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Managing trap-nesting bees as crop pollinators: Spatiotemporal effects of floral resources and antagonists

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Abstract

1. The decline of managed honeybees and the rapid expansion of mass-flowering crops increase the risk of pollination limitation in crops and raise questions about novel management approaches for wild pollinators in agroecosystems. Adding artificial nesting sites, such as trap nests, can promote cavity-nesting bees in agroecosystems, but effectiveness could be limited by the availability of floral resources in the surrounding landscape and by natural antagonists.
2. In two European regions, we exposed artificial trap nests in paired field boundaries adjacent to oilseed rape (OSR) fields or non-flowering crops for 2 years within 32 landscapes covering two independent gradients of OSR cover and semi-natural habitat (SNH) cover in the landscape. We analysed the effects of local and landscape-wide floral resource availability, land-use intensity, landscape complexity and natural antagonists on community composition and population dynamics of trap-nesting bees.
3. Numbers of brood cells showed a strong, three-fold increase in response to the additional nesting sites. Species richness and abundance of cavity-nesting bees that were active during OSR flowering increased significantly with increasing amounts of early season landscape-wide floral resource availability, such as the cultivation of OSR. Later foraging species benefited instead from the availability of late-season alternative flower resources or SNH cover once the mass-flowering had ceased. Density-dependent parasitism increased following mass-flowering, while no density-dependent effect was found during mass-flowering.
4. Structural equation modelling revealed that the influence of floral resource availability on community growth rate was mediated by community size. Community size showed a strong negative effect on community growth rate. Despite positive density-dependent parasitism, antagonists had only weak regulating effects on community growth rate.
5. *Synthesis and applications.* Trap-nesting bee populations grow markedly with the increasing availability of food resources in the landscape and effectiveness of trap nests is only marginally limited by natural antagonists. Thus, trap nests could be a simple pollinator-supporting strategy to accompany the current expansion of mass-flowering crops and to ensure pollination services for insect-pollinated crops. Trap nests benefit, not only early season active generalist bees during oilseed rape

flowering, but also species with later phenology if accompanied by other pollinator-supporting practices.

KEYWORDS

ecosystem services, landscape context, mass-flowering crops, natural enemies, nesting resources, off-field practices, oilseed rape, resource limitation, solitary bees, top-down or bottom-up control

1 | INTRODUCTION

Wild bees are a crucial component of terrestrial ecosystems, playing an important functional role as pollinators of many crops (Garibaldi et al., 2013; Klein et al., 2007) and wild plants (Ollerton, Winfree, & Tarrant, 2011). The 'global pollinator crisis' has led to considerable research on the numerous pressures threatening bees in the modern world (see a review by Goulson, Nicholls, Botías, & Rotheray, 2015). Habitat loss and agricultural intensification are two of the main drivers of wild bee declines (Potts et al., 2010). Although the increased use of managed honeybees may mitigate the loss of pollination services caused by the decline of wild bees, they cannot entirely substitute the contribution of wild bees to crop pollination (Garibaldi et al., 2013). Also, the area of pollinator-dependent crops is increasing more than the supply of honeybee colonies (Aizen & Harder, 2009; Breeze et al., 2014). To limit potential pollination deficits in crops, there is a need for effective management approaches to conserve and maintain wild pollinators in agroecosystems (Garibaldi et al., 2014; Scheper et al., 2015).

Bees largely depend on floral nectar and pollen for food and rely on undisturbed nest sites to fulfil their reproduction cycle (Potts et al., 2005; Roulston & Goodell, 2011; Wcislo & Cane, 1996). However, these bottom-up resources have become increasingly scarce in agroecosystems (Potts et al., 2010). Adding artificial nesting sites, such as trap nests for above-ground nesting bees, can be a prominent intervention to improve the availability of nesting resources for solitary cavity-nesting bees (Garibaldi et al., 2014; Goulson et al., 2015; Tschardtke, Gathmann, & Steffan-Dewenter, 1998). In particular, trap nests have been found to promote crop pollinators (Artz, Allan, Wardell, & Pitts-Singer, 2013; Bosch & Kemp, 2002; Gruber, Eckel, Everaars, & Dormann, 2011) and wild pollinator conservation (Maclvor & Packer, 2015). Yet, the effectiveness of such interventions could be limited by floral resource (FR) availability in the surrounding landscape. In agroecosystems, the conservation or creation of flower-rich habitats is, therefore, essential for providing food resources for wild bee populations (Garibaldi et al., 2014; Scheper et al., 2013). Pollen and nectar resources from crops may also contribute substantially to habitat quality (Holzschuh, Dormann, Tschardtke, & Steffan-Dewenter, 2013). For example, mass-flowering crops (MFCs) like oilseed rape (OSR) can provide large, albeit temporally restricted, amounts of food resources for pollinators. The rapid expansion of MFCs in Europe, largely due to an increased demand for biofuel, raises new questions about their potential role to counteract the decline of food resources for pollinators in agroecosystems (Diekötter, Peter, Jauker, Wolters, &

Jauker, 2014; Holzschuh, Dormann, Tschardtke, & Steffan-Dewenter, 2011; Holzschuh et al., 2013, 2016). Although MFCs provide a pulse of flowering resources, the short duration of floral availability may not be sufficient to enhance bee populations proportionally to the MFC area (Holzschuh et al., 2016). In addition, the lack of sufficient nesting sites (Roulston & Goodell, 2011) and the discontinuity of food resources after OSR flowering (Riedinger, Renner, Rundlöf, Steffan-Dewenter, & Holzschuh, 2014; Riedinger et al., 2015; Williams & Kremen, 2007) can be other factors that limit bee populations. The current understanding of the effects of resource availability on trap-nesting bee populations is, however, largely informed by snapshot surveys conducted during only part of the season without accounting for the spatiotemporal distribution of these resources (Schellhorn, Gagic, & Bommarco, 2015). Previous studies did not directly quantify the landscape-wide FR availability, but rather used proxies such as the amount of MFCs and semi-natural habitats (SNHs) in the landscape, as well as local floral diversity. Such approaches, however, neglect seasonal variation in FRs (Scheper et al., 2015).

