (Decourtye, Mader, & Desneux, 2010) may increase floral abundance in periods when no major cash crop is flowering. More abundant grassland in organic farming may further increase the temporal continuity of resource availability (Bengtsson et al., 2005), which is supported by the finding that the size of the estimated organic farming effect on worker brood area during the dearth period decreased when incorporating the proportion of grassland in the model. As expected, positive effects on worker brood area translated into positive effects on number of adults (Requier et al., 2016), although with a lower effect size, possibly because worker brood area fluctuates more than adult number. In addition, positive effects on number of adults may have been in part offset by a trade-off between colony size and individual bee longevity, as honeybees in larger colonies tend to forage at a younger age, which reduces their lifespan (Rueppell, Kaftanouglu, & Page Jr., 2009).

Positive relationships between organic farming and worker brood area or number of adults were only observed at the local scale suggesting that organic fields impact colony size especially when they are nearby. Fields in proximity of hives are more likely to be foraged on (Couvillon et al., 2014), since honeybees attempt to minimize their energy consumption (Stabentheiner & Kovac, 2016). Therefore, organic fields near hives may reduce foraging efforts of honeybees more strongly than fields at greater distance. Honeybee colonies next to organic fields may be less impacted by pesticide drift, forage on a wider diversity of pollen sources and suffer therefore from fewer micro-nutrient deficiencies (Filipiak et al., 2017). During the sunflower bloom, no relationship between organic farming and worker brood area or number of adults could be observed. In this period, organic farming may provide fewer benefits to bees as sunflower is approximately equally used in organic and conventional agriculture and less intensively treated than oilseed rape (AGRESTE, 2013).

Honey reserves is the colony trait that has the most complex relationship to organic farming. Organic farming can directly affect honey reserves through the availability of melliferous flowers or indirectly through effects on worker brood area and number of adults, which then affect honey reserves through trade-offs or cascading effects (Requier et al., 2016). In the dearth period and at the beginning of the sunflower bloom, colonies exposed to organic farmland at the landscape scale had larger honey reserves, suggesting that colonies in landscapes rich in organic farmland benefitted from increased availability of melliferous flowers after the oilseed rape bloom. It is also conceivable that colonies with access to organic farming could satisfy their pollen demands more easily, which allowed them to forage more intensively on nectar sources.

At the local scale, strong positive effects in some years offset similarly strong negative effects in other years. This may potentially be due to trade-offs between worker brood and honey production, as suggested by the finding that the most pronounced negative effects on honey reserves occurred with a short delay but in the same year as the strongest positive effects on worker brood area (2015; Fig. S6 & S8).

Conclusions

Our study presents evidence that organic farming increases honeybee colony performance. Several pathways through which organic farming may act on honeybee colonies, including insecticide reduction, herbicide reduction, crop choice and provision of semi-natural elements and cover crops, need to be studied in isolation or in fully crossed experiments, because they may counteract each other. In our study, we found, however, that positive effects (wild flower resources, pesticide ban) prevailed over negative ones (reduced oilseed rape occurrence). We suspect that organic farming may provide benefits to beekeepers by increasing colony survival. Winter colony mortality has previously been linked to reduced pollen collection and brood production in the period between the blooms of oilseed rape and sunflower, which is characterized by flower scarcity (Requier et al., 2016). Our results suggest that organic farming may counteract declines in worker brood production in this period and therefore potentially increase long-term colony survival. We, therefore, conclude that organic farming can buffer adverse effects of intensive agriculture on honeybee colonies. Increased vitality of honeybee colonies, which forage at a large scale and are crucial pollinators of natural vegetation and cropland (Potts et al., 2016), suggests that organic farming may enhance pollination not only on field but also in the wider landscape. This remains to be confirmed, but such an effect would suggest that organic farming could provide benefits to both biodiversity conservation and agricultural production.

Authors' contributions

J-FO and VB designed the monitoring scheme; J-FO and DW engaged in data collection; VB, DW and J-FO defined the research questions and hypotheses; DW, VB and JC conducted the statistical analysis; DW and VB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Data available via the Zenodo open-access repository https://doi.org/10.5281/zenodo.3089481 (Wintermantel, Odoux, Chadœuf, & Bretagnolle, 2019).

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Figures

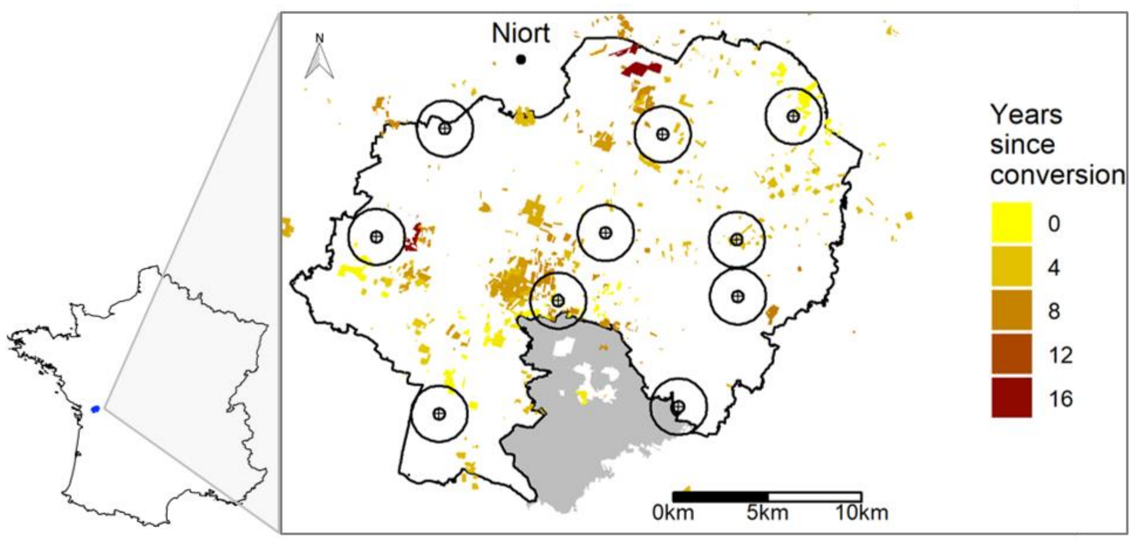

Fig. 1. Location of the Long-Term Social-Ecological Research (LTSER) site '*Zone Atelier Plaine & Val de Sèvre'* within France and a map extract showing the LTSER site, the bordering forest reserve (in grey) and organic fields in 2016, which are color-coded according to the number of years since conversion to organic farmland. Crosses indicate locations of experimental apiaries in 2016. The small circles touching the crosses indicate 300 m buffer areas and large circles show 1500 m buffer areas.

