





## RESEARCH ARTICLE

# Organic farming and annual flower strips reduce parasite prevalence in honeybees and boost colony growth in agricultural landscapes

Patrycja Pluta<sup>1</sup>  | Kathrin Czechofsky<sup>2</sup> | Annika Hass<sup>2</sup> | Lena Frank<sup>3</sup> | Ansgar Westerhoff<sup>3</sup> | Heiner Klingenberg<sup>3</sup> | Panagiotis Theodorou<sup>1,4</sup>  | Catrin Westphal<sup>2</sup>  | Robert J. Paxton<sup>1,4</sup> 

<sup>1</sup>General Zoology, Institute for Biology, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany

<sup>2</sup>Functional Agrobiodiversity, Department of Crop Sciences, University of Göttingen, Göttingen, Germany

<sup>3</sup>bienenprojekte.de UG, Göttingen, Germany

<sup>4</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

**Correspondence**

Patrycja Pluta

Email: [patrycja.pluta@gmail.com](mailto:patrycja.pluta@gmail.com)

**Funding information**

Federal Ministry of Food and Agriculture (BMEL), Grant/Award Number: 2819OE115 and 2819OE156; Deutsche Forschungsgemeinschaft, Grant/Award Number: 405945293 and 493487387

**Handling Editor:** Tien Ming Lee

**Abstract**

1. Despite the major role that insect pollinators play in crop production, agricultural intensification drives them into decline. Various conservation measures have been developed to mitigate the negative effects of agriculture on insect pollinators.
2. In a novel comparison of the efficacy of three conservation measures on honeybee colony growth, we monitored experimental honeybee colonies in 16 landscapes that comprised orthogonal gradients of organic agriculture, annual flower strips and perennial semi-natural habitats. Using structural equation modelling, we assessed the effects of conservation measures on the prevalence of 11 parasites, *Varroa destructor* loads and their collective impact on colony growth.
3. Increasing area coverage of perennial semi-natural habitat related to higher *V. destructor* load and indirectly to lower colony growth.
4. Increasing area of annual flower strips was associated with lower *V. destructor* load and indirectly with higher colony growth.
5. Increasing area of organic farming related to lower parasite richness and also directly to improved colony growth.
6. *Synthesis and applications:* Landscape features can affect pollinators directly through the provision of food resources and indirectly through modulation of parasite prevalence. To promote honeybee colony health in agro-ecosystems, our results suggest that organic agriculture and annual flower strips should be prioritized conservation measures. Landscape management should consider the merits and demerits of different measures to sustain healthy populations of pollinators in agro-ecosystems.

**KEYWORDS**

annual flower strip, honeybee, landscape, organic farming, parasite, pathogen, semi-natural habitat

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). *Journal of Applied Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

## 1 | INTRODUCTION

Pollinators contribute significantly to agricultural production (Klein et al., 2007; Potts et al., 2016), with the farmed area devoted to pollinator-dependent crops rising disproportionately faster than pollinator supply (Aizen & Harder, 2009). Many wild pollinators face declines due to agricultural intensification (Dicks et al., 2021); thus, managed pollinators, especially honeybees (*Apis mellifera*), are often the principal means of providing adequate pollination services to farms (Osterman, Aizen, et al., 2021). However, managed honeybees also suffer losses due to lack of floral resources, increased parasitism and pesticide (mis-)use (Dicks et al., 2021). Agri-environment schemes (AES), such as organic farming and annual flower strips, as well as the conservation of semi-natural habitats (SNH) aim to mitigate the impacts of agricultural intensification on insect pollinators (Batáry et al., 2015; European Commission, 2018) and can also be effective modulators of parasite prevalence in wild pollinators (Manley et al., 2023).

It is often unclear whether and how such conservation measures can improve the health and performance of insect pollinators (Marselle et al., 2021; Tschardt et al., 2021). Direct benefits of these measures include improved nutritional resources (Geppert et al., 2020; Jachuta et al., 2022), which are crucial for the growth and survival of honeybee colonies (Wintermantel et al., 2019). Conservation measures can also benefit pollinators through restricted use of pesticides that could otherwise increase mortality, compromise the immune system and reduce foraging efficiency (Di Prisco et al., 2013).

Conservation measures can also affect honeybee colonies indirectly through better resource provisioning; well-nourished bees are more tolerant not only of pesticides (Barascou et al., 2021) but also of their parasites (Frizzera et al., 2022; Manley et al., 2017). High availability of flowers can lower the visitation rate per flower (Holzschuh et al., 2011) or increase insect richness in the area, diminishing contact among susceptible individuals and subsequent parasite transmission (Graystock et al., 2020). On the other hand, flowers can attract bees, increasing exposure to parasites and leading to higher parasite prevalence (Cohen et al., 2021; Piot et al., 2019). The overall long-term impact of conservation measures on pollinators, especially on honeybees that live in a perennial colony, remains an open question.

Parasitism is considered a major cause of poor health of managed pollinators, undermining colony growth and increasing mortality (Dicks et al., 2021; Pluta & Paxton, 2022). A notorious honeybee pest, the exotic *Varroa destructor* (*V. destructor*) mite, is widely regarded as one of the main causes of high honeybee colony losses (Rosenkranz et al., 2010) due to its ability to vector multiple harmful viruses (Möckel et al., 2011), most notably deformed wing virus (DWV; Di Prisco et al., 2016; Natsopoulou et al., 2017). Other known honeybee parasites, such as black queen cell virus (BQCV), Microsporidia (*Nosema ceranae*) and Protozoa (*Crithidia mellificae*), have also been linked to colony losses (Evans & Schwarz, 2011; Natsopoulou et al., 2015). However, there is a lack of knowledge of

how conservation measures can modulate honeybee parasitism and ensuing colony health.