In addition to bees being limited by foraging and nesting resources, the effectiveness of trap nests in enhancing bee populations may also be limited by top-down forces such as natural antagonists. However, despite the hypothesized importance of natural antagonists (also called natural enemies) in regulating populations, limited knowledge exists about their impact on wild bee populations (Roulston & Goodell, 2011). Host-natural enemy interactions are assumed to be density-dependent processes, where parasitism and predation increase with host density (Hassell, 2000; Vandermeer & Goldberg, 2003). Bees support numerous parasitic guilds that attack offspring or the stored food in brood cells (Roulston & Goodell, 2011; Wcislo & Cane, 1996). However, previous studies report mixed results for top-down regulation of populations of solitary bees, including both density dependence and inverse density dependence (Palladini & Maron, 2014; Rosenheim, 1990; Steffan-Dewenter & Schiele, 2008).

Here, we assessed the interplay of bottom-up effects of floral and nesting resources vs. top-down forces of antagonists on trap-nesting bees at local and landscape scales. Considering bottom-up resources, we directly quantified the landscape-wide FR availability both during (spring) and after (summer) the OSR flowering, in addition to the amount of OSR and SNHs in the landscape. In two European regions, we exposed artificial trap nests in paired field boundaries adjacent to OSR fields or non-flowering crops for 2 years within 32 landscapes covering two independent gradients of OSR cover and SNH cover in the landscape. We hypothesized that:

1. *Trap-nesting bees are limited by the quantity of nesting and flower resources in the landscape.* Increasing cover of early flowering OSR would provide more resources in spring, thereby enhancing population size of early trap-nesting bees, as well as community diversity (mainly early generalist species). Such effects may depend on the amount of SNH in the surrounding landscape, showing greater benefits in complex landscapes where nest site availability is less limited (i.e. cross-habitat spillover from SNH to OSR; Holzschuh et al., 2013) and flower resources are more abundant and relatively stable over time. In summer, we expected that later foraging species benefit from the availability of alternative flower resources other than OSR (Mandelik, Winfree, Neeson, & Kremen, 2012) and the amount of SNH in the landscape. Further evidence for resource limitation should result from a negative relationship between community growth rate and community size.
2. *Trap-nesting bees are top-down regulated by natural antagonists.* We expected a positive density-dependent parasitism and a negative density-dependent regulation of bee host population growth rates (Vandermeer & Goldberg, 2003). Natural antagonists would follow the local abundance and regional distribution of their hosts (Steffan-Dewenter, 2003).
3. *Additional resources provided by OSR reduce the impact of top-down regulation of bee populations by natural antagonists.* During mass-flowering, the top-down regulation by natural antagonists may be diluted by an increase in nest-building resulting from an increase in the amount of OSR in the landscape (Jauker, Peter, Wolters, & Diekötter, 2012).

2 | MATERIALS AND METHODS

2.1 | Sampling design

The study was conducted in 2011 and 2012 in two regions, one in Germany in the surroundings of Würzburg (Bavaria, 49°44'53"N, 9°51'34"E) and the other in the Netherlands in the surroundings of Lochem (Gelderland, 52°9'31"N, 6°24'33"E). In each study region, we selected 16 non-overlapping landscapes along two independent gradients of cover of OSR (from 0% to 20%) and SNH (from 1% to 26%) in the landscape. In each landscape, the trap nests were established in two types of field boundaries (see Appendix S1): (1) a field boundary adjacent to a non-flowering crop (mean \pm SE distance to nearest OSR field was 227.8 \pm 30.3 m, range from 75 to 550 m) and used as a control site, and (2) a field boundary directly adjacent to an OSR field.

Around each of the selected field boundaries, we quantified proportions of OSR and SNH in a 1 km buffer (i.e. for field boundaries directly adjacent to an OSR field, landscape context was characterized around the OSR field). To ensure that proportion of OSR and SNH were uncorrelated, we replicated as far as possible the landscapes with low, intermediate and high proportion of OSR along the gradient of SNH (see Appendix S2, Tables S1 and S2). In the Dutch region, the 16

landscapes had either low or no OSR cover (and consequently only eight boundaries adjacent to OSR were selected), as it was not possible to establish a low-high gradient in OSR in this region. Overall, 32 field boundaries adjacent to a non-flowering crop and 24 field boundaries directly adjacent to an OSR field were selected in 2011. Due to crop rotation, only nine field boundaries were directly adjacent to an OSR field in 2012. Information on landscape composition was derived using national topographical maps and aerial photographs, validated by field inspections. In GIS (ArcMap 9.3.1; ESRI), we quantified the relative cover of the land-use types in each landscape.