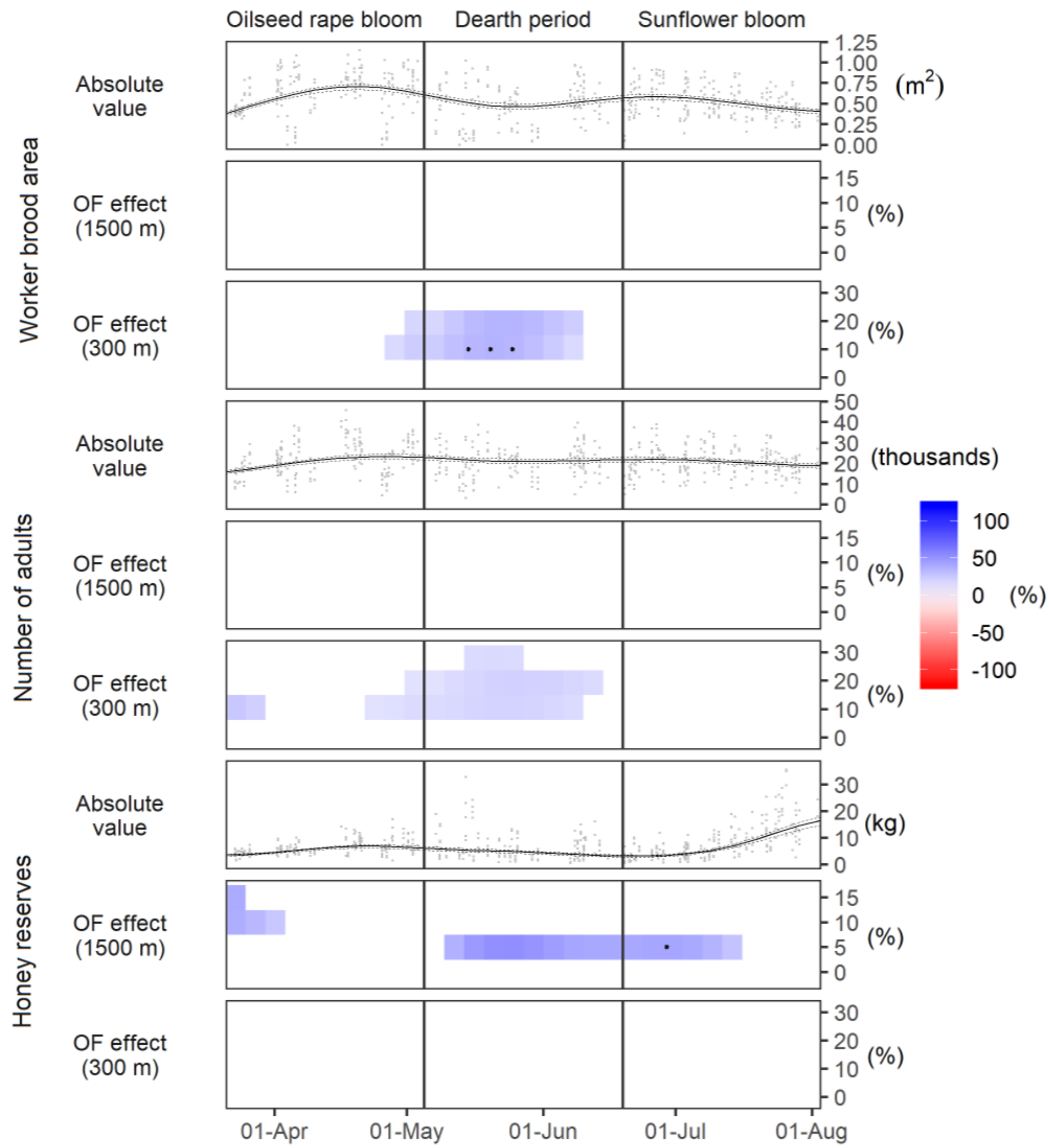

Fig. 2. Variation of worker brood area, number of adults and honey reserves across spring and summer. Solid lines denote GAMM estimates, dashed lines bootstrapped 95%-confidence intervals and dots mean values per apiary and day. The relation between colony performance traits and the proportion of organic farmland in a 1500 m or 300 m radius around the hives is illustrated as a color-coded percentage difference between colonies with and without exposure to organic farmland (*OF effect*, equation. 1). The colour gradient

shows positive differences (i.e. higher values in colonies exposed to organic farmland) in blue and negative ones in red. *OF effect* has been calculated for 5-15% organic farmland at the landscape scale (1500 m) and 10-30% organic farmland at the local scale (300 m). Cells in white indicate that $P>0.05$ and dots that $P<0.001$. *P*-values of different point estimates are not independent and have not been corrected for multiple testing. Estimates are based on data collected in 2-week intervals over six years.

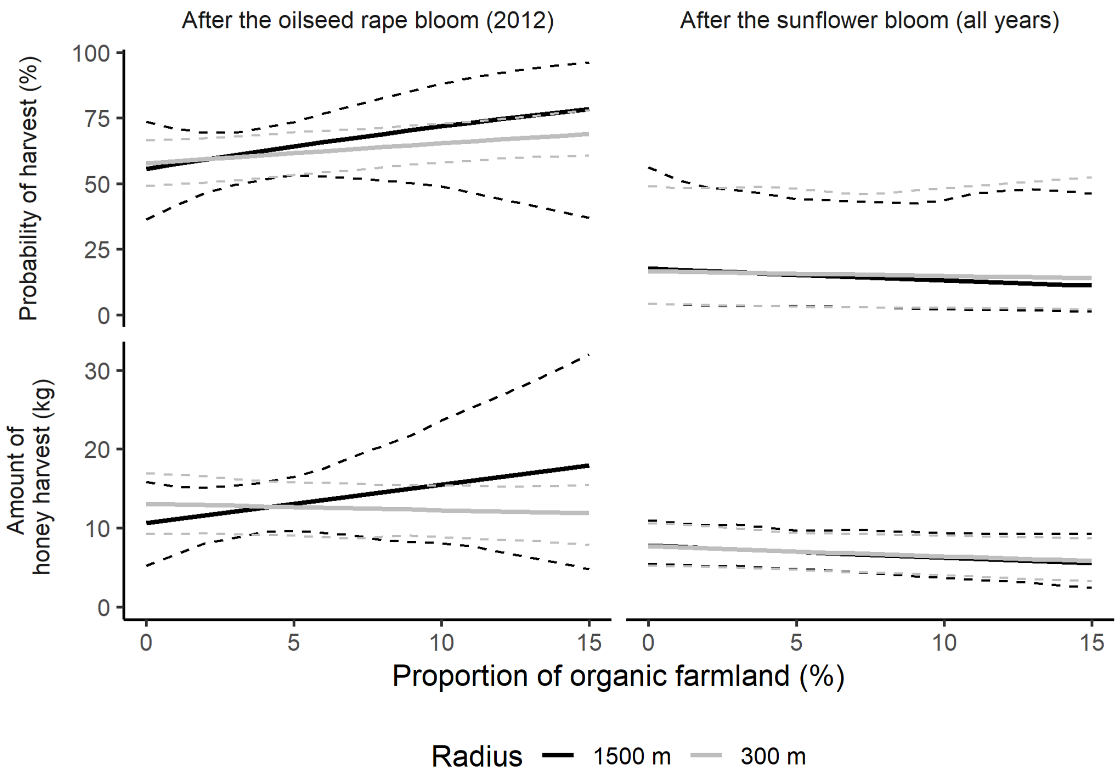

Fig 3. Honey harvest after the oilseed rape bloom in 2012 and after the sunflower bloom in all years (2012-2017) in relation to the proportion of organic farmland in a 1500 m and a 300 m radius around the honeybee hives. Honey harvest is characterized by two parameters: the probability that honey could be harvested from a colony & the amount of honey harvest among those colonies with harvest.

Supporting Information for

Effects of organic farming on the seasonal dynamics of honeybee colony performance

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This PDF file includes:

Appendix S1

Tables S1-2

Figures S1-11

Appendix S1. Adjustment of Julian days according to growing degree days.

To correct for inter-annual differences in ambient temperature, Julian days were adjusted according to growing degree days (GDDs) for oilseed rape (base temperature = 5 °C). GDDs were calculated by subtracting the base temperature from the mean of the daily minimum and maximum ambient temperature. Negative values were set to zero, as no (oilseed rape) plant growth occurs below the base temperature. GDDs were then accumulated from the first day of the year to each other day. Afterwards, Julian days between 2009 and 2017 were linked to their cumulative GDDs by a locally weighted regression (LOESS). Adjusted Julian days were then obtained by predicting them based on the LOESS fit and the measured cumulative GDDs of each regarded date.

Table S1. Spearman correlations between the proportions of organic farmland and oilseed rape, grassland and sunflower in a 1500 m and 300 m radius around 60 apiaries.

Field cover types		r_s **(1500 m)**	***P*** **(1500 m)**	r_s **(300 m)**	***P*** **(300 m)**
Organic land	Oilseed rape	-0.13	0.324	-0.12	0.336
Organic land	Grassland	-0.03	0.847	0.11	0.420
Organic land	Sunflower	0.08	0.554	0.13	0.339
Oilseed rape	Grassland	**-0.36**	**0.005**	**-0.26**	**0.046**
Oilseed rape	Sunflower	0.04	0.761	0.06	0.650
Grassland	Sunflower	**-0.28**	**0.033**	-0.19	0.143

Table S2. Model statistics of generalized additive mixed-effects models (GAMMs). Julian day numbers have been adjusted to cumulative oilseed rape growing degree days (see Appendix S1). Effective degrees of freedom (e.d.f.) were selected based on maximum likelihood without setting an upper limit (k).