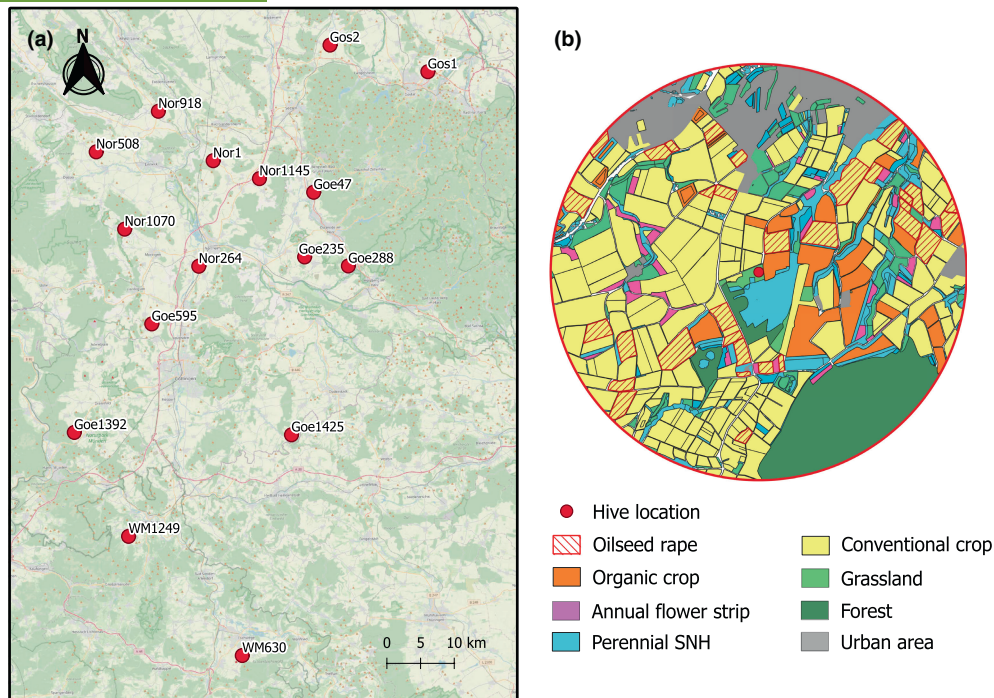
To fill this knowledge gap, we evaluated the effects of three conservation measures at the landscape scale on honeybee colony growth in the agricultural environment. We introduced standardized honeybee colonies to 16 agricultural landscapes that varied in the proportion of surrounding (a) organic agriculture, (b) annual flower strips and (c) perennial SNH. We then monitored the number of *V. destructor* and the prevalence of 11 parasites within colonies, which we relate to colony growth and ensuing overwinter survival, with the aim of answering three questions: (i) Do organic farming, annual flower strips and perennial SNH diminish parasite prevalence in honeybee colonies? (ii) Do these three measures improve honeybee colony growth and (iii) do their effects ultimately improve the survival of honeybee colonies? We hypothesized that conservation measures directly benefit colony growth through their greater supply of food resources and reduced use of pesticides, and indirectly through better nutrition and a dilution of parasites across the abundance of flowers that they offer.

## 2 | MATERIALS AND METHODS

### 2.1 | Study landscapes and landscape characterization

We selected 16 landscapes in southern Lower Saxony and northern Hesse, Germany, representing three independent gradients of the percentage of organic crop fields, annual flower strips and fields, and perennial SNH (Figure 1; Table S1; Appendix S1). We focused on extensively managed and restored SNH, thus excluded forests and grasslands. We distinguished between perennial flower strips and annual flower strips because the former are often scarce in flowers and do not provide as many food resources or attract as many pollinators as annual flower areas (Krimmer et al., 2019; Piko et al., 2021). As mass-flowering crops have been reported to increase the prevalence of parasites in pollinators (Cohen et al., 2021) yet represent an important food resource for them (Bänsch, Tschardt, Wünschiers, et al., 2020; Westphal et al., 2009), we calculated the percentage of oilseed rape field area (*Brassica napus*, OSR), the most abundant mass-flowering crop, and the percentage of organic mass-flowering crops (*Vicia faba* and *Trifolium campestre*) in our landscapes.

Land-use maps were created in Quantum GIS (QGIS Development Team, 2018) at seven radii (from 500m to 2000m in 250m increments). Field shapes and crop types for Lower Saxony in 2021 were downloaded from the 'Servicezentrum Landentwicklung und Agrarförderung' (LEA-Portal: <https://sla.niedersachsen.de/landentwicklung/LEA>). We obtained data on the AES from Integrated Administration and Control System (IACS) and mapped missing SNH manually (Table S1). We validated the geospatial data in each study landscape by ground-truthing. We also estimated flower cover for each conservation measure across all landscapes (Appendix S1).



**FIGURE 1** (a) Map of the 16 experimental landscapes located in the federal states of Lower Saxony and Hesse (Germany). (b) Study landscape WM630 and its landscape composition within a 2000 m radius around the four experimental hives that were located in the centre of the landscape. This map is licenced under the Open Data Commons Open Database Licence (ODbL) by the OpenStreetMap Foundation (OSMF) (<https://www.openstreetmap.org/copyright>; OpenStreetMap contributions).

## 2.2 | Honeybee colony monitoring

In May 2021, we placed four colonies of honeybees (*Apis mellifera carnica*) in the centre of each landscape (64 hives; Table S1). Colonies were standardized to four frames (fully occupied by workers), including two brood frames per colony. Adult workers and brood frames were mixed and randomly assigned to the hives from 100 source colonies. Colony growth (absolute number of honeybees; Imdorf et al., 1987) and the monthly 'bottom board' count of *V. destructor* fall were assessed each month from May to December 2021. The overwinter survival of colonies was assessed in March 2022 (detailed description in Appendix S1). We acquired permission to conduct the fieldwork from the landowners. Our study did not require an ethical approval.

## 2.3 | Parasite sampling and screening

To screen experimental colonies for parasites, bulk samples of worker honeybees (30 individuals per colony) from the inside of two randomly chosen colonies per landscape were collected in July and from the same colonies at the end of August/beginning of September. Honeybees were collected on dry ice in the field and transferred to  $-80^{\circ}\text{C}$  before further processing.

Detailed molecular methods are provided in Appendix S1. Primer sequences and PCR/qPCR protocols are given in Tables S2 and S3. Briefly, we extracted RNA from the samples with RNeasy Mini Kit (Qiagen, Hilden, Germany) and synthesized cDNA using M-MLV

Reverse Transcriptase (Promega, Mannheim, Germany). We used cDNA in qPCRs to screen for the presence of seven viral targets (DWV-A, DWV-B, BQCV, ABPV, SBV, CBPV and SBPV) and residual DNA from RNA extracts in PCRs to screen for four eukaryotic targets (Trypanosomes, Neogregarines, *N. ceranae* and *N. bombi*).

## 2.4 | Statistical analysis

### 2.4.1 | Response variables

We used colony assessment data (mite fall, parasite presence and colony growth) from August 2021 (second sampling for parasites), as it expressed the peak strength (Appendix S1) of the colonies and was undertaken during the last assessment of natural mite fall. This allowed experimental colonies to be maximally exposed to their respective landscapes and for collection of colony data before varroa control treatment. Colony growth was expressed as the absolute number of bees. The varroa mite fall per 100 bees per 30 days was calculated as a measure of *V. destructor* infestation intensity. The presence of other parasites was denoted as a binary variable that we used to generate parasite richness (sum of parasite species found in each colony), as it may reflect the vulnerability of a colony to an infection and the immunological cost that may affect other colony parameters such as colony growth. We did not use the data on flower cover in our analysis due to missing information from multiple landscapes (Appendix S1).

## 2.4.2 | Multi-scale modelling approach

Honeybee foraging range varies greatly (Bänsch, Tschardtke, Ratnieks, et al., 2020; Winston, 1987), and bees prioritize attractive over poorly rewarding resources (Cohen et al., 2021; Osterman, Theodorou, et al., 2021). Since our landscape variables can vary in attractiveness and quality, so can the scale at which each of them affects colony growth. Choosing an appropriate scale for a landscape study is thus difficult as foraging distances are rarely explicitly measured. An arbitrary scale might miss important relationships if the actual foraging distance differed from the chosen one (Martin, 2018). To address the issue, we used a multi-scale modelling approach (Martin & Fahrig, 2012; McGarigal et al., 2016). We selected the best spatial scale for each landscape-level variable based on its highest absolute Pearson correlation coefficient with the response variable, as proposed by Holland et al. (2004). In our case, the response variable was the absolute number of bees per colony in August. This method determines the radius at which the relationship between the response and a given predictor is the strongest, elucidating the effects of each landscape variable at a scale that can be biologically most relevant (Bartholomé et al., 2020; Boscolo & Metzger, 2009); it is robust and can estimate potential relationships more efficiently than single-scale models (Martin & Fahrig, 2012).

