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RESEARCH ARTICLE

Landscape-level synergistic and antagonistic effects among conservation measures drive wild bee densities and species richness

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Abstract

1. Pollinators face significant global decline due to agricultural intensification. Local conservation measures (CMs), such as an annual flower field, an organic crop field, or a perennial semi-natural habitat (SNH), are implemented to counteract this negative trend, with variable success, as local CMs may not support ecological processes at spatially larger landscape scales. This can be achieved by planning CMs at the landscape level (landscape CMs), for example multiple fields with a specific CM or combinations of different types of CMs. However, interactive effects between combined landscape CMs may limit their efficacy.
2. It remains unclear whether multiple combined landscape CMs can be more efficient than single landscape CMs (synergistic effect), reduce each other's effectiveness (antagonistic effect) or sum together (additive effect) to promote biodiversity.
3. We assessed the interactive effects of three landscape CMs: organic crops, annual flower fields and perennial SNH, on wild bee species richness and densities at the landscape scale. We surveyed wild bees within multiple transects in 32 landscapes and upscaled bee densities to the landscape scale.
4. We observed a synergistic effect between landscape-scale organic crops and perennial SNH. Specifically, non-*Bombus* wild bee densities increased with higher area shares of organic crops in landscapes with high area shares of perennial SNH. This is likely due to their provision of complementary resources.
5. For bumblebees, we found an additive effect of organic crops and perennial SNH, suggesting that bumblebees benefit from both landscape CMs regardless of their respective availability.
6. However, antagonistic effects were more common, for example between landscape-scale annual flower fields and organic farming, both providing similar floral resources and disturbance regimes. Only in landscapes with a low area of annual flower fields did bee densities and species richness increase with area shares of organic crops.

7. *Synthesis and applications*. Interactive effects of combined landscape CMs determine landscape-scale bee densities and species richness. In particular, functionally different and complementary resources of landscape CMs can create synergistic effects while antagonistic effects occur when similar resources are provided in different landscape CMs. Hence, we recommend that future bee conservation schemes should use smart mixing of landscape CMs, based on judicious evaluation to maximize complementary benefits and reduce redundancy with respect to landscape-scale floral resources and provision of nesting habitat, while considering the habitat requirements of different bee taxonomic groups.

KEYWORDS
agri-environment scheme, annual flower field, diversity, interactive effect, organic agriculture, pollinator decline, semi-natural habitat

1 | INTRODUCTION

Biodiversity decline in agro-ecosystems has been particularly severe in recent decades (Gregory et al., 2019; Warren et al., 2021). In response, agri-environment schemes (AES) have been developed to restore and sustain biodiversity within agricultural landscapes (Batáry et al., 2015; European Commission & Directorate-General for Environment, 2020). AES include various measures, often focussing on increasing floral resources and promoting pollinators in farmland. Indeed, there is strong evidence that flower-rich AES enhance both the abundance and diversity of pollinators (Carvell et al., 2015; Haaland et al., 2011; Scheper et al., 2013, 2015).

The effectiveness of AES on pollinators has mostly been evaluated at the local field scale, typically up to a few hectares in size and focussing on a single AES measure (Batáry et al., 2015). This is problematic, as many pollinator groups may be influenced more by spatially larger landscape processes, usually operating at scales of up to several square kilometres, than by specific local field-site conditions (Bänsch et al., 2021; Concepción & Díaz, 2011). Local field-scale studies may therefore overlook larger scale processes at the landscape level, resulting in dilution or concentration effects of AES in promoting biodiversity. For instance, AES might attract pollinators from neighbouring habitats (Bänsch et al., 2021; Holzschuh et al., 2011), leading to locally high concentrations in AES without increasing populations at the landscape level (Kleijn et al., 2018). Thus, it is essential to assess AES effectiveness at the landscape scale (Beyer et al., 2020; Zingg et al., 2019).

Furthermore, two or more AES implemented at the landscape scale (hereafter landscape conservation measures, landscape CMs) often have interactive effects (Martin et al., 2019; Sirami et al., 2019), though such interdependence among landscape CMs is rarely studied. Recent research found landscape-scale habitats complement each other in promoting bees, but interactive effects were not explicitly investigated (Maurer et al., 2022). Effects of combined landscape CMs on landscape-wide abundance and richness of pollinators and their interactions remain unclear. The following hypothetical scenarios could be anticipated, with far-reaching consequences for optimal landscape-scale design with multiple CMs (Figure 1). First, an additive effect would occur if landscape CMs act independently to promote pollinators, meaning the impact of one landscape CM does not depend on the presence of others; their effects simply add up. However, this scenario is unlikely, as evidence suggests interplay between landscape CMs, indicated by dilution effects among flowering resources in agricultural landscapes (Bänsch et al., 2021; Osterman et al., 2021; Riggi et al., 2024). Second, a synergistic effect would manifest when the combined impact of two landscape CMs is amplified, surpassing their individual effects. This would occur if the landscape CMs provide complementary resources, supporting bee species dependent on both (Beyer et al., 2021). In this case, combining both landscape CMs is recommended. Finally, an antagonistic effect suggests a limit to the benefits derived from one landscape CM when another is present. This scenario would arise if both landscape CMs are functionally similar, implying that the introduction of the second landscape CM may not enhance pollinators further due to the lack of other crucial resources, such as nesting sites.