Response	Spatial scale	Predictor	*F*	*e.d.f.*	*P*
Worker brood area	n/a	s(Julian day)	**145.1**	**8.8**	**<0.001**
Number of adults	n/a	s(Julian day)	**40.9**	**8.0**	**<0.001**
Honey reserves	n/a	s(Julian day)	**177.4**	**8.6**	**<0.001**
Worker brood area	1500 m	s(Julian day, organic farmland)	**47.6**	**27.5**	**<0.001**
Worker brood area	300 m	s(Julian day, organic farmland)	**50.0**	**26.2**	**<0.001**
Number of adults	1500 m	s(Julian day, organic farmland)	**15.6**	**24.4**	**<0.001**
Number of adults	300 m	s(Julian day, organic farmland)	**17.3**	**22.4**	**<0.001**
Honey reserves	1500 m	s(Julian day, organic farmland)	**58.2**	**26.9**	**<0.001**
Honey reserves	300 m	s(Julian day, organic farmland)	**60.5**	**24.9**	**<0.001**
Worker brood area	1500 m	s(Julian day, organic farmland)+	**11.0**	**27.5**	**<0.001**
		s(Julian day, oilseed rape)	**2.7**	**18.7**	**<0.001**
Worker brood area	300 m	s(Julian day, organic farmland)+	**12.8**	**26.8**	**<0.001**
		s(Julian day, oilseed rape)	**2.7**	**12.6**	**0.001**
Worker brood area	1500 m	s(Julian day, organic farmland)+	**9.0**	**27.3**	**<0.001**
		s(Julian day, grassland)	**3.5**	**20.3**	**<0.001**
Worker brood area	300 m	s(Julian day, organic farmland)+	**8.9**	**25.4**	**<0.001**
		s(Julian day, grassland)	**6.0**	**23.4**	**<0.001**
Worker brood area	1500 m	s(Julian day, organic farmland)+	**9.0**	**27.0**	**<0.001**
		s(Julian day, sunflower)	**5.0**	**22.1**	**<0.001**
Worker brood area	300 m	s(Julian day, organic farmland)+	**10.8**	**26.5**	**<0.001**
		s(Julian day, sunflower)	**2.8**	**15.4**	**<0.001**
Number of adults	1500 m	s(Julian day, organic farmland)+	**6.2**	**23.9**	**<0.001**
		s(Julian day, oilseed rape)	**2.2**	**10.5**	**0.009**
Number of adults	300 m	s(Julian day, organic farmland)+	**5.1**	**20.6**	**<0.001**
		s(Julian day, oilseed rape)	1.2	14.5	0.259
Number of adults	1500 m	s(Julian day, organic farmland)+	**15.6**	**24.5**	**<0.001**
		s(Julian day, grassland)	0.9	1.0	0.339
Number of adults	300 m	s(Julian day, organic farmland)+	**5.7**	**18.3**	**<0.001**
		s(Julian day, grassland)	**3.6**	**22.5**	**<0.001**
Number of adults	1500 m	s(Julian day, organic farmland)+	**4.8**	**21.4**	**<0.001**
		s(Julian day, sunflower)	**6.0**	**22.1**	**<0.001**
Number of adults	300 m	s(Julian day, organic farmland)+	**5.8**	**16.9**	**<0.001**
		s(Julian day, sunflower)	**6.5**	**20.0**	**<0.001**
Honey reserves	1500 m	s(Julian day, organic farmland)+	**21.2**	**26.5**	**<0.001**
		s(Julian day, oilseed rape)	**3.0**	**10.8**	**0.001**
Honey reserves	300 m	s(Julian day, organic farmland)+	**21.1**	**2.0**	**<0.001**

		s(Julian day, oilseed rape)	**41.1**	**25.1**	**<0.001**
Honey reserves	1500 m	s(Julian day, organic farmland)+	**9.1**	**25.1**	**<0.001**
		s(Julian day, grassland)	**3.5**	**17.2**	**<0.001**
Honey reserves	300 m	s(Julian day, organic farmland)+	**4.7**	**4.5**	**<0.001**
		s(Julian day, grassland)	**24.6**	**24.9**	**<0.001**
Honey reserves	1500 m	s(Julian day, organic farmland)+	**11.4**	**25.4**	**<0.001**
		s(Julian day, sunflower)	**4.0**	**19.4**	**<0.001**
Honey reserves	300 m	s(Julian day, organic farmland)+	**12.1**	**23.9**	**<0.001**
		s(Julian day, sunflower)	**2.2**	**14.0**	**0.006**

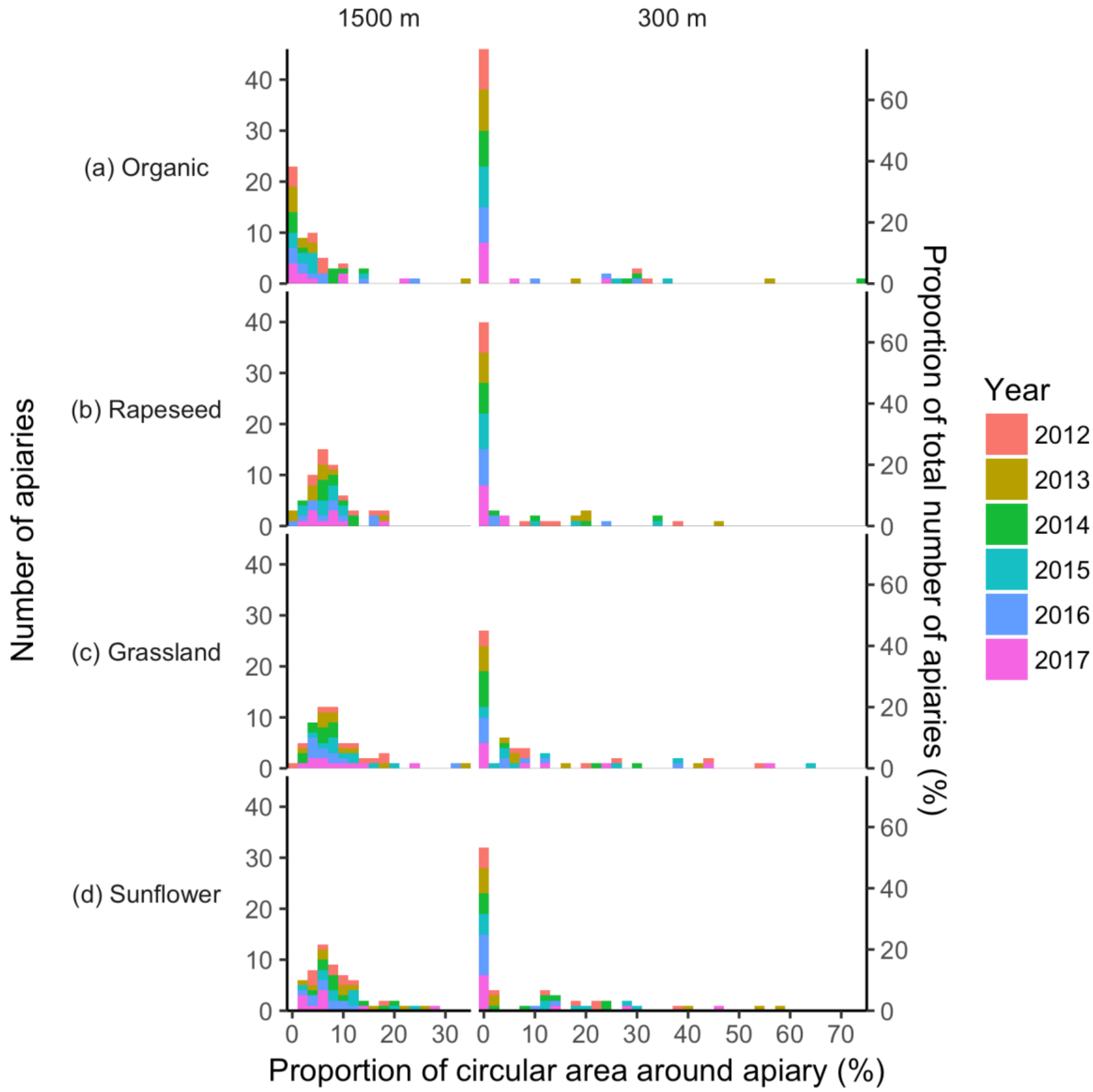


Fig. S1. Histograms of the percentage of (a) organic farmland, (b) oilseed rape (c) grassland and (d) sunflower in 300 m and 1500 m circular buffers around the apiaries expressed in absolute numbers and as a share of the total number of apiaries.