## 2.4.3 | Statistical models

All statistical analyses were performed in RStudio (v. 2022.07.1) using R (v. 4.2.2) (R Core Team, 2022). All models were fitted using the 'lme4' package (Bates et al., 2015). We used linear mixed models (LMM) and generalized linear mixed models (GLMM) to explain: mite fall with gamma distribution (varroa model), log-transformed parasite richness with Gaussian distribution (parasite richness model), the absolute number of bees with negative binomial distribution (colony growth model) and overwinter survival with binomial distribution (survival model; Table S4). All models included landscape variables as predictors. Additionally, the parasite richness model included mite fall as a predictor. The colony growth and survival models included both mite fall and parasite richness as predictors. We examined the potential outlier in the colony growth model (Appendix S1, Table S5).

To avoid overfitting, we used the Akaike information criterion corrected for small sample size (AICc; 'MuMin' package, Bartoń, 2020) and chose only the landscape predictors in the models with the lowest AICc scores (Table S4). Parasite richness and varroa fall were always included as predictors in respective models to account for their potential confounding effect.

We performed an additional analysis to see if the effect of organic farming is driven by mass-flowering crops (Appendix S1; Table S6). We also investigated the relationship between the landscape variables and the presence of each parasite species in a series of GLMMs (Appendix S1).

Each model included 'landscape\_ID' as a random factor. The predictor variables were standardized to a mean of 0 and a standard

deviation of 1. We checked residuals, dispersion, variance inflation factors and Moran's *I* of each model using the 'DHARMA' package (Hartig, 2020). The significance of parameters was assessed using Type III Wald tests (package 'car', Fox et al., 2022). We calculated estimated marginal means using 'emmeans' (Lenth, 2022).

## 2.4.4 | Structural equation modelling

To evaluate possible direct and indirect relationships between conservation measures, mites, parasites and colony growth, we used piecewise structural equation modelling (SEM, package 'piecewiseSEM', Lefcheck, 2016). We used the best models that describe varroa mite fall, parasite richness and colony growth to construct the SEM. Hypothesized and non-hypothesized paths were assessed with the d-separation test while the fit of the SEM was evaluated using Fisher's *C* statistic. We omitted the colony survival model in our SEM because the results carried very little information and strained the capacity of the SEM with additional pathways. Estimates were scale standardized to produce total effects (TE), expressed as a product of the indirect effects summed with the direct effects (Lefcheck, 2016) on a standard deviation scale.

## 3 | RESULTS

### 3.1 | Scale-dependency of conservation measures effects

The spatial scales at which honeybee colony growth was best associated with conservation measures were as follows: 500m for OSR and annual flower strips, 750m for SNH and 2000m for organic farming (Table S7). Although different scales resulted in slightly different *p*-values favouring the scales chosen by multi-scale approach, there were no qualitative changes in the results across scales (Appendix S2), suggesting that our landscape variables affected colony growth across different spatial scales in similar ways.

### 3.2 | Effect of conservation measures on *V. destructor* infestation intensity and parasite prevalence in honeybees

The mean monthly varroa fall per 100 bees ranged from 0 to 1 ( $0 \pm 0.01$  in July,  $0.23 \pm 0.20$  in August; mean  $\pm$  SD). On average, a colony was infected with  $1.7 \pm 1.16$  and  $2.4 \pm 0.93$  viral or eukaryotic parasites in July and August, respectively. Overall, parasite prevalence was higher in August (July—84.4% and August—100% of colonies infected with at least one parasite). DWV-B, BQCV and trypanosomes increased in prevalence from July to August from 21% to 65%, from 71% to 81% and from 56% to 78%, respectively. Meanwhile, DWV-A and ABPV maintained the same prevalence in both months (3%). SBV and neogregarines decreased between the

2 months (from 15% to 6%, and from 6% to 3%, respectively). CBPV, SBPV, *N. ceranae* and *N. bombi* were not detected in any of the colonies (Figure 2). For all further statistical analyses, we used August data because the mite fall was higher and colonies were exposed longer to a landscape.

The intensity of *V. destructor* infestation (varroa model) was explained by a negative relationship with the percentage of annual flower area ( $\chi^2=9.89$ ,  $p<0.01$ ; Table 1, Figure 3) and a positive relationship with the percentage of perennial SNH ( $\chi^2=4.87$ ,  $p=0.03$ ; Table 1, Figure 3). In the parasite richness model, parasite richness was positively related to mite fall ( $\chi^2=16.21$ ,  $p<0.01$ ; Table 1, Figure 4), and negatively related to the percentage of organic crops ( $\chi^2=4.79$ ,  $p=0.03$ ; Table 1, Figure 4). Estimated marginal means from the models are presented in Table S8. Our models explaining

individual parasite presence/absence did not show any significant relationships (Table S9).

### 3.3 | Effects of conservation measures and parasites on colony growth

The mean absolute number of bees was  $7847.22 \pm 2115.46$  in July and  $8276.61 \pm 3189.86$  in August. In the colony growth model, the absolute number of bees decreased with increasing parasite richness ( $\chi^2=6.22$ ,  $p=0.01$ ; Figure 5) but increased with the percentage of organic crops ( $\chi^2=4.03$ ,  $p=0.04$ ; Table 1, Figure 5). Mite fall was not related to the number of bees ( $\chi^2=0.01$ ,  $p=0.97$ ; Table 1).

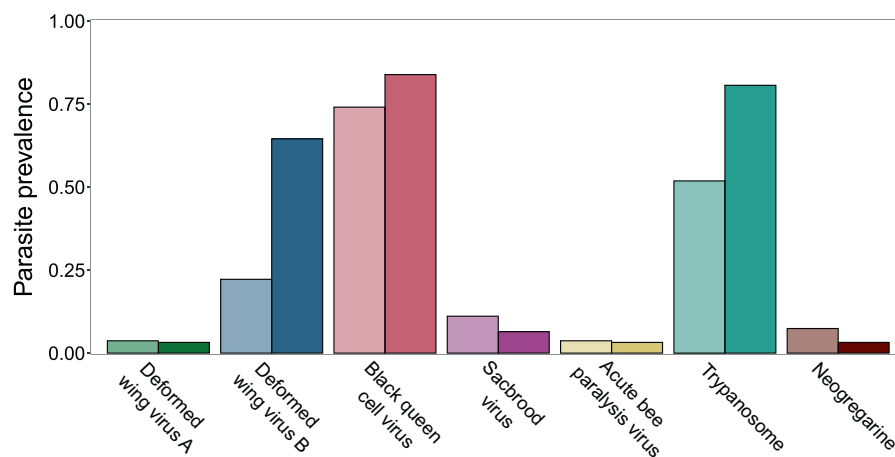
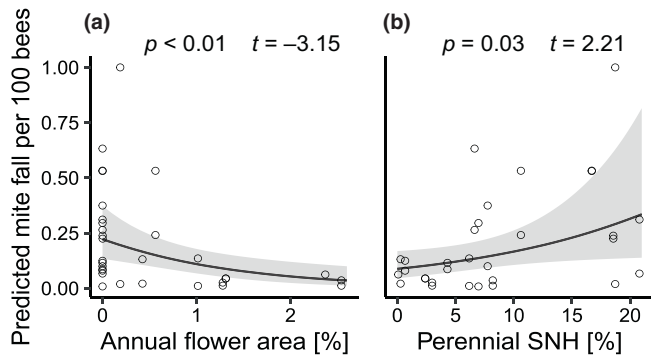


FIGURE 2 Parasite prevalence in honeybee colonies in July (first column for each parasite; faded colours) and August (second column). Presented are only parasites that were detected in at least one colony in one of the sampling rounds.