The study landscapes were also characterized by measuring land-use intensity (LI) and landscape-wide FR availability. LI was calculated by quantifying the nitrogen input per hectare of arable land per year (see Appendix S1). Nitrogen input is commonly used as a key indicator of LI which is well correlated with other farming intensity measures as well as plant diversity (Kleijn et al., 2009). Flower resources in the landscape (FR) were quantified to capture the landscape-wide availability of pollinator food resources. A stratified sampling approach was applied to determine the FR, both during (FR_{early}, early season landscape-wide FR availability, in May) and after (FR_{late}, late-season landscape-wide FR, in July–August) OSR flowering (see Scheper et al., 2015 for exact methodology).

2.2 | Trap nests

In each field boundary, six trap nest tubes were fixed on three wooden poles (two tubes per pole; see Appendix S1). In March 2011, before the beginning of OSR flowering, the trap nests were placed in the study sites and removed in autumn between mid- and the end of September. The collected trap nests were then stored at 4°C in a cooling chamber. In the following year, all nests were returned to the original field site in an emergence tube together with new trap nests (Steffan-Dewenter & Schiele, 2008). In each year, all occupied nests were marked at two different points in the season to record when a nest was built: (1) during OSR flowering and (2) after OSR flowering (6 weeks after mass-flowering). During the winter months, the nests were analysed in the laboratory. For each brood nest, the total number of brood cells, the number of brood cells attacked by parasitoids and the number of dead brood cells due to other causes (e.g. pathogen infections) were recorded. The brood nest values from the same field boundary were then summed together (2 trap nest tubes \times 3 poles), but separately for each year and season within year. We quantified the following parameters to characterize the local communities within each field boundary and for each season and year, separately: (1) bee species richness, (2) the total number of brood cells (N , used as a measure of community size; Steffan-Dewenter & Schiele, 2008), (3) parasitism rate (P , calculated as the ratio of parasitized brood cells to the total number of brood cells), and (4) mortality rate (M , calculated as the ratio of dead brood cells due to other causes to the total number of brood cells). Finally, annual community growth rate was calculated as $r_t = \ln(N_t/N_{t-1})$, where N_t and N_{t-1} were the total number of brood cells at time t (second year) and $t - 1$ (first year) (Turchin, 2003).

2.3 | Statistical analysis

We used linear mixed models (LMMs) to assess the effect of bottom-up and top-down forces on wild bee populations and community structure. Region ID and landscape ID were included in the models as random factors ('random intercept models'). In a preliminary analysis, we tested for random slope effects (region-level slope for the landscape effect, that is, OSR or SNH cover), but found no evidence that such effects improved model fit (Akaike information criterion [AIC] was always lower in random intercept models and the likelihood ratio tests were non-significant). To improve normality and homoscedasticity of residuals, abundance data (total number of brood cells) were log-transformed, proportion data (parasitism and mortality rates) were logit transformed and bee richness was square-root transformed. Finally, we calculated Cook's distance to verify whether extreme observations represented influential points using the R package 'influence.ME' (Nieuwenhuis, te Grotenhuis, & Pelzer, 2012). In some models, we identified influential observations, but the exclusion of these data points did not affect the results of the analyses. All analyses were conducted using R version 3.2.2 (R Development Core Team 2015).

2.3.1 | Annual changes in community and population size

We built a model containing the fixed factors: year, season and their interactions, to assess whether the effect of year on nest colonization (number of brood cells) differed across seasons. As *Osmia bicornis* is often a dominant trap-nesting species (e.g. Diekötter et al., 2014), we performed the same analysis considering whether season variations in nest colonization differed between *O. bicornis* populations and non-*O. bicornis* species, separately. In these cases, field boundary ID was also included in the model as a random factor. We used the 'lmerTest' R package to calculate *p*-values using Satterthwaite approximations to determine degrees of freedom. Models were simplified using a backward deletion procedure ($p > .05$).

2.3.2 | Local and landscape effects on community richness and size

We built four different models (*i–iv*) analysing each season and year, separately. In this way, we could determine the influence of various resources over the year (e.g. OSR in spring or alternative flower resources in summer) or between year (e.g. crop rotation) on population and community dynamics (Riedinger et al., 2015). In the four models (*i–iv*), we used bee richness and community size (number of brood cells) as response variables. *Model i*: we used the trap nest data collected during OSR flowering in the first year of the experiment to test the effect of OSR on bees using field boundary type and OSR cover as predictors in the model. *Model ii*: we assessed the effect of late-season landscape-wide FR availability (FR_{late}) on bees and field boundary type in the model using the trap nest data collected after OSR flowering. *Models iii and iv*: we analysed the data in the same

way as we did in models (*i*) and (*ii*), using the trap nest and landscape data collected in the second year. Also, we tested the possible effect of crop rotation using the interannual change of OSR proportions (ΔOSR) as a covariate in the models (*iii*) and (*iv*) and calculated as follows: $\Delta OSR = (OSR_{2012} - OSR_{2011}) / OSR_{2011}$. In all the models (*i–iv*), we included SNH cover and LI as covariates. Then, we compared model performance using early season landscape-wide FR availability (FR_{early}) instead of OSR cover in models (*i*) and (*iii*) as the two measures showed strong correlation ($r_{2011} = 0.94$ and $r_{2012} = 0.83$). We applied an information-theoretic model selection procedure (Burnham & Anderson, 2002) to evaluate alternative competing models (models *i–iv*) using second-order AIC_c (see Appendix S1 for more details). For each parameter in the candidate model set ($\Delta AIC_c < 7$), we used model averaging to incorporate model selection uncertainty into our parameter estimates (Burnham & Anderson, 2002). We reported 95% confidence intervals (CIs) around model-averaged partial slope coefficients.