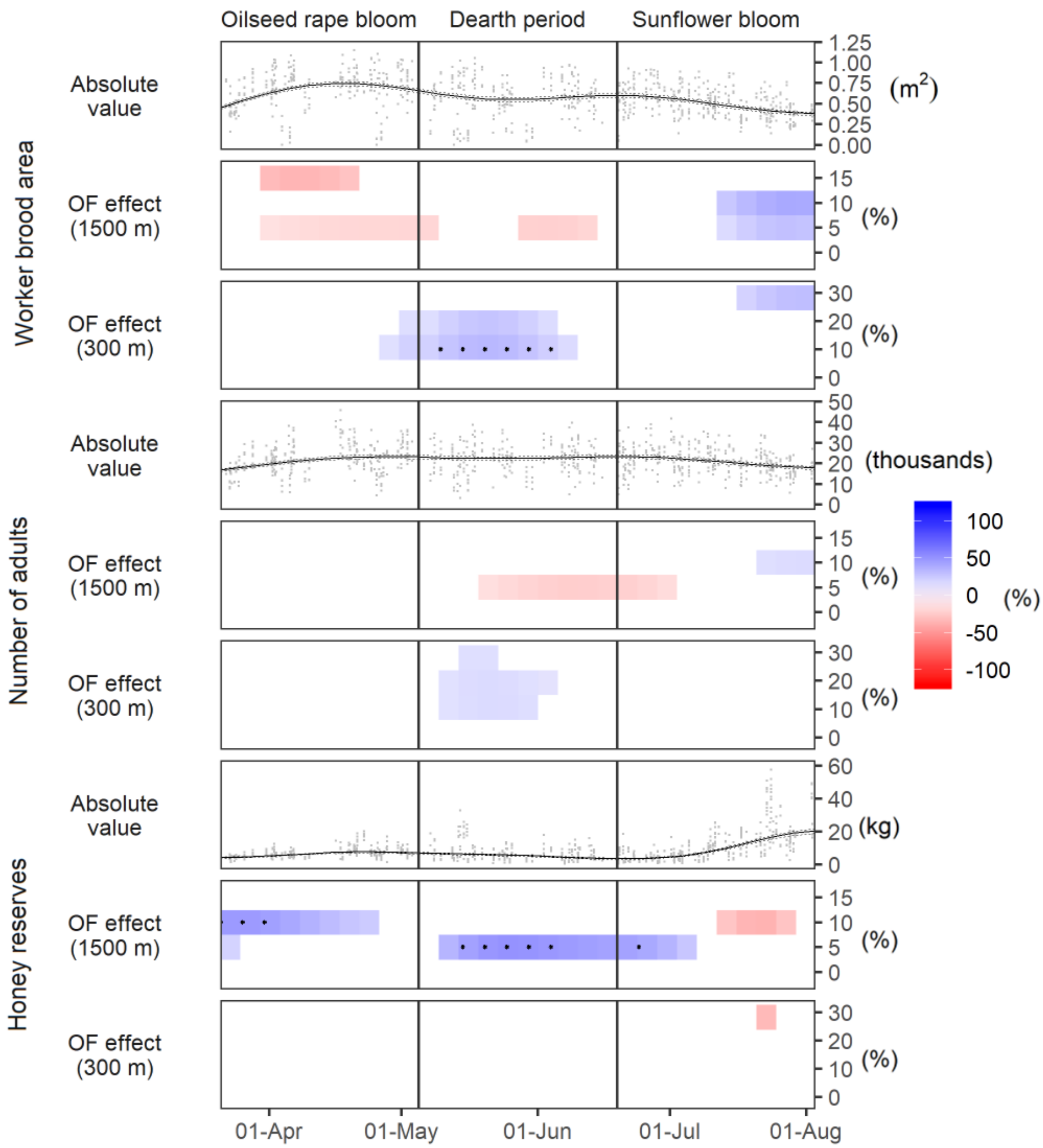


Fig. S2 Variation of worker brood area, number of adults and honey reserves across spring and summer for the years 2009-2017. Solid lines denote estimates of generalized additive mixed models, dashed lines bootstrapped 95%-confidence intervals and dots measured mean values per apiary and day. The relation between life-history traits and the proportion of organic farmland in a 1500 m or 300 m radius around the hives is illustrated as a color-coded percentage difference between colonies with and without exposure to organic farmland (*OF effect*, equation. 1). The color gradient shows positive differences (i.e. higher values in colonies exposed to organic farmland) in blue and negative ones in red. Cells in white indicate that $P>0.05$ and dots that $P<0.001$. *P*-values of different point estimates are not independent and have not been corrected for multiple testing. Estimates are based on data collected in 2-week intervals over nine years.

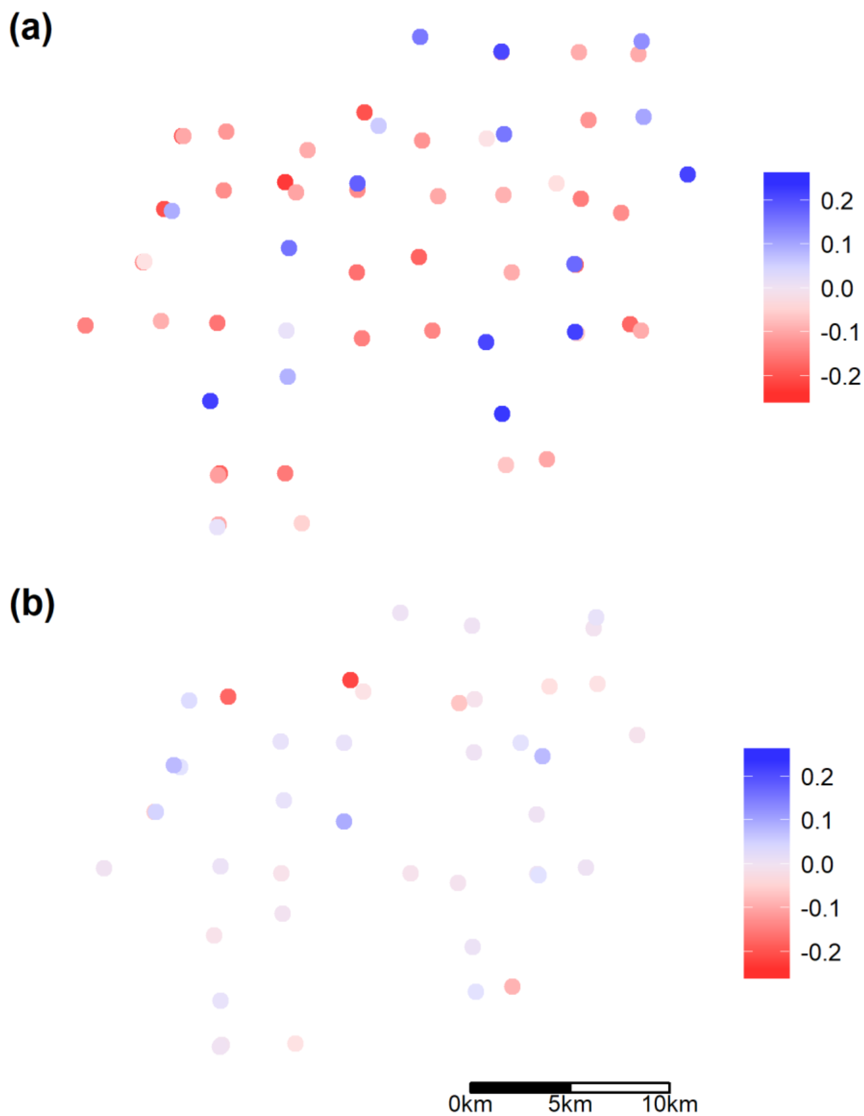


Fig. S3. Mean model residuals per apiary of models on **(a)** the probability of honey harvest after the sunflower bloom (in log odds ratios) and **(b)** the amount of honey harvest among those colonies with honey harvest after the sunflower bloom (in $kg^{0.5}$) in the years between 2012-2017.