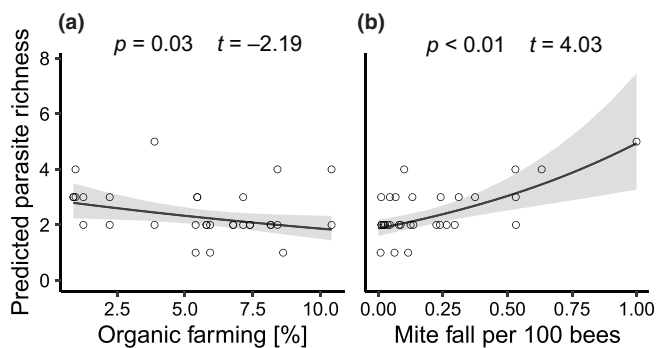
TABLE 1 Best models explaining parasite richness in honeybee colonies, their *Varroa destructor* mite fall, absolute number of bees and colony survival. Bold terms indicate significant relationships. Upward pointing arrows indicate positive relationships and downward pointing arrows indicate negative relationships.

Response variables	Explanatory variables	Estimate	$\chi^2$	$p$	Marginal $R^2$	Conditional $R^2$
Mite fall	Perennial SNH [%]	<b>0.43</b> ↑	4.87	<b>0.03</b>	0.50	0.52
	Annual flower strips [%]	<b>-0.57</b> ↓	9.89	<b>&lt;0.01</b>		
Log-parasite richness	Mite fall	<b>0.23</b> ↑	16.21	<b>&lt;0.01</b>	0.40	0.46
	Organic farming [%]	<b>-0.13</b> ↓	4.79	<b>0.03</b>		
Absolute number of bees	Log-Parasite richness	<b>-0.52</b> ↓	6.62	<b>0.01</b>	0.41	0.41
	Organic farming [%]	<b>0.19</b> ↑	4.03	<b>0.04</b>		
	Mite fall	<0.01	0.01	0.97		
Absolute number of bees	Trypanosome presence	<b>-0.31</b> ↓	4.22	<b>0.04</b>	0.37	0.37
	Organic farming [%]	<b>0.26</b> ↑	8.84	<b>&lt;0.01</b>		
	Mite fall	-0.10	2.28	0.13		
Colony survival	Absolute number of bees	1.42	2.72	0.10	0.20	0.20
	Log-Parasite richness	3.80	1.10	0.30		
	Mite fall	-1.09	1.32	0.25		





**FIGURE 3** Mite (*Varroa destructor*) fall in honeybee colonies in relation to: (a) the percentage of annual flower area (negative relationship); and (b) the percentage of perennial SNH (positive relationship). Plotted lines show the predicted relationships of the GLMMs and shaded areas indicate the 95% confidence intervals. Dots show raw data.

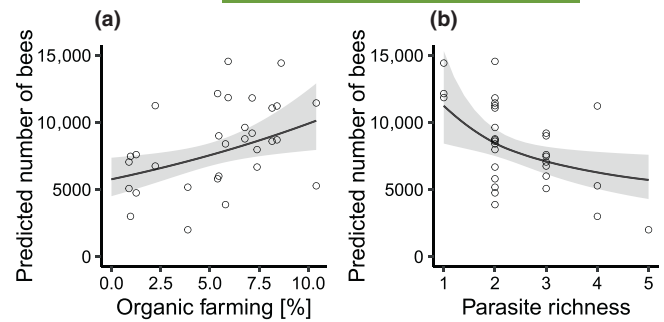


**FIGURE 4** Parasite richness in honeybee colonies in relation to: (a) the percentage of organic agriculture (negative relationship); and (b) natural varroa mite fall (positive relationship). Plotted lines show the predicted relationships of the LMMs and shaded areas indicate the 95% confidence intervals. Dots show raw data.

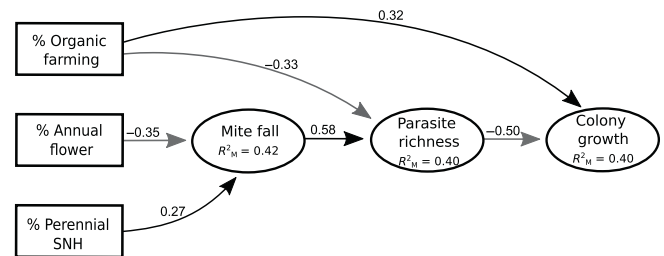
The best model examining the relationship between individual parasites and colony growth included a negative relationship with the prevalence of trypanosomes ( $\chi^2=4.42$ ,  $p=0.04$ ; Table 1), a positive relationship with the percentage of organic crops ( $\chi^2=8.84$ ,  $p<0.01$ ; Table 1) and an insignificant relationship with the mite fall ( $\chi^2=2.28$ ,  $p=0.13$ ; Table 1). Estimated marginal means from the models are presented in Table S8.

### 3.4 | Effects of conservation measures, parasites and colony growth on colony survival

Throughout the study period, six of 60 colonies died before winter (90% survival), and another six colonies died during winter (80% annual survival). The best model explaining colony survival included insignificant relationships with the absolute number of bees ( $\chi^2=2.72$ ,  $p=0.10$ ), parasite richness ( $\chi^2=1.10$ ,  $p=0.30$ ) and mite fall ( $\chi^2=1.32$ ,  $p=0.25$ ; Table 1).



**FIGURE 5** Growth of honeybee colonies in relation to: (a) the percentage of organic farming (positive relationship); and (b) parasite richness (negative relationship). Plotted lines show predicted relationships of the GLMM and shaded areas indicate the 95% confidence intervals. Dots show raw data.



**FIGURE 6** Structural equation model describing the direct and indirect relationships between conservation measures, mite fall (*Varroa destructor*), other parasites and honeybee colony growth (absolute number of bees). Black solid arrows reflect significant positive relationships and grey solid arrows represent significant negative relationships. Insignificant relationships were excluded from the graph. Standardized estimates are given above the arrows and marginal  $R^2$  inside the boxes.

### 3.5 | Structural equation model

Our SEM included three best models explaining mite fall, parasite richness and colony growth with seven direct paths (Figure 6; Table S10). Non-hypothesized paths were non-significant (Fisher's C statistic=7.84,  $p=0.65$ ,  $df=10$ ). Through model selection, the percentage of OSR was omitted in every model and thus was not included in the SEM.