In this study, we address the research gap regarding interactive effects between combined landscape CMs. In focussing on the landscape scale, we investigate the interactive effects among three landscape CMs that provide floral resources: organic crops, annual flower fields and perennial semi-natural habitats (SNH), assessing their impact on wild bee species richness and density through an empirical approach.

Organic crops are managed without herbicides, insecticides or synthetic fertilizers. They enhance wild bee diversity and abundance (Batáry et al., 2017; Kennedy et al., 2013) and promote bumblebee colony growth and reproduction (Carrié et al., 2018; Rundlöf

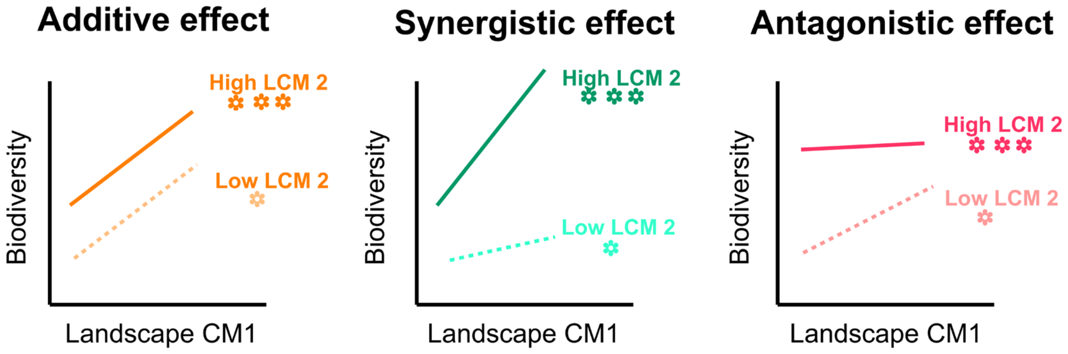

FIGURE 1 Schematic characterization of different interactive effects between landscape conservation measures (landscape CMs/LCM). Additive effects occur when the combined impact of two or more landscape CMs equals the sum of their individual effects on biodiversity metrics, like species richness or population densities. Synergistic effects occur when the combined impact exceeds the sum of individual effects, indicating facilitation. Antagonistic effects emerge when the combined effect is less than the sum, suggesting one factor mitigates the other.

et al., 2008) by providing additional floral resources. However, habitat structures may modulate this impact, suggesting that the value of organic crops as a landscape CM may interact with other landscape CMs.

Annual flower fields are another popular landscape CM specifically designed to promote pollinators in agricultural settings. Annual flower fields are ploughed and replanted each year. Generally, they tend to offer high flower cover (Williams et al., 2015) potentially attracting large numbers of foraging pollinator individuals (Krimmer et al., 2019). How annual flower fields interact with other landscape CMs in promoting wild bees is, however, less well known.

Perennial SNHs in agricultural landscapes encompass a large spectrum of habitat types, including meadows, hedgerows, herbaceous field boundaries and tree groups. These structures play a pivotal role, particularly for wild bees (Steffan-Dewenter et al., 2002). Moreover, local conservation measures are particularly effective in agricultural landscapes with 1%–20% of SNH (‘intermediate landscape-complexity hypothesis’), (Tscharntke et al., 2012), suggesting interactive effects with other landscape CMs.

Here, we test whether there are additive, synergistic or antagonistic effects among landscape CMs in enhancing landscape-scale biodiversity. This approach advances theories in landscape ecology by improving our understanding of landscape dynamics (Tscharntke et al., 2012) and their relevance for new agricultural policies. Considering the EU's goal to increase organic farming to 25% of total agricultural land by 2030, it is crucial to determine where to focus this increase to maximize biodiversity benefits. Specifically, we hypothesized that the landscape-scale density and richness of wild bees increase with higher coverage of three different landscape CMs and that synergistic effects among these landscape CMs enhance bee densities and species richness. Synergistic effects between annual flower fields and organic crops are expected due to their provision of complementary floral resources (Szitár et al., 2022). Moreover, combinations with perennial SNH are also expected to result in synergistic effects because, for example, they provide additional nesting sites (Martínez-Núñez et al., 2022) that are lacking in annual landscape CMs, such as annual flower fields and organic crops.

2 | MATERIALS AND METHODS

2.1 | Study design and landscape composition

The study was conducted in 32 study landscapes, each represented by a circular sector of 1000 m radius (Figure 2). These landscapes were located in the counties of Göttingen, Northeim, Goslar and Werra-Meißner in Lower Saxony and Hesse, Germany. To ensure independence, the minimum distance between landscapes was 2 km (from their outer circumferences) and thus beyond the flight range of the majority of bee species (Greenleaf et al., 2007; Zurbuchen et al., 2010). Landscapes were selected along three independent (orthogonal) gradients of landscape CMs: organic crops [%], annual flower fields [ha] and perennial SNH [%]. See Supporting Information S1 for more details on landscape composition and area shares of landscape CMs (Table S1.1).

2.2 | Bee and flower surveys

In 2021, we surveyed bumblebees (*Bombus* spp.) and non-*Bombus* wild bees using seven standardized transect walks per landscape. The transects, located within the central 500 m radius of each study landscape (Figure 2), were conducted on three sampling runs between late May and August 2021: Run 1 (30.05.-25.06.), Run 2 (26.06.-21.07.), Run 3 (22.07.-07.08.). Each transect was placed in its entirety in the most attractive, flower-rich areas of one of the following habitat types that represented the landscape CMs: organic crop fields (0–4 transects per landscape), annual flower fields (0–4 transects per landscape) and perennial SNH including grassy field margins (3–7 transects per landscape). Each transect covered 200 m^2 (usually 200 × 1 m, with adjustments for smaller field margins, e.g. 100 × 2 m). The transect locations remained consistent unless habitats were mowed or harvested. Observations were randomized between 9 AM and 6 PM on favourable weather days (minimum 15°C, no precipitation, low wind speed). See Supporting Information S1 for more details on transect methodology.