2.3.3 | Top-down regulation by natural antagonists

We tested whether parasitism and mortality rates presented a positive density dependence by testing the effects of year, season, community size and their interaction. We also assessed the effect of local and landscape factors on parasitism rate using the same procedure described for the analysis of community models.

2.3.4 | The effects of bottom-up and top-down forces on community dynamics

Although a 2-year study is not ideal in revealing community dynamics, our data offer a unique opportunity to develop a probabilistic model that unites multiple predictors and response variables in a single causal network. We used piecewise structural equation modelling (SEM) and constructed the model using prior knowledge of the system to define the paths of interest (see Appendix S1 for more details). Specifically, we simultaneously tested the effects of landscape-wide FR availability, cover of SNHs, LI, parasitism rate (P_{t-1}), mortality rate (M_{t-1}) and community size (N_{t-1}) on community growth rate (r_t) in a single network. Because the aim of this analysis was to obtain a general picture of the direct and indirect effects on trap-nesting bee community dynamics, we only considered the overall-year effects in the SEM.

3 | RESULTS

Altogether, we analysed 18,730 nests containing 76,466 brood cells (see Appendix S2, Table S3). A total of 43,738 brood cells were constructed during mass-flowering, of which 92% was *O. bicornis*. In summer after mass-flowering, *O. bicornis* occupied only 26% of brood cells, while we found an increased presence of different bees such as *Hylaeus* spp. (26%), *Heriades truncorum* (20%), *Osmia brevicornis* (13%) and *Megachile* spp. (5%).

3.1 | Annual changes in community and population size

We found a significant interaction effect of season and year on the number of brood cells (LMMs: $F_{1,144.1} = 7.12$, $p = .009$). The average number of brood cells per site and year (mean \pm SE) significantly increased from 180 ± 30 in 2011 to 567 ± 89 in 2012. While there was no difference comparing the nest colonization during (192 ± 55) and after OSR flowering (170 ± 30) in the first year of the experiment, we found a stronger increase in brood cells during (666 ± 150) compared to after OSR flowering (465 ± 94) in the second year. At the population level, we also found a significant interaction of season and year for *O. bicornis* (LMMs: $F_{1,144.4} = 4.15$, $p = .043$). In this case, a larger number of brood cells was constructed during rather than after OSR flowering in both years (Figure 1a). Considering non-*O. bicornis* species, we only found a significant effect of the season (LMMs: $F_{1,148.2} = 132.7$, $p < .001$) inferring an increase in brood cells after OSR flowering (Figure 1b).

3.2 | Local and landscape effects on community richness

In the first year, none of the predictors were related to bee species richness during OSR flowering (all predictors with low summed Akaike weights, $\Sigma w_i < 0.50$ and 95% CIs including zero) (Figure 2a; see Appendix S2, Table S6). After mass-flowering, species richness was best predicted by field boundary type, SNH cover and LI ($\Sigma w_i > 0.70$) (Figure 2a; see Appendix S2, Table S6). SNH cover had a positive effect on species richness, while LI had a negative effect (Figure 2a; see Appendix S2, Figure S1a). Species richness was higher in field boundaries adjacent to non-flowering crops (Figure 2a; see Appendix S2, Figure S1a).

In the second year, species richness during OSR flowering was best predicted by field boundary type, flower resource availability (both OSR cover and FR_{early}) and SNH cover ($\Sigma w_i > 0.80$; Figure 2a; see Appendix S2, Table S6). Species richness was positively related to OSR at local (field boundaries adjacent to OSR) and landscape (OSR cover) scale, as well as to FR_{early} and SNH cover (Figure 2a; see

Appendix S2, Figure S1b). The model including FR_{early} or OSR cover as covariate showed a quite similar performance ($\Delta AIC_c = 1.8$). After mass-flowering, species richness was predicted by field boundary type ($\Sigma w_i = 0.65$) and SNH cover ($\Sigma w_i = 0.72$; Figure 2a; see Appendix S2, Table S6). Species richness was higher in field boundaries adjacent to OSR and in landscapes with a higher cover of SNH (Figure 2a; see Appendix S2, Figure S1c).

3.3 | Local and landscape effects on community size

In the first year, the number of brood cells was best explained by OSR cover ($\Sigma w_i = 0.91$) or FR_{early} ($\Sigma w_i = 0.98$) during the mass-flowering (Figure 2b; see Appendix S2, Table S7). OSR cover and FR_{early} had a positive effect on community size (Figure 2b; see Appendix S2, Figure S2a), showing a twofold increase in the number of brood cells for each 0.5 percentage increase in FR_{early} . The model including FR_{early} as a covariate showed a better performance than that with OSR cover ($\Delta AIC_c = 2.4$). After mass-flowering, the number of brood cells was only predicted by FR_{late} ($\Sigma w_i = 0.65$) showing a positive effect (Figure 2b; see Appendix S2, Table S7 and Figure S2b).

In the second year, the number of brood cells was best predicted by field boundary type ($\Sigma w_i = 0.73$), FR_{early} ($\Sigma w_i = 0.94$) and LI ($\Sigma w_i = 0.64$) during OSR flowering (Figure 2b; see Appendix S2, Table S7). OSR showed a positive effect on number of brood cells at the local scale (field boundaries adjacent to OSR), as well as early season landscape-wide FR availability, while LI had a negative effect (Figure 2b; see Appendix S2, Figure S2c). Also in this case, the model including FR_{early} as a covariate was ranked higher in model selection ($\Delta AIC_c = 3.5$). The effect of FR_{early} on the number of brood cells was comparable to that found in the first year. The positive effect of OSR at the local scale and the negative effect of LI were also observed after OSR flowering (Figure 2b; see Appendix S2, Figure S2d).