In landscapes with higher perennial SNH cover, the mite fall increased ( $\beta=0.27$ ,  $p=0.03$ ). In contrast, with increasing coverage of annual flowers, varroa loads decreased ( $\beta=-0.35$ ,  $p<0.01$ ). Higher mite fall was associated with higher parasite richness ( $\beta=0.58$ ,  $p<0.01$ ), which in turn was associated with lower numbers of bees ( $\beta=-0.50$ ,  $p=0.01$ ). There was no direct relationship between mite fall and colony growth ( $\beta=0.01$ ,  $p=0.97$ ). Both perennial SNH and annual flower strips were associated with colony growth indirectly, through varroa and parasites, though in qualitatively different ways (SNH: negatively; annual flower strips: positively). *V. destructor* infestation was also indirectly associated with reduced colony growth through increasing parasite richness.

An increase in organic crop cover was associated with a direct decrease in parasite richness ( $\beta = -0.33$ ,  $p = 0.05$ ) and a direct increase in colony growth ( $\beta = 0.32$ ,  $p = 0.04$ ), potentially benefiting colony growth indirectly and directly. Parasite richness had the greatest total effect on colony growth ( $TE = -0.50$ ), followed by organic farming ( $TE = 0.49$ ) and intensity of varroa infestation ( $TE = -0.29$ ). The total effect of annual flower strips and perennial SNH with colony growth were minor ( $TE = 0.10$  and  $-0.08$ , respectively; Table S11).

## 4 | DISCUSSION

Here, we compared the relation of three conservation measures to the growth, parasitism and survival of experimental honeybee colonies in agricultural landscapes. With an increasing proportion of organic farming, parasite richness decreased and colony growth increased. An increase in annual flower strips and perennial SNH was associated with a respective decrease and an increase in mite fall. Higher mite fall was linked to higher parasite richness, and thereby lower colony growth. Ultimately, organic farming and annual flower strips seemed to benefit colony growth while perennial SNH detracted from colony growth.

The growth of a honeybee colony is largely dependent on food resources provided by its surroundings. Annual flower strips offer abundant floral resources that secure a colony's nutritional needs throughout the season (Klatt et al., 2020). Our results suggest that the annual flower area might support honeybees indirectly as it was related to lower *V. destructor* loads. Organic farming has previously been reported to benefit colony growth (Wintermantel et al., 2019). Besides this pronounced relation, we found that organic farming also related to lower parasite diversity in a colony. Organic farming not only provides food resources in the form of flowering crops but also weeds growing within and along the edges of fields (Geppert et al., 2020). By meeting their nutritional needs in organically managed farmland, a honeybee colony may be less vulnerable to the detrimental effects of parasite infestation or infection (Frizzera et al., 2022). Moreover, both annual flower strips and organic agriculture can contribute to the dilution of parasites, annual flower strips through the sheer abundance of flowers (Graystock et al., 2020; Manley et al., 2023) and organic farming through weeds scattered in small patches within crops (Crochard et al., 2022), which allows bees to disperse over larger areas. We also found that the relationship of colony growth and parasitism to organic farming is not driven by mass-flowering crops, but rather by a complementary effect of mass-flowering and non-mass-flowering organic agriculture.

In surprising contrast, we found that perennial SNH in the landscape was associated with higher varroa loads and, indirectly, lower colony growth. In our study, flower cover in perennial SNH was similar to that in organic fields, though much lower than in annual flower strips. Perennial SNH are often less attractive to pollinators than

annual flower strips (Piko et al., 2021), and some flowering SNH, such as grassy strips, are cut multiple times throughout the season. This abrupt disruption in food provision and possible concentration of bees on small flowering areas may increase parasite transmission. In previous studies, abundant SNH has been associated with an increase (Fearon et al., 2022) but also a decrease (Cohen et al., 2021) in parasite prevalence among diverse bee species, and an increase in pollinator species diversity, which highlights the importance of SNH to non-*Apis* pollinators (Krimmer et al., 2019; Piko et al., 2021). The discrepancies between habitat types considered as 'SNH' or 'natural/green area' in the literature make it difficult to elucidate the effects of these habitats on pollinators.

Parasitism is an important, although often unexplored, link between the landscape and honeybee colony growth. We report that the richness of parasites may be detrimental to colony fitness, but possibly mitigated by conservation measures. Our SEM showed a clear link between the landscape, varroa mites, parasite richness and colony growth, with no direct connection between the intensity of varroa infestation and colony growth. The level of infestation with varroa mites in our colonies was generally low and might have been too low to directly affect colony growth. On the other hand, it suggests that the indirect effect of varroa on colonies through parasite diversity is more pronounced than the direct effect of its feeding on honeybees. Varroa not only vectors viruses but also compromises the immune system of honeybees, which in turn makes hosts more vulnerable to other infections such as DWV (Nazzi et al., 2012). Although we did not find any relationship between viral agents and colony growth, we found a negative relationship of trypanosome (*Crithidia* spp., *Lotmaria* spp.) presence with honeybee colony growth. In support, recent studies (Gómez-Moracho et al., 2020; Liu et al., 2020) reported malnutrition and a shorter lifespan of honeybees infected with *C. melliferae* and *L. passim*. It is important to note that parasite prevalence is not an ideal estimate of parasitic burden and may not relate to lower fitness. It may fluctuate across or between years and can be biased by the initial parasite community of a colony. We could not make certain that our colonies were varroa- and other parasite-free at the beginning of the study, although we homogenized the workers and brood frames drawn from a large pool of source colonies to ensure an even distribution of parasites.

Although all three conservation measures and parasites were related to colony growth, there was ultimately no relationship with overwinter mortality of colonies. Potential effects on colony survival in our study might have been nullified by supplying colonies with food according to their individual needs and by treatment against varroa. These common beekeeping practices were conducted after parasite sampling and colony assessment at the end of the beekeeping season.

In our comparison of the total effects of the conservation measures, organic farming had potentially the greatest impact on honeybee colony growth, while the effects of annual flower strips and perennial SNH were markedly lower. Conservation measures are

aimed at supporting a diversity of pollinators. While efficiency in the provision of that support for honeybees is highly desirable and policies should strive to maximize their benefits, other bee species and other flower visitors also need to be taken into consideration. Although we inferred SNH to have a negative impact on honeybee colonies, it plays an important role in supporting wild bee species (Eeraerts, 2023; Geppert et al., 2020; Krimmer et al., 2019) and provides long-term stability in the provision of floral resources (Ammann et al., 2024) and the ecosystem service of pollination to crops and wild plant species alike.

## 5 | CONCLUSIONS

Our results contribute to the ongoing debate on whether the implementation of conservation measures benefits the health and fitness of a major commercial pollinator, *A. mellifera*, by showing that it depends on the type of conservation measure. Furthermore, they highlight how a comprehensive landscape-scale assessment of environmental variables can elucidate crucial links with honeybee colony health. We provide evidence that organic farm management and annual flower strips limit parasite presence and improve honeybee colony growth, although the efficiency of organic farming is superior. Our study supports the initiative of the European Green Deal to achieve 25% organic farming coverage in agricultural land by 2030 (Pe'er et al., 2022). The slight negative effect of perennial SNH on honeybee health calls for a closer inspection of these habitats as, even though they did not prove to be beneficial to honeybee colonies in our study, there is still considerable evidence of their benefits to other pollinators (Eeraerts, 2023; Martínez-Núñez et al., 2022). Provision of additional flowering resources and promotion of organic agriculture might be important in creating suitable landscapes for a broader range of bee species and other insect pollinators.