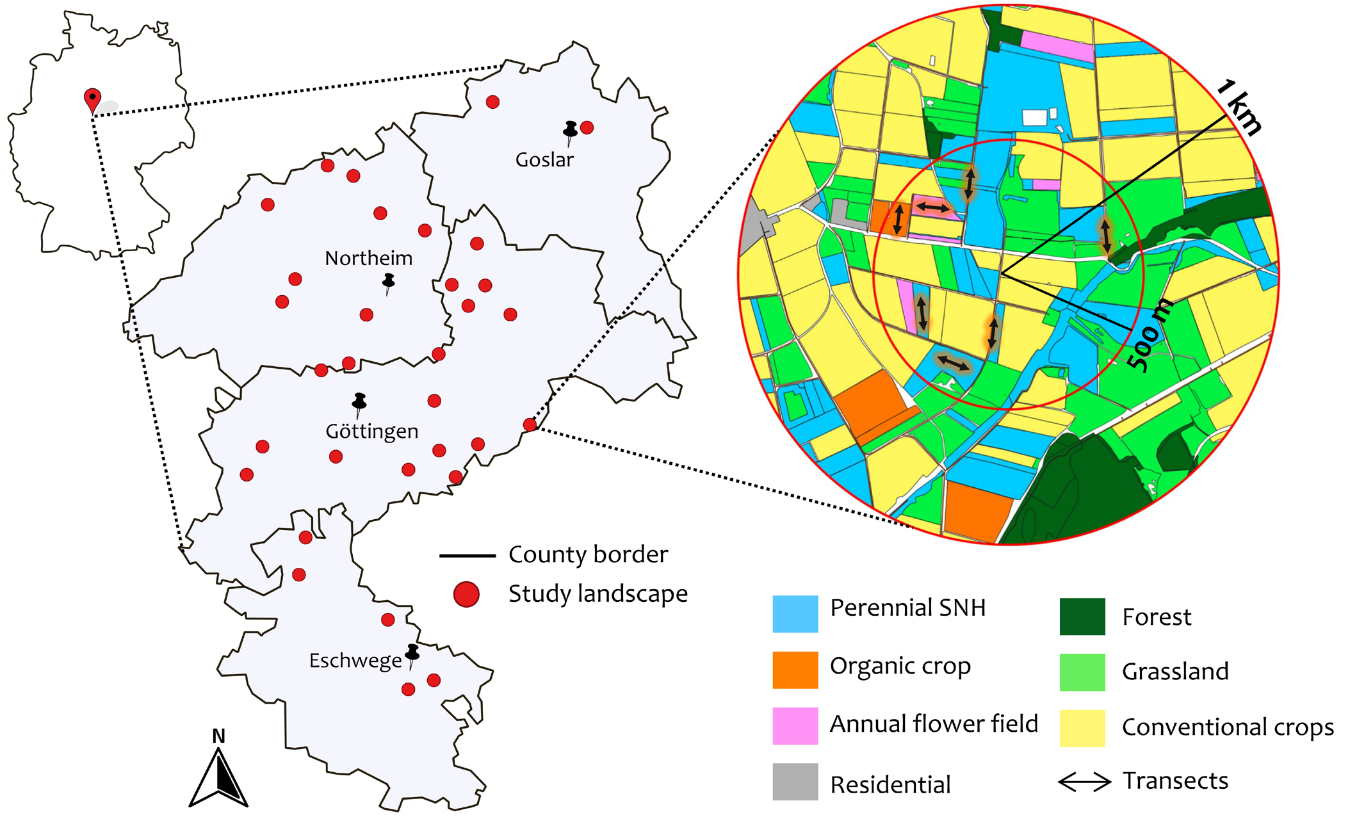

FIGURE 2 Map of the 32 study landscapes located in four counties of southern Lower Saxony and northern Hesse (Germany). Exemplary study landscape of one site with a 1000 m radius. Black arrows within the central sampling area (500 m radius) indicate the seven transect walks, each located in one of the three landscape CMs.

Bee densities were recorded as the number of all flower-visiting bees per transect (bees/200 m^2) within a 10-min observation period, excluding handling time. If species identification was not feasible in the field, specimens were collected for identification. Due to difficulties in distinguishing *Bombus terrestris* and *B. lucorum* in the field, these two cryptic species were aggregated. Bumblebees were identified using standard keys (Amiet et al., 2017; Mauss, 1994), while all other bees were sent to an expert for species identification (Jenny Förster, Dresden). After completing each transect walk, flower cover within the 200-m^2 transect was evaluated by estimating the percentage area covered by open flowers. Flowering plant species were identified using the Flora Incognita identification app (Mäder et al., 2021). Fieldwork was conducted under permits issued by Niedersächsischen Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz (NLWKN) (permit number [H42L 22,202/2021-Czechofsky]) and Werra-Meißner-Kreis, Fachdienst 8.3 Natur- und Landschaftsschutz, Immissionsschutz (permit number [60.23-wmk-04/21–339]), in accordance with all relevant regulations. Our study did not require an ethics approval.