3.4 | Top-down regulation by natural antagonists

We found that 15.3% of the brood cells were attacked by parasitoids or parasites (see Appendix S2, Table S4), while nest dissection showed 16.8% were dead due to other causes, for example, pathogen infections. Parasitism rate was significantly affected by year (LMMs: $F_{1,137.5} = 48.23$, $p < .001$) and the interaction between community size and season (LMMs: $F_{1,184.4} = 5.23$, $p = .023$; see Appendix S2, Table S8). Parasitism rate was higher in the second year of the experiment increasing from 7% to 18%. A positive density-dependent parasitism was found after mass-flowering, while no density-dependent effect was found during OSR flowering (Figure 3). Parasitism rate was generally not related to local or landscape variables, except for a significant positive effect of SNH cover after the mass-flowering in the first study year (see Appendix S2, Table S9). Mortality rate was found to vary only across the season (LMMs: $F_{1,153.1} = 14.31$, $p < .001$) and the years (LMMs: $F_{1,153.7} = 26.45$, $p < .001$; see Appendix S2, Table S8). A higher mortality rate was found after OSR flowering (25%) than during

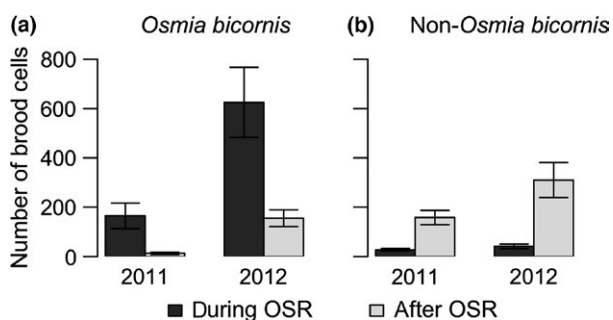


FIGURE 1 Mean (\pm SE) number of (a) *Osmia bicornis* and (b) non-*O. bicornis* brood cells in relation to year (2011 and 2012) and season within each year (during OSR flowering and after OSR flowering)