### AUTHOR CONTRIBUTIONS

Robert John Paxton, Catrin Westphal, Annika Hass and Ansgar Westerhoff conceived and designed the study; Ansgar Westerhoff, Lena Frank and Heiner Klingenberg collected the bee data; Annika Hass, Patrycja Pluta and Kathrin Czechofsky collected the landscape data; Patrycja Pluta collected the parasite data; Patrycja Pluta and Panagiotis Theodorou analysed the data; Patrycja Pluta drafted the manuscript. All the authors assisted in revising the manuscript and gave final approval for publication.

### ACKNOWLEDGEMENTS

We thank the Lower Nature conservation authorities of Göttingen and Werra-Meißner Kreis for providing the data on AES, and landowners for permission to place out hives. We also thank Susanne Jahn and assisting students for help in field sampling, and the reviewers for their valuable comments. Open Access funding enabled and organized by Projekt DEAL.

### FUNDING INFORMATION

Research reported here is supported by funds from the Federal Ministry of Food and Agriculture (BMEL) based on a decision of the parliament of the Federal Republic of Germany via the Federal Office for Agriculture and Food (BLE) under the Federal Programme for Ecological Farming and Other Forms of Sustainable Agriculture (grant numbers 2819OE115 and 2819OE156). Catrin Westphal is grateful for being funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation)—Project numbers: 405945293 and 493487387.

### CONFLICT OF INTEREST STATEMENT

The authors report no conflict of interests.

### DATA AVAILABILITY STATEMENT

Data and code are available from Zenodo Digital Repository <https://doi.org/10.5281/zenodo.12515616> (Pluta et al., 2024) and from Github [https://github.com/papluta/Honeybees\\_AES\\_2021](https://github.com/papluta/Honeybees_AES_2021).

### ORCID

Patrycja Pluta  <https://orcid.org/0000-0002-3600-5001>

Panagiotis Theodorou  <https://orcid.org/0000-0002-4056-5300>

Catrin Westphal  <https://orcid.org/0000-0002-2615-1339>

Robert J. Paxton  <https://orcid.org/0000-0003-2517-1351>

### REFERENCES

- Aizen, M. A., & Harder, L. D. (2009). The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Current Biology*, 19, 915–918. <https://doi.org/10.1016/j.cub.2009.03.071>
- Ammann, L., Bosem-Baillood, A., Herzog, F., Frey, D., Entling, M. H., & Albrecht, M. (2024). Spatio-temporal complementarity of floral resources sustains wild bee pollinators in agricultural landscapes. *Agriculture, Ecosystems & Environment*, 359, 108754. <https://doi.org/10.1016/j.agee.2023.108754>
- Bänsch, S., Tschardtke, T., Ratnieks, F. L. W., Härtel, S., & Westphal, C. (2020). Foraging of honey bees in agricultural landscapes with changing patterns of flower resources. *Agriculture, Ecosystems and Environment*, 291, 106792. <https://doi.org/10.1016/j.agee.2019.106792>
- Bänsch, S., Tschardtke, T., Wünschiers, R., Netter, L., Brenig, B., Gabriel, D., & Westphal, C. (2020). Using ITS2 metabarcoding and microscopy to analyse shifts in pollen diets of honey bees and bumble bees along a mass-flowering crop gradient. *Molecular Ecology*, 29(24), 5003–5018. <https://doi.org/10.1111/mec.15675>
- Barascou, L., Sene, D., Barraud, A., Michez, D., Lefebvre, V., Medrzycki, P., Di Prisco, G., Strobl, V., Yañez, O., Neumann, P., Le Conte, Y., & Alaux, C. (2021). Pollen nutrition fosters honeybee tolerance to pesticides. *Royal Society Open Science*, 8, 210818. <https://doi.org/10.1098/rsos.210818>
- Bartholomé, O., Aullo, A., Becquet, J., Vannier, C., & Lavorel, S. (2020). Pollinator presence in orchards depends on landscape-scale habitats more than in-field flower resources. *Agriculture, Ecosystems & Environment*, 293, 106806. <https://doi.org/10.1016/j.agee.2019.106806>
- Bartoń, K. (2020). *MuMIn: multi-model inference*. R package version 1.43.15. <https://cran.r-project.org/web/packages/MuMIn/index.html>