2.3 | Extrapolation to landscape-level bee densities in crop-dominated landscapes

To analyse the landscape-level response of wild bee densities to different landscape CMs in the agricultural matrix, we scaled up bee density to the landscape level (Fijen et al., 2024) and calculated extrapolated bee densities to the total area of all landscape CMs and conventional crops per landscape (***Dj***):

$$D_j = \frac{\sum_{i=1}^{n} B_{ij*} CM_{ij}}{T_j}$$

As a first step, we calculated the average bee density per m^2 (***Bij***) by dividing the average number of bee individuals per transect in landscape CM***i*** in landscape ***j*** by transect area (200 m^2) (Step 1, Supporting Information S2, Figure S2.1). Subsequently, we multiplied the mean bee densities per landscape CM with the corresponding area of each landscape CM***i*** in landscape ***j*** in m^2 within the 1000 m radius (***CM***$_{ij}$), resulting in the mean landscape-level bee abundance per landscape CMs (***Bij * CMij***) (Step 2, Supporting Information S2, Figure S2.1). By summing the mean landscape-level bee abundances in each of the three landscape CMs, we calculated the hypothetical landscape-level bee abundance in all landscape CMs (**∑ (*Bij * CMij*)**) (Step 3, Supporting Information S2, Figure S2.1). To finally standardize bee densities by the area of landscape CM and intensively managed crops in each landscape (***Dj***), we divided the hypothetical landscape CM landscape-level bee abundance of each study landscape by the total area of all landscape CMs and conventional crops in landscape **j** in ha (***Tj***) (excluding grassland) (Step 4, Supporting Information S2, Figure S2.1).

This approach allowed us to extrapolate bee densities across the dominant land-use types of each landscape. *Dj* was calculated for each run and non-*Bombus* and *Bombus* wild bee individuals separately. Moreover, we extrapolated flower cover and computed total wild bee species richness (including bumblebees and non-*Bombus* species) at the landscape-level (see Supporting information S2). We assumed that no bees were present in conventionally managed crops, given that our fieldwork took place after the mass-flowering of oilseed rape. Moreover, a previous investigation in our study region has demonstrated that the number of bees in conventional cereal fields is negligible (Piko et al., 2021). We excluded grasslands, which we did not sample.

2.4 | Statistical analyses

To identify the impacts of the three landscape CMs on the landscape-level density and species richness of wild bees, we fitted generalized linear mixed models using the 'glmmTMB' package (Brooks et al., 2017). We initially ran four general linear mixed models (GLMM) with the response variables landscape-level density of bumblebees, landscape-level density of non-*Bombus* wild bees and landscape-level species richness of all wild bees as well as total flower cover per run. In each GLMM, we included the explanatory variables: run, area shares of perennial SNH, organic crops and annual flower fields, as well as all two-way interactions between the three landscape CMs. Study landscape was included as a random effect. For all models we used a Gaussian error distribution because extrapolation resulted in non-integer values for the landscape-level response variables, that is landscape-level densities of bumblebees, non-*Bombus* wild bees and total flower cover (Supporting Information S3, Table S3.1). This approach also optimized model fit for total species richness.

We log-transformed the response variable for landscape-level density of bumblebees and non-*Bombus* wild bees and sqrt-transformed the response variable for annual flower cover prior to model fitting to improve normality. We checked for multi-collinearity using variance inflation factors (VIFs); all VIFs were below the collinearity threshold (<2.5) in all models (Dormann et al., 2013). Diagnostic plots and tests for overdispersion and zero-inflation were undertaken with the 'DHARMa' package (Hartig, 2022). Predictions and confidence intervals in scatter plots were obtained from the 'ggeffects' package (Lüdecke, 2018). All figures were generated with the 'ggplot2' package (Wickham, 2016).

For visualization of interactive effects, we determined the 1st and 3rd quartile of each landscape CM variable and categorized these into 'low' and 'high', respectively. Additionally, we calculated for each interactive effect the threshold value of a landscape CM above which (synergistic effect), or the threshold value of the landscape CM below which (antagonistic effect), the slope of another interacting landscape CM reached positive values for wild bee abundance, bumble bee abundance and species richness. By using model data, we fixed one landscape CM variable at its average value and calculated the threshold of the other landscape CM at which we found it had a slope of zero.

All statistical analyses were conducted in R version.12.0 (R Core Team, 2021).

3 | RESULTS

Overall, we observed 4527 wild bee individuals; 4,453 individuals were identified to the species level. In total, 69 different wild bee species were recorded (Supporting Information S3, Table S3.2). Bumblebees ($n = 4110$) made up 89% of all observed individuals. All three landscape CMs had a positive effect on landscape-wide flower cover, although this was only marginally significant for annual flower fields (Supporting Information S3, Figure S3.1 and Table S3.3). We found several positive main effects of the three landscape CMs on landscape-level non-*Bombus* wild bee densities, bumblebee densities and species richness (Supporting Information S3, Table S3.4). All interactive effects are presented below. Thresholds for interactive effects are presented in Supporting Information S3, Table S3.5.