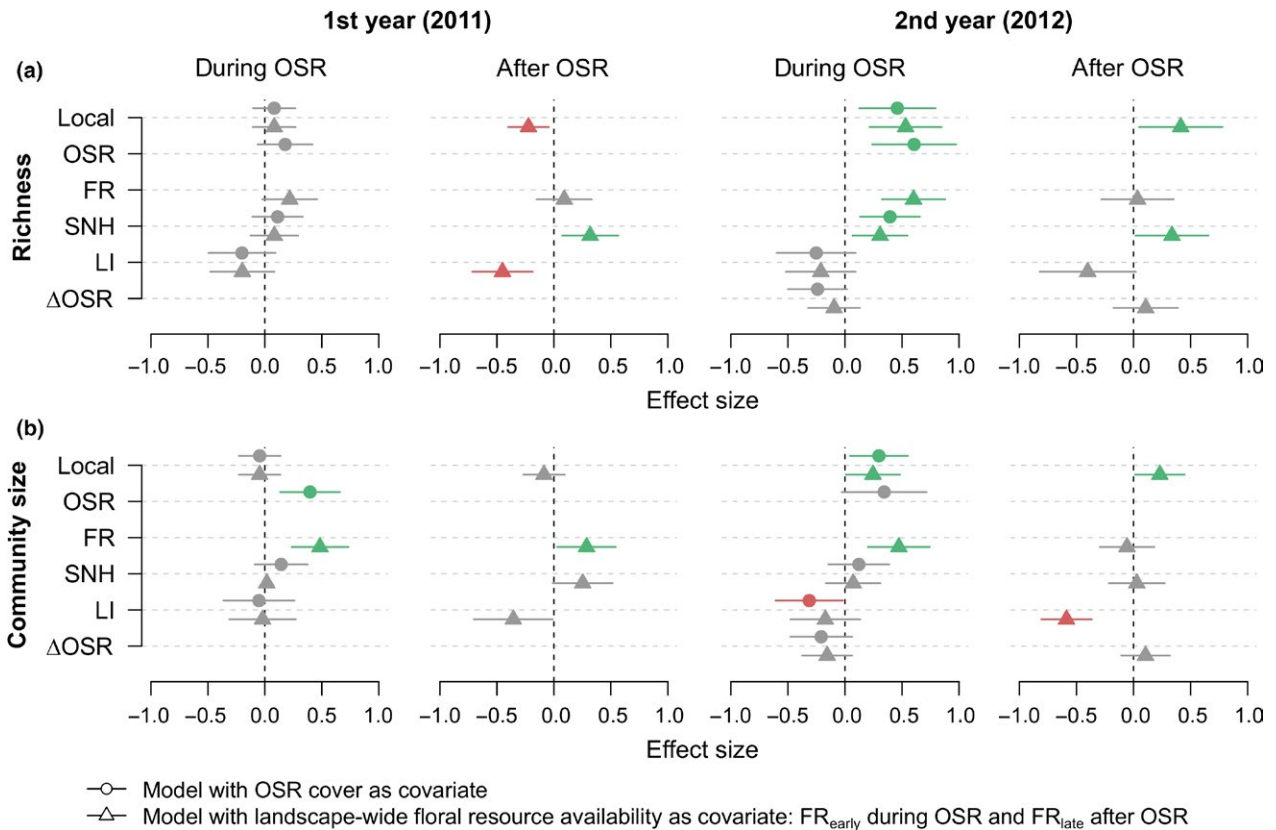


FIGURE 2 Standardized model-averaged effect sizes and 95% confidence intervals for the local and landscape parameters included in the model with $\Delta AICc \leq 7$ explaining (a) species richness and (b) community size (number of brood cells) of trap-nesting bees. Models were carried out separately for each year (2011 and 2012) and season within each year (during OSR flowering and after OSR flowering). Symbols reflect estimates with intervals that include (grey) and do not include 0 (negative in red and positive in green). Where the confidence intervals do not overlap 0 (red or green symbols), a significant effect is indicated. Dots and triangles reflect estimates from models including OSR cover in the landscape or landscape-wide floral resource availability as covariates respectively (see Appendix S2, Table S7). Local and landscape parameter abbreviations: (1) Local, field boundary type (a positive effect size inferred a positive effect of field boundary adjacent to OSR); (2) OSR, proportion of OSR; (3) FR, landscape-wide floral resource availability (FR_{early} during OSR or FR_{late} after OSR); (4) SNH, proportion of semi-natural habitat; (5) LI, land-use intensity (nitrogen input); (6) ΔOSR , interannual change in OSR proportions [Colour figure can be viewed at wileyonlinelibrary.com]

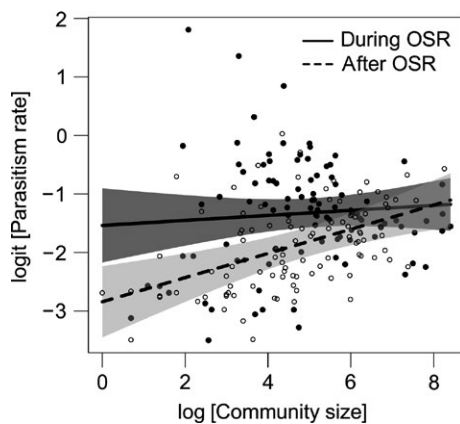


FIGURE 3 Conditional partial regression plot explaining the interactive effects of season (during oilseed rape [OSR] flowering, filled dots and solid line; after OSR flowering, open dots and dashed line) and local bee community size (number of brood cells) on parasitism rate. Plotted points are partial residuals; shaded areas indicate 95% confidence intervals

OSR flowering (15%) and in the second year of the experiment (22%) compared to the first year (18%).

3.5 | The effects of bottom-up and top-down forces on community dynamics

The piecewise SEM was well supported by the data (Fischer's $C = 7.88$, $df = 12$, $p = .795$) and none of the independence claims implied by the model were statistically significant ($p > .05$) suggesting that all the important relationships were specified in the model (Figure 4). We found that the influence of FR availability on community growth rate was mediated by community size ($\beta = 0.41$, standardized coefficient). Community size showed a strong negative effect on community growth rate ($\beta = -0.51$; Figures 4 and 5a). Despite a positive density-dependent relationship between community size and parasitism rates ($\beta = 0.38$), top-down forces had only weak regulating effects on community growth rates (parasitism rate $\beta = -0.15$, Figures 4 and 5b; mortality rate $\beta = -0.05$).

FIGURE 4 Structural equation model (SEM) of bottom-up and top-down control of wild bee community dynamics. Solid colour arrows represent positive paths ($p < .05$, piecewise SEM), dotted colour arrows represent negative paths ($p < .05$, piecewise SEM) and dotted grey arrows non-significant paths ($p > .05$, piecewise SEM). The path coefficients were reported as standardized effect sizes. R^2 (marginal coefficient of determination) are given in the boxes of response variables [Colour figure can be viewed at wileyonlinelibrary.com]

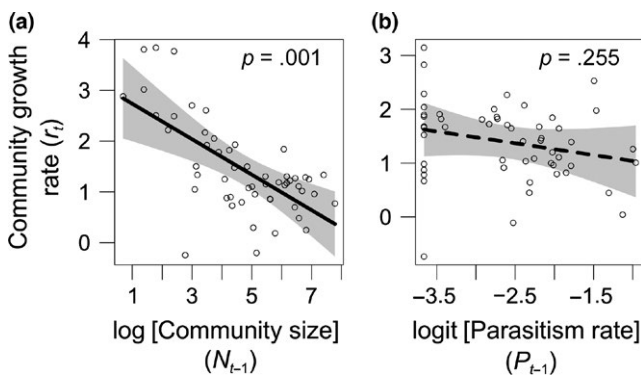
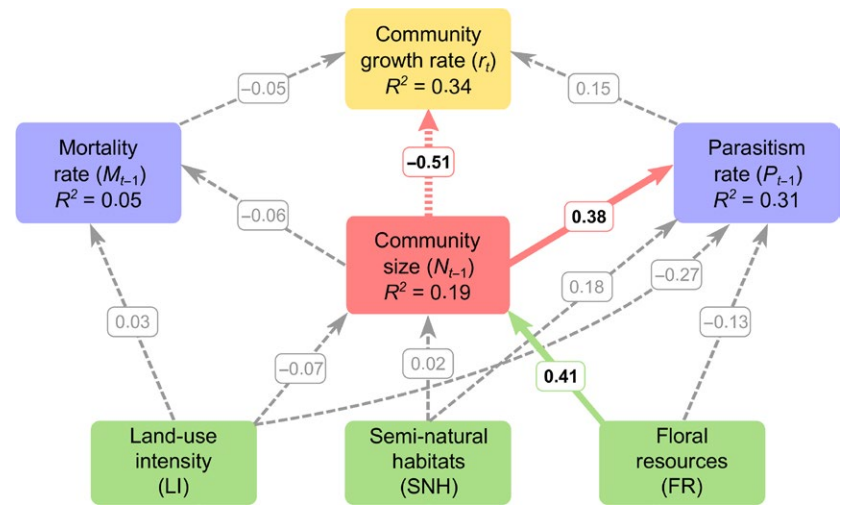