- Batáry, P., Dicks, L. V., Kleijn, D., & Sutherland, W. J. (2015). The role of agri-environment schemes in conservation and environmental management. *Conservation Biology*, 29(4), 1006–1016. <https://doi.org/10.1111/cobi.12536>
- Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Boscolo, D., & Metzger, J. P. (2009). Is bird incidence in Atlantic forest fragments influenced by landscape patterns at multiple scales? *Landscape Ecology*, 24, 907–918. <https://doi.org/10.1007/s10980-009-9370-8>
- Cohen, H., Smith, G. P., Sardiñas, H., Zorn, J. F., McFrederick, Q. S., Woodard, S. H., & Ponisio, L. C. (2021). Mass-flowering monoculture attracts bees, amplifying parasite prevalence. *Proceedings of the Royal Society B: Biological Sciences*, 288(1960), 20211369. <https://doi.org/10.1098/RSPB.2021.1369>
- Crochard, L., Julliard, R., Gaba, S., Bretagnolle, V., Baude, M., & Fontaine, C. (2022). Weeds from non-flowering crops as potential contributors to oilseed rape pollination. *Agriculture, Ecosystems and Environment*, 336, 108026. <https://doi.org/10.1016/J.AGEE.2022.108026>
- Di Prisco, G., Annoscia, D., Margiotta, M., Ferrara, R., Varricchio, P., Zanni, V., Caprio, E., Nazzi, F., & Pennacchio, F. (2016). A mutualistic symbiosis between a parasitic mite and a pathogenic virus undermines honey bee immunity and health. *Proceedings of the National Academy of Sciences of the United States of America*, 113(12), 3203–3208. <https://doi.org/10.1073/pnas.1523515113>
- Di Prisco, G., Cavaliere, V., Annoscia, D., Varricchio, P., Caprio, E., Nazzi, F., Gargiulo, G., & Pennacchio, F. (2013). Neonicotinoid clothianidin adversely affects insect immunity and promotes replication of a viral pathogen in honey bees. *Proceedings of the National Academy of Sciences of the United States of America*, 110(46), 18466–18471. <https://doi.org/10.1073/PNAS.1314923110>
- Dicks, L. v., Breeze, T. D., Ngo, H. T., Senapathi, D., An, J., Aizen, M. A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L. A., Gemmill-Herren, B., Howlett, B. G., Imperatriz-Fonseca, V. L., Johnson, S. D., Kovács-Hostyánszki, A., Kwon, Y. J., Lattorff, H. M. G., Lungharwo, T., Seymour, C. L., ... Potts, S. G. (2021). A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nature Ecology & Evolution*, 5(10), 1453–1461. <https://doi.org/10.1038/s41559-021-01534-9>
- Eeraerts, M. (2023). A minimum of 15% semi-natural habitat facilitates adequate wild pollinator visitation to a pollinator-dependent crop. *Biological Conservation*, 278, 109887. <https://doi.org/10.1016/j.biocon.2022.109887>
- European Commission, Directorate-General for Environment. (2018). EU pollinators initiative. *Publications Office*, 5(2), 40–51. <https://data.europa.eu/doi/10.2779/88885>
- Evans, J. D., & Schwarz, R. S. (2011). Bees brought to their knees: Microbes affecting honey bee health. *Trends in Microbiology*, 19(12), 614–620. <https://doi.org/10.1016/j.tim.2011.09.003>
- Fearon, M. L., Wood, C. L., & Tibbetts, E. A. (2022). Habitat quality influences pollinator pathogen prevalence through both habitat-disease and biodiversity-disease pathways. *Ecology*, 104(2), 1–15. <https://doi.org/10.1002/ecy.3933>
- Fox, J., Weisberg, S., & Price, B. (2022). *Car: Companion to applied regression*. R package version 3.0-0. <https://cran.r-project.org/web/packages/car/index.html>
- Frizzera, D., Ray, A. M., Seffin, E., Zanni, V., Annoscia, D., Grozinger, C. M., & Nazzi, F. (2022). The beneficial effect of pollen on varroa infested bees depends on its influence on behavioral maturation genes. *Frontiers in Insect Science*, 2, 1–10. <https://doi.org/10.3389/finsc.2022.864238>
- Geppert, C., Hass, A., Földesi, R., Donkó, B., Akter, A., Tschartke, T., & Batáry, P. (2020). Agri-environment schemes enhance pollinator richness and abundance but bumblebee reproduction depends on field size. *Journal of Applied Ecology*, 57(9), 1818–1828. <https://doi.org/10.1111/1365-2664.13682>
- Gómez-Moracho, T., Buendía-Abad, M., Benito, M., García-Palencia, P., Barrios, L., Bartolomé, C., Maside, X., Meana, A., Jiménez-Antón, M. D., Ollas-Molero, A. I., Alunda, J. M., Martín-Hernández, R., & Higes, M. (2020). Experimental evidence of harmful effects of *Crithidia mellificae* and *Lotmaria passim* on honey bees. *International Journal for Parasitology*, 50(13), 1117–1124. <https://doi.org/10.1016/j.ijpara.2020.06.009>
- Graystock, P., Ng, W. H., Parks, K., Tripodi, A. D., Muñoz, P. A., Fersch, A. A., Myers, C. R., McFrederick, Q. S., & McArt, S. H. (2020). Dominant bee species and floral abundance drive parasite temporal dynamics in plant-pollinator communities. *Nature Ecology & Evolution*, 4(10), 1358–1367. <https://doi.org/10.1038/s41559-020-1247-x>
- Hartig, F. (2020). *DHARMa: Residual diagnostics for hierarchical regression models*. R package v 0.4.6. <https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html>
- Holland, J. E. Y. D., Bert, D. G., & Fahrig, L. (2004). Determining the spatial scale of species' response to habitat. *Bioscience*, 54, 227. [https://doi.org/10.1641/0006-3568\(2004\)054\[0227:DTSSOS\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0227:DTSSOS]2.0.CO;2)
- Holzschuh, A., Dormann, C. F., Tschartke, T., & Steffan-Dewenter, I. (2011). Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proceedings of the Royal Society B: Biological Sciences*, 278(1723), 3444–3451. <https://doi.org/10.1098/RSPB.2011.0268>
- Imdorf, A., Buehlmann, G., Gerig, L., Kilchenmann, V., & Wille, H. (1987). Überprüfung der Schätzmethode zur Ermittlung der Brutfläche und der Anzahl Arbeiterinnen in freifliegenden Bienenvölkern. *Apidologie*, 18(2), 137–146. <https://doi.org/10.1051/apido:19870204>
- Jachufa, J., Denisow, B., Wrzesień, M., & Ziółkowska, E. (2022). The need for weeds: Man-made, non-cropped habitats complement crops and natural habitats in providing honey bees and bumble bees with pollen resources. *Science of the Total Environment*, 840, 156551. <https://doi.org/10.1016/J.SCITOTENV.2022.156551>
- Klatt, B. K., Nilsson, L., & Smith, H. G. (2020). Annual flowers strips benefit bumble bee colony growth and reproduction. *Biological Conservation*, 252, 108814. <https://doi.org/10.1016/j.biocon.2020.108814>
- Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tschartke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, 274(1608), 303–313. <https://doi.org/10.1098/rspb.2006.3721>
- Krimmer, E., Martin, E. A., Krauss, J., Holzschuh, A., & Steffan-Dewenter, I. (2019). Size, age and surrounding semi-natural habitats modulate the effectiveness of flower-rich agri-environment schemes to promote pollinator visitation in crop fields. *Agriculture, Ecosystems and Environment*, 284, 106590. <https://doi.org/10.1016/J.AGEE.2019.106590>
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579. <https://doi.org/10.1111/2041-210X.12512>
- Lenth, R. V. (2022). “emmeans: Estimated marginal means, aka least-squares means.” R package version 1.7.3. <https://cran.r-project.org/web/packages/emmeans/index.html>
- Liu, Q., Lei, J., Darby, A. C., & Kadowaki, T. (2020). Trypanosomatid parasite dynamically changes the transcriptome during infection and modifies honey bee physiology. *Communications Biology*, 3(1), 1–8. <https://doi.org/10.1038/s42003-020-0775-x>