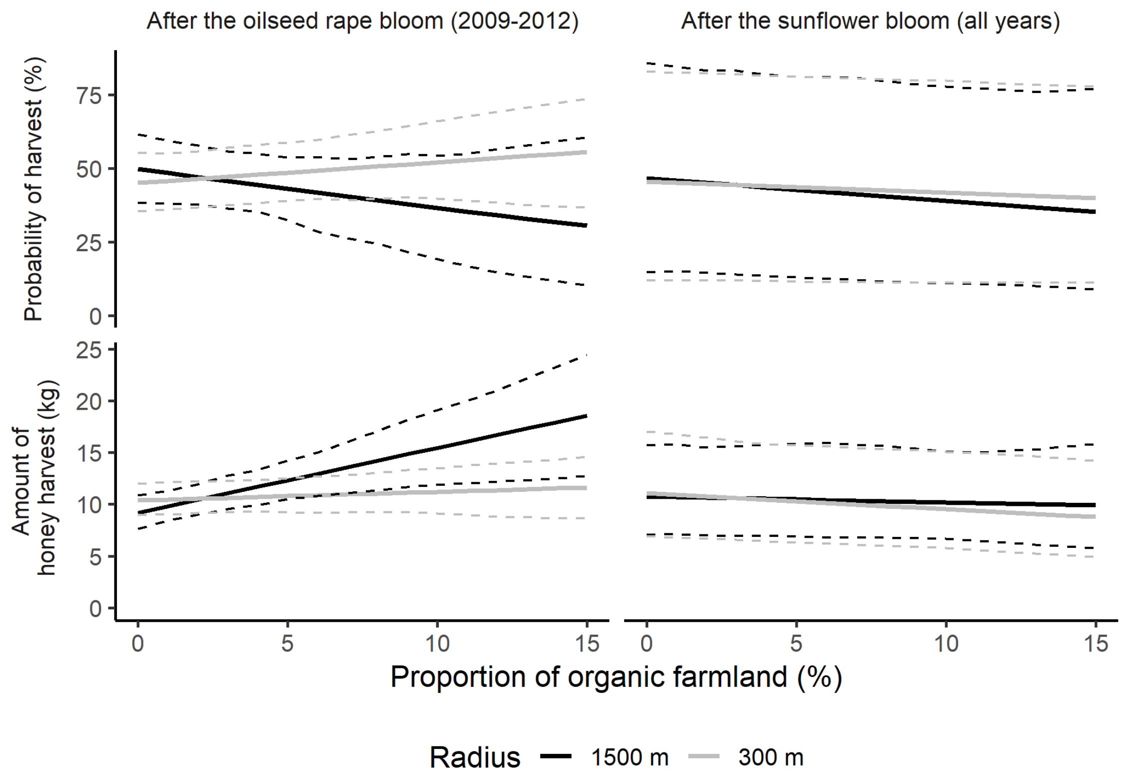


Fig. S4. Honey harvest after the oilseed rape bloom in 2009-2012 and after the sunflower bloom in all years (2009-2017) in relation to the proportion of organic farmland in a 1500 m and a 300 m radius around the honeybee hives. Honey harvest is characterized by two parameters: the probability of honey harvest per colony & the amount of honey harvest among those colonies with harvest.

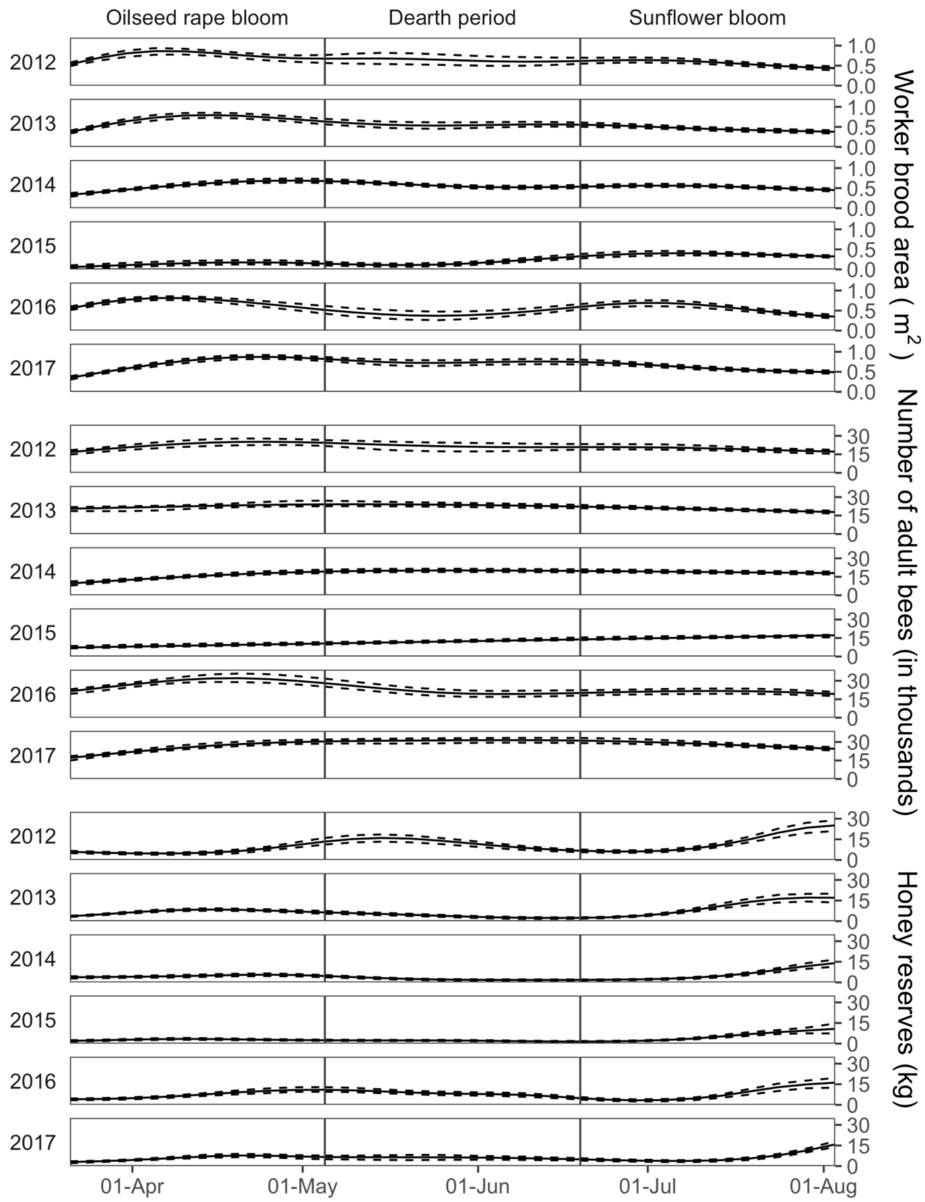


Fig. S5. Seasonal variation of colony performance traits separately for each year. Solid lines denote predictions of generalized additive mixed models, dashed lines indicate bootstrapped 95% confidence intervals and dots show measured mean values per apiary and day. Confidence intervals were calculated by 1100 bootstrap simulations.