3.1 | Effects of landscape CMs on landscape-level non-*Bombus* wild bee densities

Regarding the interactive effects between the landscape CMs, we found an antagonistic effect on the non-*Bombus* wild bee densities of organic crops and annual flower fields; non-*Bombus* wild bee densities increased with the area share of organic crops, but this effect was observed only in landscapes with a low area of annual flower fields ($p < 0.001$, Figure 3a). Additionally, we found a synergistic effect between organic crops and perennial SNH; the density of non-*Bombus* wild bees showed an increase with the area share of organic crops in landscapes with a higher area share of perennial SNH, but not in landscapes with low amounts of perennial SNH ($p = 0.003$, Figure 3b). Furthermore, we found a significant antagonistic effect between annual flower fields and perennial SNH; non-*Bombus* wild bee densities increased with the area of annual flower fields, but this effect was observed only in landscapes with a low amount of perennial SNH ($p = 0.052$, Figure 3c).

3.2 | Effects of landscape CMs on landscape-level bumblebee densities

As with non-*Bombus* wild bee densities, we also found an antagonistic effect between organic crops and annual flower fields on the landscape-level densities of bumblebees; bumblebee densities increased in landscapes with high area shares of organic crops, particularly when the available area of annual flower fields was low in the landscapes ($p = 0.025$, Figure 3d). In contrast to non-*Bombus* wild bees, there was an additive effect between organic

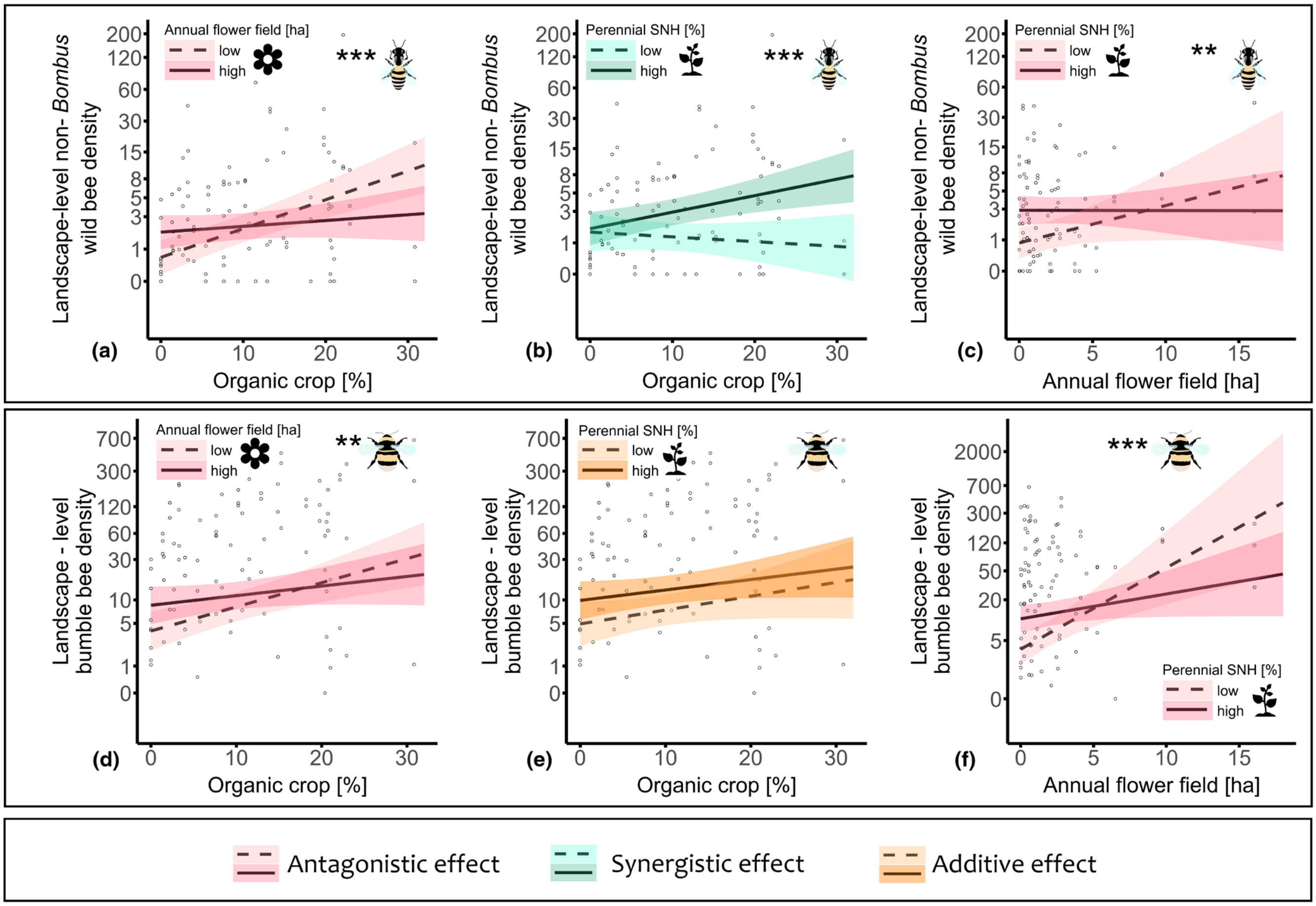

FIGURE 3 Interactive effects of landscape CMs on landscape-level bee densities per ha: Antagonistic effects of area share of organic crop and area of annual flower fields on non-*Bombus* wild bee densities (a) and bumblebee densities (d). Effects of area share of organic crop and area share of perennial semi-natural habitat (SNH) on non-*Bombus* wild bee densities (synergistic effect; interaction significant; (b)) and bumblebee densities (additive effect, interaction not significant; (e)). Effects of the area of annual flower fields and area share of perennial SNH on non-*Bombus* wild bee (antagonistic effect, interaction significant; (c)) and on bumblebee densities (antagonistic effect; interaction significant; (f)). Stars indicate level of significance for the interactive effects (**$p \leq 0.01$; ***$p \leq 0.001$). *Y*-axes are log-transformed for ease of-visualization. (Annual flower field [ha]: Low: 1st Quartile = 0.53, high: 3rd Quartile = 2.69; Perennial SNH [%]: Low: 1st Quartile = 3.29, high: 3rd Quartile = 10.28).