FIGURE 5 Conditional partial regression plot explaining the effect of (a) bee community size (N) and (b) parasitism rate (P) at time $t - 1$ on bee community growth rate [$r_t = \ln(N_t/N_{t-1})$]. Plotted points are partial residuals; shaded areas indicate 95% confidence intervals

4 | DISCUSSION

Our study shows that mainly bottom-up forces drive wild bee populations and communities in agroecosystems (Figure 4). We found, firstly, that trap-nesting bee populations were limited by the availability of nesting sites. Secondly, landscape-level FR availability showed a direct effect on trap-nesting bee population and community dynamics. In spring, we found that abundance (in both years) and species richness (in the second year) of bees significantly increased with an increasing amount of early season landscape-wide FR availability, such as the cultivation of OSR. Later foraging species benefited instead from the availability of late-season alternative flower resources once the mass-flowering had ceased. We also found a positive relationship between parasitism rate and community size but a marginal top-down regulation on bee populations (Figure 4).

4.1 | Bottom-up control

Considering resource-based forces, we found that solitary bees are limited by both nesting and foraging resources (Goulson et al., 2015;

Roulston & Goodell, 2011). Community size showed a strong increase in response to the additional trap-nesting sites. The number of brood cells was three times higher in the second year. At the population level, this increase was even more pronounced for *O. bicornis* (i.e. five times higher). Although the short temporal scale used in this study is not an ideal approach to measuring limitation in nesting resources, our results are in line with a previous study where population dynamics of *O. bicornis* was monitored for a longer period (Steffan-Dewenter & Schiele, 2008), suggesting for a possible nest site limitation effect in above-ground nesting solitary bees. However, it would be interesting to verify the effect of nest site limitation on cavity-nesting bees using a more appropriate experimental design that considers, for example, the immigration and emigration rates of individuals.

Besides nesting sites, wild bee populations were also significantly limited by foraging resources (Figure 4). FRs represent the primary energy source for both adult and larval bees and as such are considered to be a major driver of wild bee populations and community dynamics (Roulston & Goodell, 2011; Scheper et al., 2014). We found strong evidence of a direct effect of FR availability on reproductive output of wild bees, that is, the total abundance of brood cells. Landscapes with large quantities of foraging resources are likely to facilitate brood provisioning (Roulston & Goodell, 2011) and also support larger source populations to colonize the trap nests. However, such positive effects of FR availability on bee populations depend on sufficient availability of nesting resources. Because landscape-wide FR availability was relatively stable among years (see Appendix S2, Tables S10 and S11), the negative relationship between community size and community growth rate provided further evidence for resource limitation. This would suggest that experimentally enhanced populations by adding artificial nesting sites are closer to their carrying capacity limits (Steffan-Dewenter & Schiele, 2008).

Considering the different resources that were available over the season, MFCs benefit mainly *O. bicornis* populations that can utilize this resource. In the first year, during OSR flowering, we found an increase in brood cells with an increasing amount of early season landscape-wide FR availability (i.e. mainly derived from OSR fields). This occurred irrespective of the local field boundary type. In the

second year of the experiment, we found instead that both a local effect of OSR and early season landscape-wide FR availability positively influenced the number of brood cells, as well as bee richness. Interestingly, this benefit was not only detected during the flowering period of OSR but also later in those nests built after flowering of OSR had ceased. This significant post-flowering effect was particularly evident in the second year of the experiment when we found larger and more diversified wild bee communities in trap nests established adjacent to OSR. A possible explanation could be that in landscapes with a larger amount of OSR the activity period of early active species increased. In spring, wild bees benefit from a large amount of nectar and pollen resources, especially early generalist species like *O. bicornis* (Holzschuh et al., 2013; Jauker et al., 2012). In addition, OSR may also attract other species, as confirmed by the positive effect of OSR on bee species richness. As seen above, the availability of FRs was relatively stable among years (see Appendix S2, Tables S10 and S11), we found a negligible influence of crop rotation on trap-nesting bee populations. Further studies are, however, needed to better understand how MFCs impact on bee population dynamics in consecutive years as their cover can vary widely from year to year (Riedinger et al., 2015). After mass-flowering, later foraging species contributed to the colonization of nests. However, the positive relationships with late-season landscape-wide FR availability or SNH and the negative relationships with LI suggest that the availability of alternative resources also limits later foraging females. Importantly, the negative effect of LI on wild bees became more pronounced after mass-flowering, while during flowering, OSR may outweigh the negative effects of LI. This can also be the reason why we did not find a significant causal effect of LI on community size (N_{t-1}) in the SEM. An alternative explanation could be that species emerging later in the season suffer more from LI than early generalist species like *O. bicornis*. Even if LI was measured using nitrogen input, this variable generally correlates with pesticide applications and other farming practices (e.g. Kleijn et al., 2009) that can directly affect bee survival (Goulson et al., 2015).