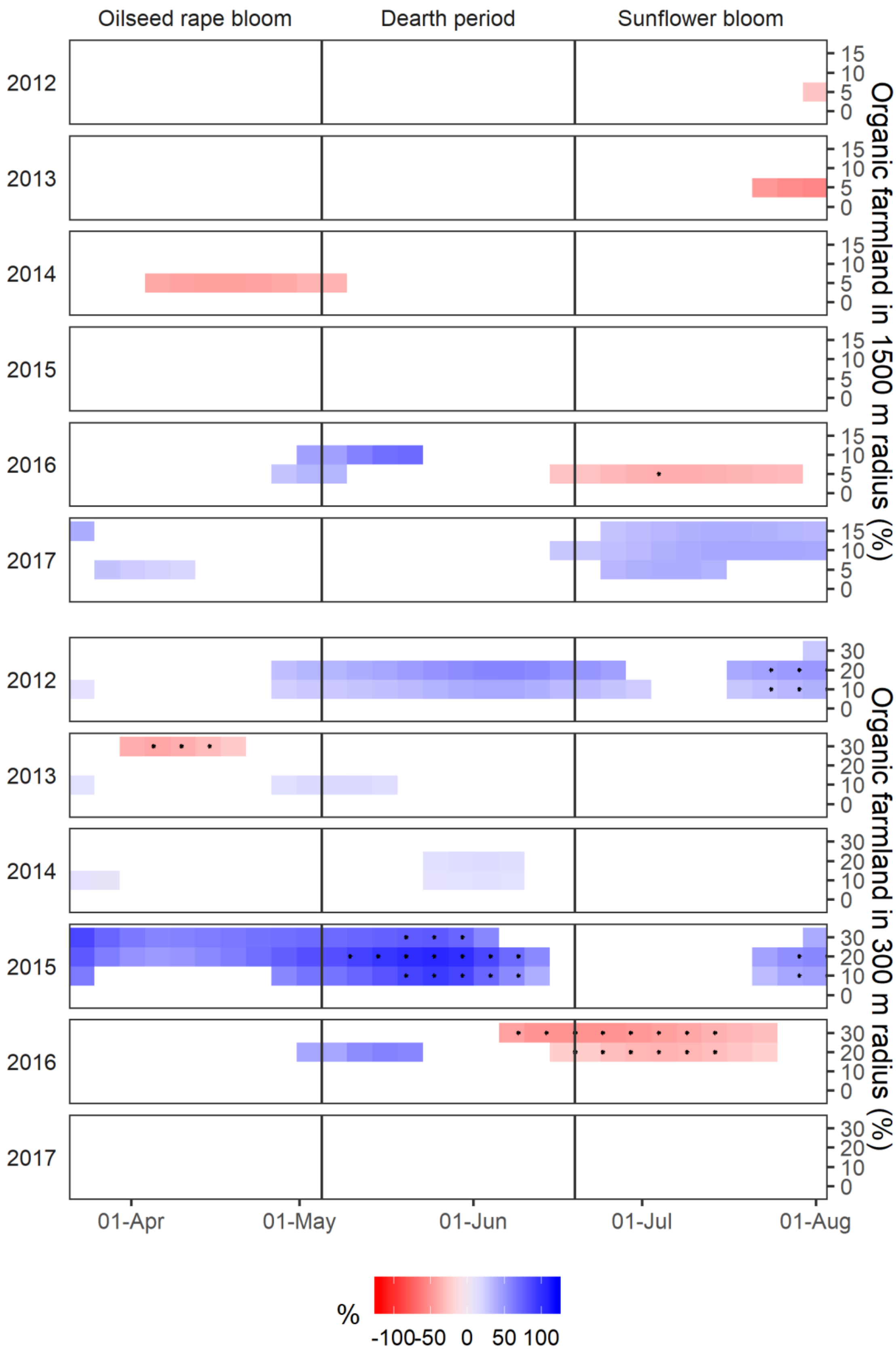
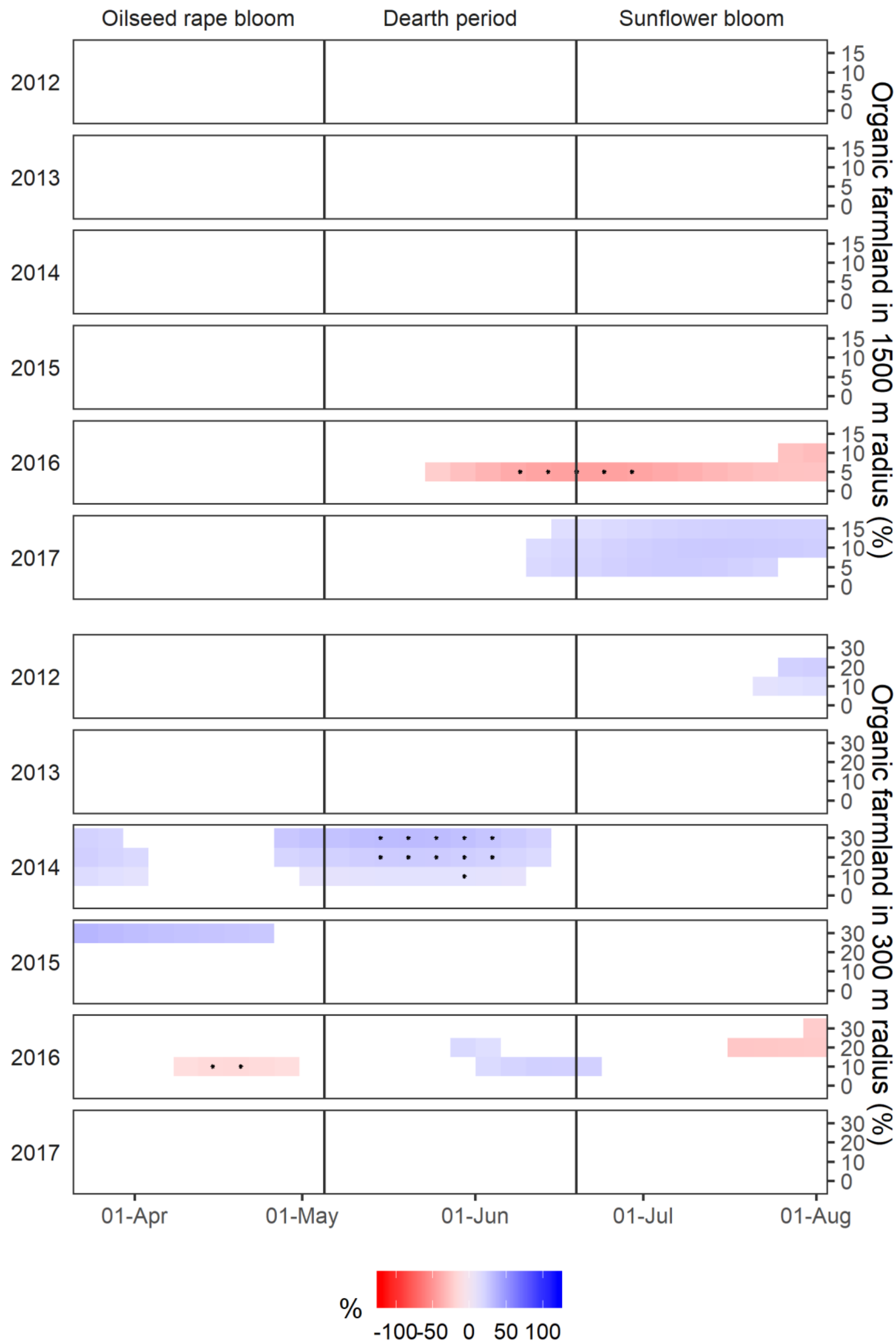
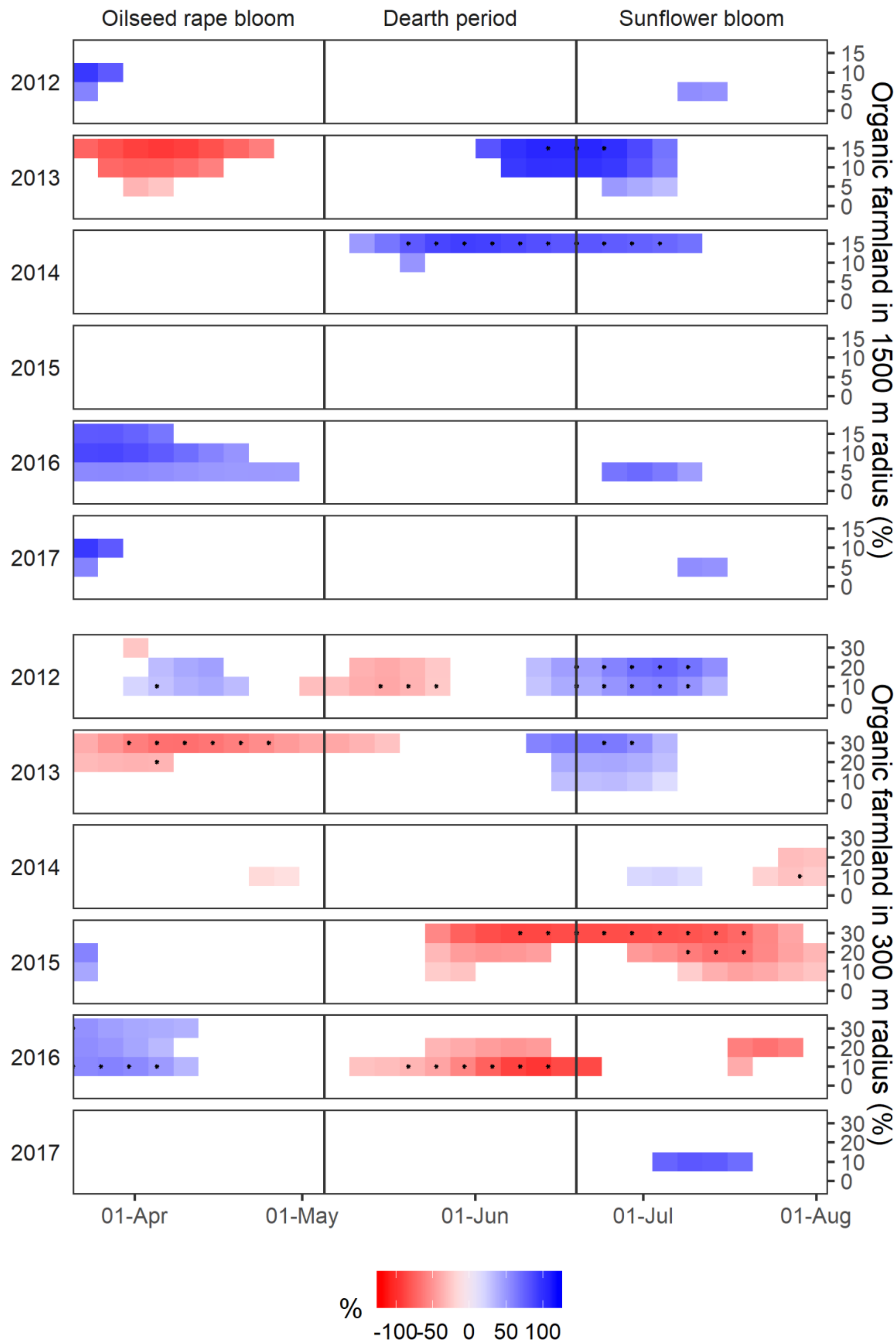

Oilseed rape bloom
Dearth period
Sunflower bloom
2012
2013
2014
2015
2016
2017
Organic farmland in 1500 m radius (%)
Organic farmland in 300 m radius (%)
01-Apr
01-May
01-Jun
01-Jul
01-Aug
%
-100 -50 0 50 100

Fig. S6. Seasonal variation of the relation between worker brood area and the proportion of organic farmland in a 1500 m or 300 m radius around the hives separately for each year. The size of the organic farming effect (*OF effect*) is color-coded with higher values in colonies with organic farmland exposure shown in blue (and the reverse in red). *OF effect* represents the weighted percentage difference in GAMM predictions of worker brood area at the same (growing degree day-adjusted) Julian day between colonies with and without exposure to organic farmland (see equation 1). Cells in white indicate that $P>0.05$ and dots that $P<0.001$. *P*-values were calculated under the null from 1100 bootstrap simulations. *P*-values of different point estimates are not independent and have not been corrected for multiple testing. Estimates are based on data collected in 2-week intervals over six years.