crops and perennial SNH; bumblebee densities increased with area shares of organic crops in landscapes with both high and low area shares of perennial SNH while bumblebee densities were generally higher in landscapes with high shares of perennial SNH, representing an additive effect ($p = 0.714$, Figure 3e). Moreover, we found another antagonistic effect on bumblebee densities for annual flower fields and perennial SNH; with increasing area of annual flower fields, the densities of bumblebees increased when the area share of perennial SNH in the landscapes was low ($p < 0.001$, Figure 3f) but not so when the area share of perennial SNH in these landscapes was high.

3.3 | Effects of landscape CMs on landscape-level species richness of all wild bees

In alignment with the density patterns observed for both landscape-level non-*Bombus* wild bees and bumblebees, the landscape-level species richness of wild bees increased with higher area shares of organic crops, but only when the coverage of annual flower fields within the landscapes was low (antagonistic effect; $p = 0.024$, Figure 4a). There was no interactive effect between organic crops and perennial SNH ($p = 0.467$, Figure 4b), nor between annual flower fields and perennial SNH for landscape-level bee species richness ($p = 0.336$, Figure 4c).

4 | DISCUSSION

Studies have demonstrated positive effects of conservation measures, such as various AES and SNH, on bees (Batáry et al., 2017; Kennedy et al., 2013; Martínez-Núñez et al., 2022; Scheper et al., 2013). However, the interplay of multiple, combined conservation measures and their effects on landscape-level pollinator densities and species richness remains largely unknown. To address this gap, we assessed landscape-scale densities of wild bee

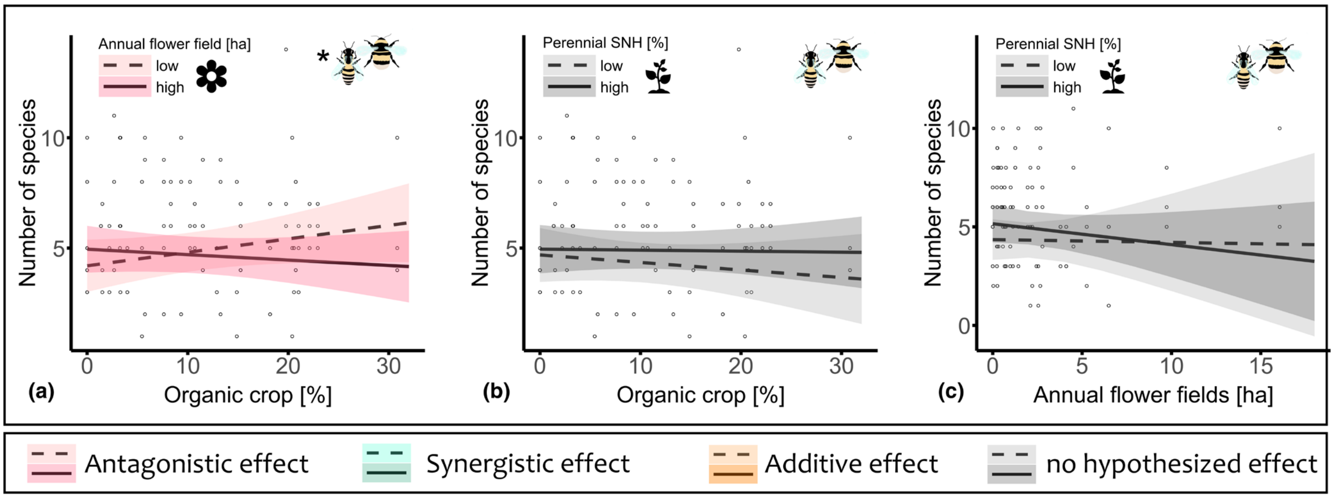

FIGURE 4 Relationships between organic crop area share and annual flower field area [ha] (a), organic crop area share and perennial SNH area share (b) and annual flower field area and perennial SNH area share (c) on wild bee total species richness (*Bombus* and non-*Bombus* analysed together). The star indicates significance of the interactive effect between cover of organic crop and annual flower field area (*0.01–0.05). (Annual flower field: Low: 1st Quartile = 0.53 [ha], high: 3rd Quartile = 2.69 [ha]).

species and interactive effects among landscape CMs in promoting wild bees. We expected synergistic effects between the three landscape CMs: organic crops, annual flower fields and perennial SNH, due to the provision of complementary resources (Szitár et al., 2022). Our comprehensive landscape approach demonstrates that interactive effects between different landscape CMs are crucial for shaping landscape-scale bee densities and species richness. We found support for one synergistic effect, indicating high benefits of combined landscape CMs. However, antagonistic effects between landscape CMs were the most frequent interaction, suggesting that combining different landscape CMs, each with high area shares, often reduces their effectiveness to promote bees, especially if both landscape CMs provide functionally similar resources.

4.1 | Antagonistic effects

First, we found evidence for an antagonistic effect between the area share of organic crops and the area of annual flower fields. Increased area shares of organic crops positively affected landscape-level densities of bumblebees and non-*Bombus* wild bees, but this effect was stronger in landscapes with low areas of annual flower fields.