According to previous studies (Diekötter et al., 2014; Jauker et al., 2012), the richness of bees also increases with an increasing amount of SNH in the landscape. Pollinator communities are often more abundant and diversified in complex landscapes where SNH are better conserved (Kennedy et al., 2013). Wild bees can benefit from the diverse and more permanent foraging as well as nesting and overwintering resources provided by SNH (Roulston & Goodell, 2011). This significant relationship was found both during (only in the second year) and after the mass-flowering (both years). During mass-flowering, this effect plus the additive effect of OSR suggests that the diversified bee communities occurring in complex landscape profit from the resources provided by MFCs (Jauker et al., 2012; Williams & Kremen, 2007). Once the mass-flowering has ceased, the role of SNH may become even more important in providing alternative resources for wild pollinators.

4.2 | Top-down control

Considering our hypothesis related to a possible top-down regulation on bee populations, we found a positive density-dependent parasitism

rate but marginal effects of top-down factors on community growth rate (Figure 4). The relationship between parasitism rate and community size varied over the season. While a positive density-dependent parasitism was observed after mass-flowering, there was only a weak relationship during mass-flowering. During mass-flowering, top-down regulation by natural antagonists may be buffered by the increased number of brood cells with increasing amount of OSR in the landscape (Jauker et al., 2012). When the mass-flowering has ceased, this compensation disappears showing a significant density-dependent relationship. This would suggest a stronger effect of natural antagonists on small populations (Steffan-Dewenter & Schiele, 2008). This mechanism was better elucidated when we verified whether early season landscape-wide FR availability affected the relationship between parasitism rate and community size (see Appendix S2, Figure S3). During mass-flowering, the positive density-dependent parasitism disappeared in landscapes with abundant availability of flower resources. This analysis confirms that MFCs can affect the host-natural enemy interactions by outweighing the effect of top-down regulation by natural antagonists on community size. We also found that parasitism rate increased in the second year of the experiment following the growth of bee populations. Such findings further demonstrate that parasitism rates correlate positively with the local and regional abundance of hosts (Steffan-Dewenter, 2003) and might imply a further accumulation of antagonists (but see Steffan-Dewenter & Schiele, 2008). One limitation of this study is the short temporal scale used to disentangle the effects of top-down forces on trap-nesting bee community dynamics. For instance, predator-prey cycles can often occur over long time-scales and this could explain the marginal top-down regulation found in the study. Nevertheless, no support for top-down regulation by natural antagonists was also reported on a longer time-scale (Steffan-Dewenter & Schiele, 2008). Therefore, these results seem to suggest that, if sufficient food resources are available in the surrounding landscape, the effectiveness of trap nests in boosting populations of trap-nesting bees is hardly affected by natural antagonists.

Contrary to our expectations, local and landscape factors did not show a direct effect on parasitism rate. We only found a positive impact of SNH on parasitism rate after OSR flowering in the first year. In part, this reflects the effect derived from landscape complexity on natural antagonists (Steckel et al., 2014; Steffan-Dewenter, 2003; Steffan-Dewenter & Schiele, 2008) due to a higher availability of hosts and refuge sites (Rand, Tylanakis, & Tschamtkke, 2006). Taken together, these results demonstrate a stronger influence of host densities, rather than those of habitat or landscape parameters, on parasitism rate for this system.

5 | CONCLUSIONS

Our study shows that the addition of nesting resources by the use of trap nests could be a simple pollinator-supporting strategy to accompany the current expansion of MFCs. Adding trap nests designed by varying nesting tube diameter can support a large diversity

of cavity-nesting bees, and not just large populations of early generalist bees. During mass-flowering, we found a marked growth of trap-nesting bee populations with the increasing availability of food resources in the landscape. On average, we observed a twofold increase in community size for each 0.5 percentage increase in early season landscape-wide FR availability. Trap nests benefit not only early generalist bees occurring during OSR flowering but also species with later phenology. Yet, alternative FRs other than OSR are needed to maintain these later populations. This suggests that the conservation or creation of flower-rich habitats is, important for the effectiveness of trap nests over the entire season. The conservation of SNH, which provide suitable nesting sites and ensure larger availability of pollen and nectar resources throughout the entire season, is certainly essential. In simplified landscapes where flower-rich habitats have been lost, an effective solution could instead be the adoption of complementary interventions aiming to enhance FRs. The establishment of wildflower strips (Scheper et al., 2015) or hedgerows (Dainese, Montecchiari, Sitzia, Sigura, & Marini, 2017; Dainese, Riedinger et al., 2017; Morandin & Kremen, 2013) is, for instance, a simple strategy to create high-quality habitats taking little or no land from crop production. These interventions should be targeted at providing continuous bloom over the season for supporting the greatest diversity of wild pollinators (Scheper et al., 2015; Williams et al., 2015; Wood, Holland, & Goulson, 2017). In conclusion, trap nests in combination with other interventions that enhance FRs could be a successful strategy to promote the recruitment of wild pollinators in agroecosystems and potentially to ensure pollination services for insect-pollinated crops. Further studies, incorporating pollen analysis to link specific trap-nesting bees to specific crops, are needed to determine which crops benefit most from this supporting practice in order to optimize alternative pollination systems for crop production.

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AUTHORS' CONTRIBUTIONS

A.H., D.K. and I.S.-D. developed the experimental design; V.R. and J.S. collected data; M.D. analysed the data and wrote the first draft of the manuscript. All authors interpreted results and contributed to writing of the manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.b87h6> (Dainese et al., 2017).

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