Oilseed rape bloom
Dearth period
Sunflower bloom
2012
2013
2014
2015
2016
2017
Organic farmland in 1500 m radius (%)
Organic farmland in 300 m radius (%)
01-Apr
01-May
01-Jun
01-Jul
01-Aug
%
-100-50 0 50 100

Fig. S7. Seasonal variation of the relation between number of adults and the proportion of organic farmland in a 1500 m or 300 m radius around the hives separately for each year. The size of the organic farming effect (*OF effect*) is color-coded with higher values in colonies with organic farmland exposure shown in blue (and the reverse in red). *OF effect* represents the weighted percentage difference in GAMM predictions of number of adults at the same (growing degree day-adjusted) Julian day between colonies with and without exposure to organic farmland (see equation 1). Estimates are based on data collected in 2-week intervals over six years. Cells in white indicate that $P>0.05$ and dots that $P<0.001$. *P*-values were calculated under the null from 1100 bootstrap simulations. *P*-values of different point estimates are not independent and have not been corrected for multiple testing.



Oilseed rape bloom
Dearth period
Sunflower bloom
2012
2013
2014
2015
2016
2017
Organic farmland in 1500 m radius (%)
Organic farmland in 300 m radius (%)
0
5
10
15
20
30
01-Apr
01-May
01-Jun
01-Jul
01-Aug
%
-100
-50
0
50
100

Fig. S8. Seasonal variation of the relation between honey reserves and the proportion of organic farmland in a 1500 m or 300 m radius around the hives separately for each year. The size of the organic farming effect (*OF effect*) is color-coded with higher values in colonies with organic farmland exposure shown in blue (and the reverse in red). *OF effect* represents the weighted percentage difference in GAMM predictions of colony honey reserves at the same (growing degree day-adjusted) Julian day between colonies with and without exposure to organic farmland (see equation 1). Estimates are based on data collected in 2-week intervals over six years. Cells in white indicate that $P>0.05$ and dots that $P<0.001$. *P*-values were calculated under the null from 1100 bootstrap simulations. *P*-values of different point estimates are not independent and have not been corrected for multiple testing.

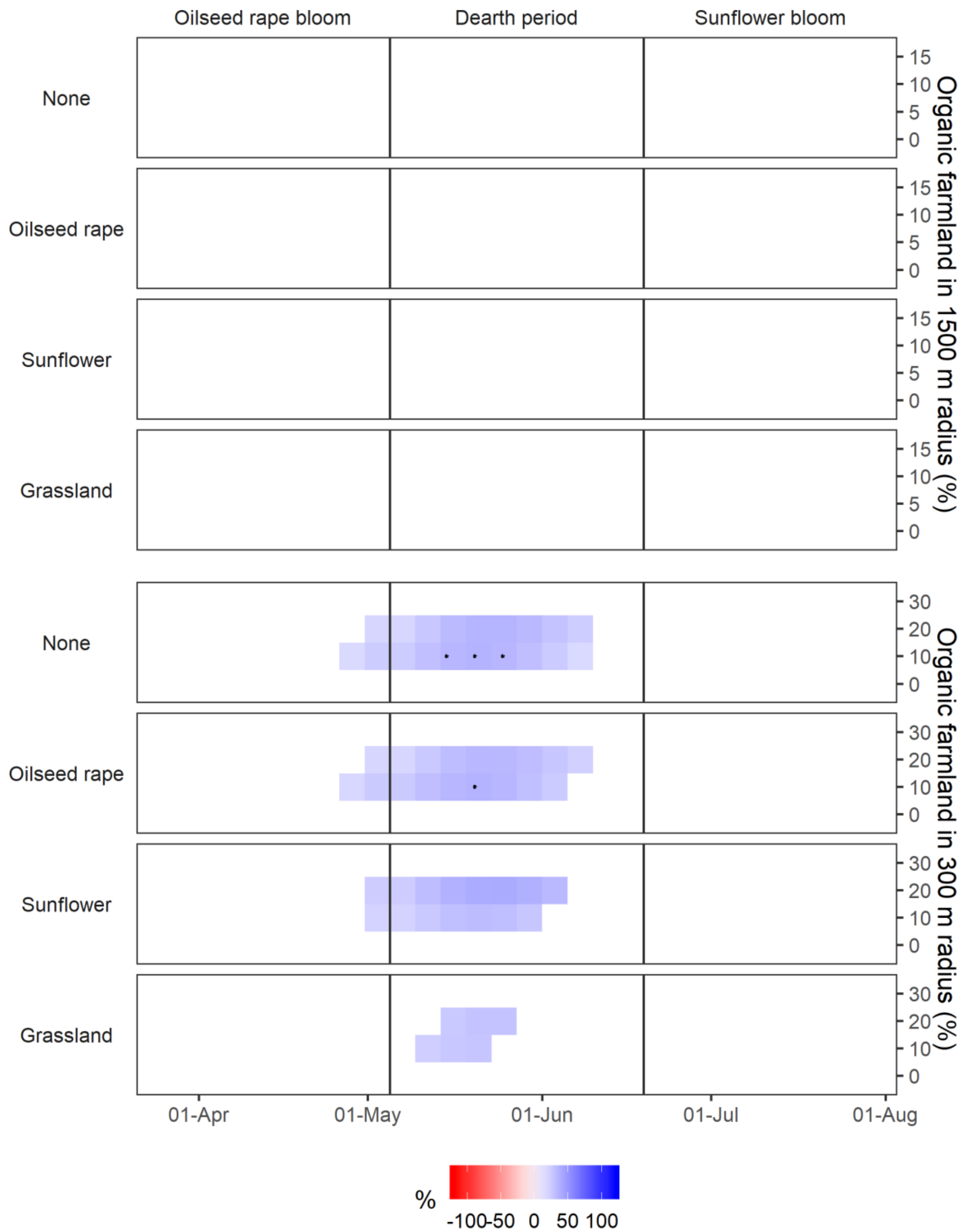


Fig. S9. Seasonal variation of the effect of organic farming on worker brood area, across spring and summer when incorporating in addition to an interaction between (growing degree day-adjusted) Julian days and the proportion of organic land either no field cover variable or an interaction between Julian days and the proportion of oilseed rape, sunflower or grassland in circular areas around the hives. The size of the organic farming effect (*OF effect*) is color-coded with higher values in colonies with organic farmland exposure shown in blue (and the reverse in red). *OF effect* represents the weighted percentage difference in Generalized Additive Mixed Model (GAMM) predictions of worker brood area at the same Julian day between colonies with and without exposure to organic farmland (see equation 1). Estimates are based on data collected in 2-week intervals over six years. Cells in white indicate that $P>0.05$ and dots that $P<0.001$. *P*-values were calculated under the null from 1100 bootstrap simulations. *P*-values of different point estimates are not independent and have not been corrected for multiple testing.