Organic farming fosters a greater abundance of native wild plants compared to conventional management, making it a beneficial provider of diverse, high-quality nectar and pollen resources for pollinators (Carrié et al., 2018; Geppert et al., 2020; Szitár et al., 2022). Similarly, numerous studies have shown positive local effects of annual flower fields on bees, providing ample and highly attractive flowering resources (Piko et al., 2021; Szitár et al., 2022). It is therefore surprising that high amounts of annual flower fields diminish the positive effect of organic farming on landscape-scale bee abundance and species richness. This may occur because the abundant floral resources from annual flower fields render additional organic farming ineffective. In particular, annual flower fields and organic crops provide functionally similar resources, as both landscape CMs are annual habitats with regular soil disturbance that inhibits the establishment of perennial plant species and destroys nesting sites for bees. Indeed, two of the five most abundant flowering plant species per landscape CM were shared between annual flower fields and organic crops (*Cirsium arvense* and *Matricaria chamomilla*, Supporting Information S3, Figure S3.2). The functional similarity and lack of nesting resources in both landscape CMs probably drive the lower effectiveness of organic crops in landscapes with high amounts of annual flower fields.

We also found this antagonistic effect for landscape-level bee species richness, which increased with the area shares of organic crops in landscapes with a low annual flower field area. Notably, in landscapes with a high area of annual flower fields, species richness declined slightly with increasing shares of organic crops. This may be due to bees' foraging preferences and temporal variation of resource availability, as bees can be attracted from one flowering habitat to another (Bänsch et al., 2021; Osterman et al., 2021). If organic crops have low area shares, more species may be attracted to smaller habitats like flower fields and grassy field margins. In contrast, in landscapes with high shares of organic crops, bee species may be more dispersed, as abundant floral resources are distributed over a larger area (Batáry & Tscharntke, 2022), which reduces local bee densities (dilution effect, Bänsch et al., 2021; Osterman et al., 2021; Riggi et al., 2024). We found this effect for bee species richness but not bee densities, probably because our extrapolation approach already corrected for the dilution effect. Yet, we could not upscale bee species richness as it remains unclear how it increases with the area of the different landscape CMs.

Additionally, we found antagonistic effects between annual flower fields and perennial SNH, both for bumblebee and non-*Bombus* wild bee densities. Higher shares of annual flower fields positively influenced landscape-level bumblebee densities, particularly in landscapes with low area shares of perennial SNH. Previous studies showed that the effectiveness of AESs such as annual flower fields often depends on existing landscape complexity, for example area shares of SNH, which mediate their attractiveness (Scheper et al., 2013; Tscharntke et al., 2012). Our results confirm these findings, showing that annual flower fields are more effective if implemented in simple landscapes with low shares of perennial SNH. The abundant and consistent source of floral resources offered by annual flower fields therefore seems to be more attractive if other flower-rich habitats are lacking in the landscape (intermediate landscape hypothesis; Tscharntke et al., 2012). Whereas previous studies focussed on the local scale, our study demonstrates that this mechanism holds true when analysing extrapolated bumblebee densities at the landscape scale.

4.2 | Synergistic effects

In addition to antagonistic effects, we also found support for a synergistic effect between different landscape CMs, as expected in our initial hypotheses. An increase in the area shares of organic crops enhanced landscape-level non-*Bombus* wild bee densities, particularly in landscapes with high area shares of perennial SNH. This indicates that the combination of these two landscape CMs is particularly beneficial for non-*Bombus* wild bees. The reason could be that organic crops and perennial SNH provide functionally different and complementary resources for this bee group, amplifying each other and therefore surpassing the sum of their individual effects (Beyer et al., 2021; Junker et al., 2015). Perennial SNH provides not only spatial but also temporal heterogeneity of crucial resources for pollinators, including nesting sites and floral resources (Martínez-Núñez et al., 2022). In particular, nesting sites in perennial SNH might be responsible for the complementary and synergistic effect, as these are lacking in organic crop fields. Moreover, our data show that the dominant flowering plant species in perennial SNH differ from those in organic crops and annual flower fields. For example, legumes such as *Trifolium pratense*, *Trifolium repens* and *Lathyrus pratensis* play a more important role in perennial SNH and might attract different bee species, especially bumblebees (Beyer et al., 2021), compared to the dominant flowering plants in organic crops. Additionally, perennial SNH, including grassy margins, might facilitate pollinator movement across landscapes (Hass et al., 2018), improving access to floral resources in organic fields and further promoting their synergistic effect.

4.3 | Additive effects

In contrast to non-*Bombus* bee density, we found an additive effect between organic crops and perennial SNH on bumblebee densities; independent of each other, both landscape CMs enhanced the landscape-level densities of bumblebees. This suggests that high area shares of organic crops are beneficial for bumblebees, irrespective of the existing perennial SNH. One possible explanation for the divergent responses of the different bee groups is that many common bumblebees are less dependent on specific nesting sites than many non-*Bombus* wild bee species (Westrich, 2019). Common bumblebee species are adaptable and can nest in field margins, demonstrating lower specificity in their nesting requirements (Westrich, 2019).