- Manley, R., Boots, M., & Wilfert, L. (2017). Condition-dependent virulence of slow bee paralysis virus in *Bombus terrestris*: Are the impacts of honeybee viruses in wild pollinators underestimated? *Oecologia*, 184(2), 305–315. <https://doi.org/10.1007/s00442-017-3851-2>
- Manley, R., Doublet, V., Wright, O. N., Doyle, T., Refoy, I., Hedges, S., Pascall, D., Carvell, C., Brown, M. J. F., & Wilfert, L. (2023). Conservation measures or hotspots of disease transmission? Agri-environment schemes can reduce disease prevalence in pollinator communities. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 378(1873), 20220004. <https://doi.org/10.1098/rstb.2022.0004>
- Marselle, M. R., Turbe, A., Shwartz, A., Bonn, A., & Colléony, A. (2021). Addressing behavior in pollinator conservation policies to combat the implementation gap. *Conservation Biology*, 35(2), 610–622. <https://doi.org/10.1111/cobi.13581>
- Martin, A. E. (2018). The spatial scale of a species' response to the landscape context depends on which biological response you measure. *Current Landscape Ecological Reports*, 3, 23–33. <https://doi.org/10.1007/s40823-018-0030-z>
- Martin, A. E., & Fahrig, L. (2012). Measuring and selecting scales of effect for landscape predictors in species-habitat models. *Ecological Applications*, 22, 2277–2292. <https://doi.org/10.1890/11-2224.1>
- Martínez-Núñez, C., Kleijn, D., Ganuza, C., Heupink, D., Raemakers, I., Vertommen, W., & Fijen, T. P. M. (2022). Temporal and spatial heterogeneity of semi-natural habitat, but not crop diversity, is correlated with landscape pollinator richness. *Journal of Applied Ecology*, 59(5), 1258–1267. <https://doi.org/10.1111/1365-2664.14137>
- McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C., & Cushman, S. A. (2016). Multi-scale habitat selection modeling: A review and outlook. *Landscape Ecology*, 31, 1161–1175. <https://doi.org/10.1007/s10980-016-0374-x>
- Möckel, N., Gisder, S., & Genersch, E. (2011). Horizontal transmission of deformed wing virus: Pathological consequences in adult bees (*Apis mellifera*) depend on the transmission route. *Journal of General Virology*, 92, 370–377. <https://doi.org/10.1099/vir.0.025940-0>
- Natsopoulou, M. E., McMahon, D. P., Doublet, V., Bryden, J., & Paxton, R. J. (2015). Interspecific competition in honeybee intracellular gut parasites is asymmetric and favours the spread of an emerging infectious disease. *Proceedings of the Royal Society B: Biological Sciences*, 282(1798), 20141896. <https://doi.org/10.1098/rspb.2014.1896>
- Natsopoulou, M. E., McMahon, D. P., Doublet, V., Frey, E., Rosenkranz, P., & Paxton, R. J. (2017). The virulent, emerging genotype B of deformed wing virus is closely linked to overwinter honeybee worker loss. *Scientific Reports*, 7(1), 1–9. <https://doi.org/10.1038/s41598-017-05596-3>
- Nazzi, F., Brown, S. P., Annoscia, D., Del Piccolo, F., Di Prisco, G., Varricchio, P., Vedova, G. D., Cattonaro, F., Caprio, E., & Pennacchio, F. (2012). Synergistic parasite-pathogen interactions mediated by host immunity can drive the collapse of honeybee colonies. *PLoS Pathogens*, 8(6), e1002735. <https://doi.org/10.1371/journal.ppat.1002735>
- Osterman, J., Aizen, M. A., Biesmeijer, J. C., Bosch, J., Howlett, B. G., Inouye, D. W., Jung, C., Martins, D. J., Medel, R., Pauw, A., Seymour, C. L., & Paxton, R. J. (2021). Global trends in the number and diversity of managed pollinator species. *Agriculture, Ecosystems and Environment*, 322, 107653. <https://doi.org/10.1016/j.agee.2021.107653>
- Osterman, J., Theodorou, P., Radzevičiūtė, R., Schnitker, P., & Paxton, R. J. (2021). Apple pollination is ensured by wild bees when honey bees are drawn away from orchards by a mass co-flowering crop, oilseed rape. *Agriculture, Ecosystems and Environment*, 315, 107383. <https://doi.org/10.1016/j.agee.2021.107383>
- Pe'er, G., Finn, J. A., Díaz, M., Birkenstock, M., Lakner, S., Röder, N., Kazakova, Y., Šumrada, T., Bezák, P., Concepción, E. D., Dänhardt, J., Morales, M. B., Rac, I., Špulerová, J., Schindler, S., Stavrínides, M., Targetti, S., Viaggi, D., Vogiatzakis, I. N., & Guyomard, H. (2022). How can the European Common Agricultural Policy help halt biodiversity loss? Recommendations by over 300 experts. *Conservation Letters*, 15(6), 1–12. <https://doi.org/10.1111/cons.12901>
- Piko, J., Keller, A., Geppert, C., Batáry, P., Tscharrntke, T., Westphal, C., & Hass, A. L. (2021). Effects of three flower field types on bumblebees and their pollen diets. *Basic and Applied Ecology*, 52, 95–108. <https://doi.org/10.1016/j.BAAE.2021.02.005>
- Piot, N., Meeus, I., Kleijn, D., Scheper, J., Linders, T., & Smagge, G. (2019). Establishment of wildflower fields in poor quality landscapes enhances micro-parasite prevalence in wild bumble bees. *Oecologia*, 189(1), 149–158. <https://doi.org/10.1007/S00442-018-4296-Y>
- Pluta, P., Czechofsky, K., Hass, A., Frank, L., Westerhoff, A., Klingenberg, H., Westphal, C., & Paxton, R. (2024). Organic farming and annual flower strips reduce parasite prevalence in honey bees and boost colony growth in agricultural landscapes. *Zenodo Digital Repository*. <https://doi.org/10.5281/zenodo.12515616>
- Pluta, P., & Paxton, J. R. (2022). Assessing the impact of disease on pollinators. In P. G. Kevan & S. W. Chan (Eds.), *Promoting pollination and pollinators in farming*. Burleigh Dodds Science Publishing.
- Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, 540(7632), 220–229. <https://doi.org/10.1038/nature20588>
- QGIS Development Team. (2018). QGIS geographic information system. QGIS Association. <http://www.qgis.org>
- R Core Team. (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rosenkranz, P., Aumeier, P., & Ziegelmann, B. (2010). Biology and control of *Varroa destructor*. *Journal of Invertebrate Pathology*, 103, S96–S119. <https://doi.org/10.1016/j.jip.2009.07.016>
- Tscharrntke, T., Grass, I., Wanger, T. C., Westphal, C., & Batáry, P. (2021). Beyond organic farming—Harnessing biodiversity-friendly landscapes. *Trends in Ecology & Evolution*, 36(10), 919–930. <https://doi.org/10.1016/j.tree.2021.06.010>
- Westphal, C., Steffan-Dewenter, I., & Tscharrntke, T. (2009). Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology*, 46(1), 187–193. <https://doi.org/10.1111/J.1365-2664.2008.01580.X>
- Winston, M. L. (1987). *The biology of the honey bee* (7th ed.). Harvard University Press.
- Wintermantel, D., Odoux, J.-F., Chadœuf, J., & Bretagnolle, V. (2019). Organic farming positively affects honeybee colonies in a flower-poor period in agricultural landscapes. *Journal of Applied Ecology*, 56(8), 1365–2664. <https://doi.org/10.1111/1365-2664.13447>

## SUPPORTING INFORMATION

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

**Appendix S1.** Extended materials and methods.

**Appendix S2.** Re-evaluation of the models at three different scales.

**Table S1.** Coordinates of the study sites and area (in %) of landscape variables at increasing spatial scales.

**Table S2.** Primer sequences used for qPCR and PCR screening.

**Table S3.** qPCR and PCR protocols.

**Table S4.** Terms included in global and final models (best AIC score).

**Table S5.** Comparison of the parasite richness model (1) with and without potential outlier.

**Table S6.** Analysis of mass-flowering and non-mass-flowering organic crops.

**Table S7.** Person's correlation coefficients of the relationship between landscape variables and the absolute number of honey bees per colony.

**Table S8.** Estimated marginal means of the significant predictors.

**Table S9.** Best models of the prevalence of individual parasites in honey bee colonies.

**Table S10.** Summary of the structural equation model.

**Table S11.** Total effects of the structural equation models.

**How to cite this article:** Pluta, P., Czechofsky, K., Hass, A., Frank, L., Westerhoff, A., Klingenberg, H., Theodorou, P., Westphal, C., & Paxton, R. J. (2024). Organic farming and annual flower strips reduce parasite prevalence in honeybees and boost colony growth in agricultural landscapes. *Journal of Applied Ecology*, 61, 2146–2156. <https://doi.org/10.1111/1365-2664.14723>