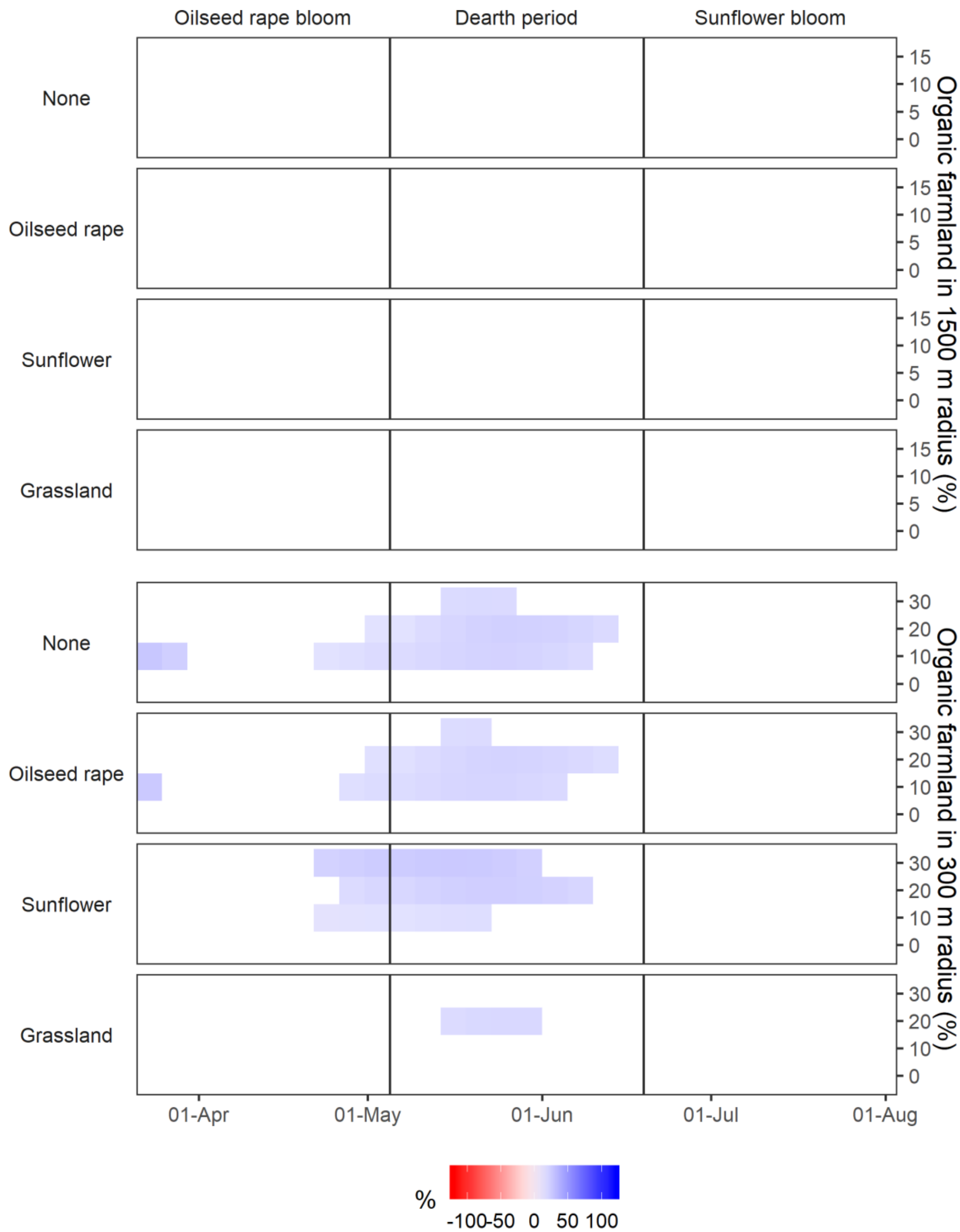


Fig. S10. Seasonal variation of the effect of organic farming on number of adults, across spring and summer when incorporating in addition to an interaction between (growing degree day-adjusted) Julian days and the proportion of organic land either no field cover variable or an interaction between Julian days and the proportion of oilseed rape, sunflower or grassland in circular areas around the hives. The size of the organic farming effect (*OF effect*) is color-coded with higher values in colonies with organic farmland exposure shown in blue (and the reverse in red). *OF effect* represents the weighted percentage difference in Generalized Additive Mixed Model (GAMM) predictions of number of adults at the same Julian day between colonies with and without exposure to organic farmland (see equation 1). Estimates are based on data collected in 2-week intervals over six years. Cells in white indicate that $P>0.05$ and dots that $P<0.001$. *P*-values were calculated under the null from 1100 bootstrap simulations. *P*-values of different point estimates are not independent and have not been corrected for multiple testing.

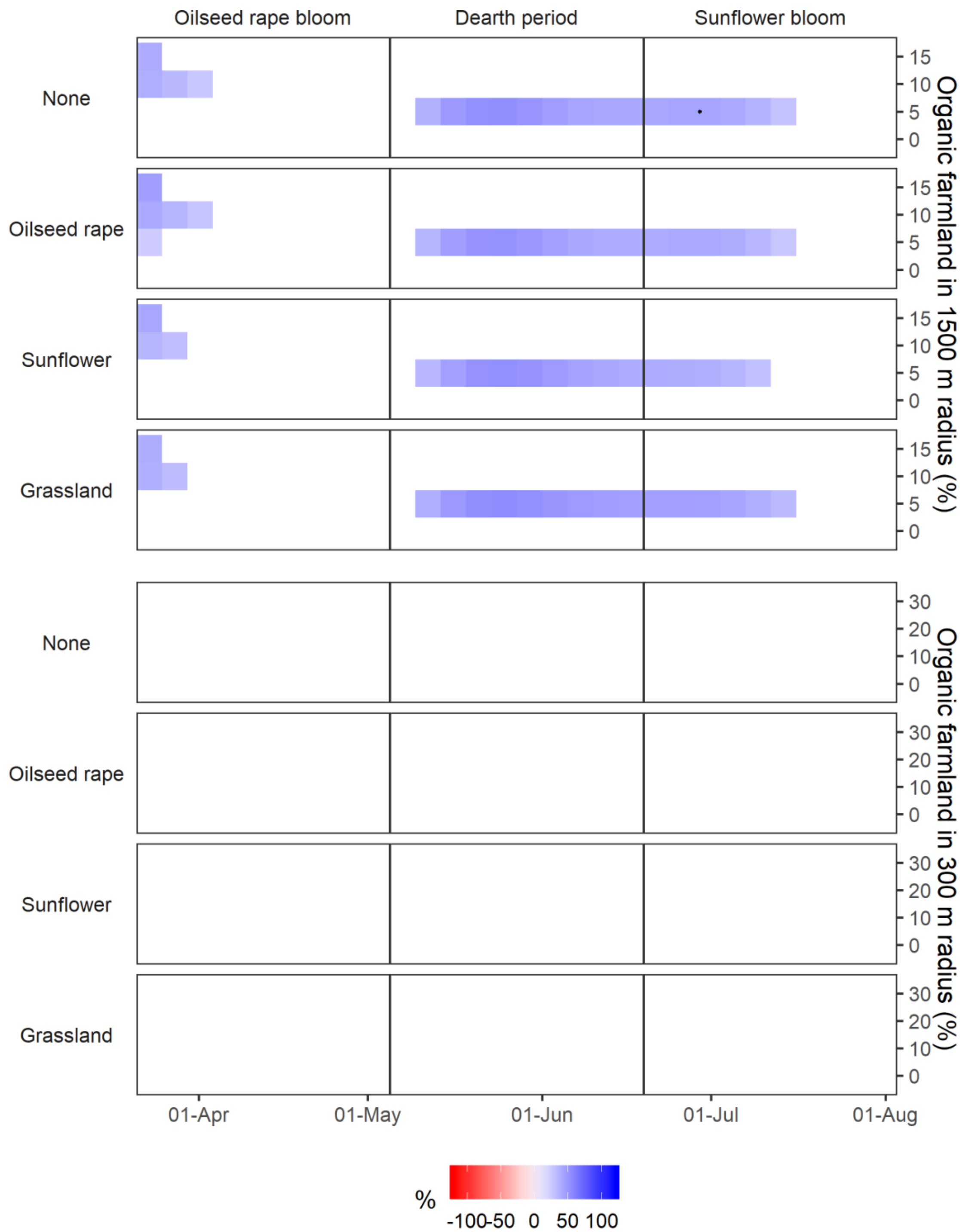


Fig. S11. Seasonal variation of the effect of organic farming on honey reserves, across spring and summer when incorporating in addition to an interaction between (growing degree day-adjusted) Julian days and the proportion of organic land either no field cover variable or an interaction between Julian days and the proportion of oilseed rape, sunflower or grassland in circular areas around the hives. The size of the organic farming effect (*OF effect*) is color-coded with higher values in colonies with organic farmland exposure shown in blue (and the reverse in red). *OF effect* represents the weighted percentage difference in Generalized Additive Mixed Model (GAMM) predictions of honey reserves at the same Julian day between colonies with and without exposure to organic farmland (see equation 1). Estimates are based on data collected in 2-week intervals over six years. Cells in white indicate that $P>0.05$ and dots that $P<0.001$. *P*-values were calculated under the null from 1100 bootstrap simulations. *P*-values of different point estimates are not independent and have not been corrected for multiple testing.