4.4 | Landscape scale sampling and extrapolation

While floral resources have been extrapolated to larger spatial scales (Bishop et al., 2024; Timberlake et al., 2019), this method has rarely been applied to bee abundances (Batáry & Tscharntke, 2022). This approach allowed us to estimate landscape-scale bee densities considering the attraction of bees from one habitat to another as well as differences between landscape CMs in local flower density and area share per landscape (Batáry & Tscharntke, 2022). However, our estimates include uncertainties. We extrapolated bee densities based on pooled data from different perennial SNH, including hedgerows, calcareous grasslands, field margins and fallows, to capture the variability of perennial SNH across each landscape. Moreover, we assumed that bees do not inhabit conventional crops after oilseed rape mass-flowering, which, though likely, may not always be the case (Piko et al., 2021). Additionally, it would be beneficial for future studies to include additional years in the analysis to assess the consistency of results over time (Karp et al., 2018; Zou et al., 2020). Moreover, even with high spatial and temporal sampling effort, transect walks only capture a small fraction of the pollinator community. Extrapolation for organic crops could be biased by inconsistencies in the area shares of different crop species. We minimized this potential bias by sampling bees in different crop species when more than one was present in the landscape. Furthermore, the interactive effects between landscape variables might depend on region-specific characteristics. Therefore, further studies are needed to generalize our findings across a wider geographic area. Despite these possible limitations, we believe extrapolation gives a more complete picture of landscape-level processes determining bee density patterns than local estimates biased by the local flower cover and surrounding landscape composition (Batáry & Tscharntke, 2022; Gillespie et al., 2024).

4.5 | Landscape management recommendations

We show that all three landscape CMs, organic crops, annual flower fields and perennial SNH, can enhance floral resource provisions at the landscape scale, with positive effects on wild bee densities and species richness. Moreover, we demonstrate that considering interactive effects between landscape CMs is crucial for effective wild bee management. We found strong evidence for saturation effects between functionally similar landscape CMs such as organic farming and annual flower fields. This indicates that organic farming should be primarily introduced in landscapes characterized by low amounts of annual flower fields to maximize its effectiveness in enhancing bees, particularly in cases where additional nesting sites are not provided. However, while landscape management might optimize conservation efficiency for mobile species such as wild bees, there can also be local benefits, for example of organic farming for plants (Tuck et al., 2014). Therefore, our results are most useful when the potential area of landscape CMs is limited and allocation decisions are required.

Moreover, we found a synergistic effect between organic crops and perennial SNH for non-*Bombus* wild bees, probably due to the provision of functionally complementary resources such as different flowering plant species and nesting sites in SNH, which are lacking in organic crops. Recently, the promotion of organic farming for biodiversity conservation has been questioned, arguing that it leads to rather low biodiversity benefits (Tscharntke et al., 2021). However, our findings demonstrate that organic crops can be an important component of diversified farming systems that strongly promote non-*Bombus* wild bees, particularly if combined with other measures such as perennial SNH.

Our approach also allows calculating thresholds for the combination of different landscape CMs (Supporting Information S3, Table S3.5). For example, organic crops show a positive effect on the landscape-level species richness of wild bees at annual flower field cover below 2 ha in the landscape. Moreover, the threshold for the synergetic effect indicates that at least 4.85% of perennial SNH should be present in a landscape for organic crops to have a positive impact on non-*Bombus* wild bee density (Supporting Information S3, Table S3.5). These thresholds can be used to develop guidelines for bee conservation in agricultural landscapes.

5 | CONCLUSIONS

Overall, our study shows that landscape-scale processes are crucial for shaping bee densities and that they require sampling across different habitats per landscape (Beyer et al., 2021; Maurer et al., 2022) as well as the use of extrapolation tools. Our study goes beyond existing knowledge on landscape-scale resources for bees (Bishop et al., 2024; Scheper et al., 2015; Timberlake et al., 2019) by highlighting the importance of interactive effects between different landscape CMs for biodiversity. We therefore expand landscape ecological theory (Tscharntke et al., 2012) by demonstrating saturation and synergistic effects based on the functional differences of resource provision in combined landscape CMs. Our findings suggest that introducing a higher area share of a landscape CM is not always more effective in simple landscapes with low amounts of other landscape CMs, as suggested by the intermediate landscape complexity hypothesis (Scheper et al., 2013; Tscharntke et al., 2012). However, smart combinations of landscape CMs can increase bee densities through synergistic effects, which can be further enhanced by cultivating functionally diverse flowering crops and concurrently underpinning pollination services (Fijen et al., 2025). Our findings can thereby guide future collaborative schemes (Petit & Landis, 2023) to optimize landscape-scale resources and their interactive effects, contributing to more effective conservation measures that promote sustainable agro-ecosystems and address the ongoing decline of pollinators in farmland.

AUTHOR CONTRIBUTIONS

Annika L. Hass, Catrin Westphal and Robert J. Paxton conceived and designed the study; Annika L. Hass developed the theory on the hypothesized effects; Kathrin Czechofsky collected the bee data; Kathrin Czechofsky collected the landscape data with the advice of Annika L. Hass; Kathrin Czechofsky and Annika L. Hass analysed the data; Kathrin Czechofsky wrote the first draft of the manuscript with contributions from Annika L. Hass and Catrin Westphal. All authors provided comments on previous drafts of the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors report no conflict of interests.

DATA AVAILABILITY STATEMENT

Data and code are available from the Zenodo Digital Repository https://doi.org/10.5281/zenodo.13347297 (Czechofsky et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. Additional information on methods.

Supporting Information S2. Additional information on material and methods.

Supporting Information S3. Additional supporting results.

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