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RESEARCH ARTICLE

Linking landscape structure, floral resource distribution, pollen use and movement distances of a generalist predator

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Abstract

1. Understanding the habitat use and movement patterns of natural enemies in agricultural landscapes is essential for enhancing biological pest control. Since many natural enemies rely on floral resources, the distribution of these resources in combination with movement behaviour likely influence biological control in field crops. Nevertheless, few studies have assessed natural enemy movement at the landscape scale.
2. Here we estimated minimal movement distances of the green lacewing *Chrysoperla carnea* based on consumed pollen and the spatial distribution of the respective plant species in 24 agricultural landscapes (500 m radius). Lacewings were sampled using sticky traps in the centre of each landscape, and the consumed pollen were identified. The location of the most important pollen-providing plants was mapped in each landscape. Distances to potential sources of pollen consumed by 346 lacewings were used to derive minimal movement distances.
3. Lacewings consumed mostly pollen from insect-pollinated plants that were present within 500 m from the sampling location. The distance to the nearest source of consumed pollen exceeded 200 m in 31% of lacewing individuals, demonstrating the relevance of the landscape scale to understand their population dynamics.
4. Distances were shorter to insect-pollinated than to wind-pollinated plants, and shorter early than late in the season. Mean and median distances to pollen sources were negatively associated to flower availability and edge density in the landscape, but this was not the case for minimal distances.
5. *Synthesis and applications*. Our findings suggest that the spatial distribution of flowering wild plants can inform movement patterns of lacewings and other flower-visiting insects in agricultural landscapes. In addition, the location of floral resources in the landscape is important for its capacity to sustain natural enemies. Given the strong reliance of lacewings on pollen from nearby insect pollinated woody plants, the promotion of native shrubs and trees, such as *Prunus*, *Salix* and *Castanea*, should be prioritized for natural enemy enhancement in agricultural landscapes. Doing this in the form of hedgerows or agroforestry systems

would lead to only minimal reduction in production areas and provide additional benefits such as biodiversity conservation.

KEYWORDS
agricultural landscapes, biological control, insect predator, movement ecology, natural enemies, pollen feeding

1 | INTRODUCTION

Humans have modified landscapes for agriculture throughout the world, thereby reducing the cover of semi-natural habitats and negatively affecting biodiversity and ecosystem functioning (Díaz et al., 2019; Tscharntke et al., 2012). These changes also impair ecosystem services such as biological control and pollination (Dainese et al., 2019). Many insects that provide ecosystem services rely on specific resources mainly found in semi-natural habitats (Bianchi et al., 2006; Samways et al., 2020). Consequently, the spatial composition and configuration of agricultural landscapes influence the movement of ecosystem service providers and ultimately the spatial distribution of the associated ecosystem services (Martin et al., 2019). However, since insect movement is governed by a range of factors (Kral-O'Brien & Harmon, 2021; Schellhorn et al., 2014) and species often show context-specific responses, landscape effects on ecosystem service providers are highly variable (Karp et al., 2018). Thus, there is a need for a more mechanistic understanding of the processes driving the movement behaviour of ecosystem service providers that takes account of the spatio-temporal distribution of (floral) resources (Lavandero et al., 2010). However, tracking the movement of individual insects is difficult because of their small size. Movement patterns of insects have been studied using different techniques, such as harmonic radar, mark-(re)capture approaches, molecular markers and dusts and dyes (Batuecas et al., 2021; Cavigliasso et al., 2020; Chapman et al., 2010; MacDonald & Loxdale, 2010; Schellhorn et al., 2010; Winder, 2010). However, some of these methods involve handling of insects for experiments, such as capturing or marking insects in the laboratory, or the application of markers in the field, which may potentially influence the behaviour and/or movement behaviour of insects (Hagler & Jackson, 2001). The use of pollen as natural markers does not have this disadvantage because there is no interference with the insects until the moment that they are captured (Silberbauer et al., 2010).

Biological control of arthropod pests is an important ecosystem service that reduces plant damage and the need for pesticide application (Rusch et al., 2017). Many natural enemies feed on both prey and additional floral resources, such as nectar and pollen, which enhance their survival and reproductive potential (He et al., 2021; Van Rijn et al., 2013). Due to the use of herbicides, weed flower availability in crops is generally low, and natural enemies then rely on floral resources from semi-natural habitats. Furthermore, due to the scattered distribution of resources in agricultural landscapes, natural enemies must move across the landscape mosaic in search of flower and prey resources that may be available at different times in the year (Schellhorn et al., 2014). Therefore, the amount and distribution of floral resources in a landscape in combination with the movement behaviour of natural enemies are likely key drivers for biological control in field crops.

Green lacewings (Neuroptera; Chrysopidae) are a globally important group of generalist predators, among which *Chrysoperla carnea* (Stephens) is the most common species in agricultural fields in the northern hemisphere (McEwen et al., 2007). Their larvae are predators of various soft-bodied arthropods, such as aphids, whereas adults feed on pollen, nectar and insect honeydew (McEwen et al., 2007). *Chrysoperla carnea* overwinters in woody and urban areas and moves to arable fields during spring (Duelli, 2007). While *C. carnea* is described as a nomadic species that is able to travel long distances, especially before reproduction (Chapman et al., 2006; Duelli, 1980a), marking studies indicated that lacewings tend to move short distances within nearby habitats (Hagler et al., 2020; Lefebvre et al., 2017). Indeed, lacewing abundance is positively associated with habitat diversity (Paredes et al., 2024) and semi-natural habitat cover (Serée et al., 2020). However, little is known about how the spatial arrangement of semi-natural habitats in the landscape that offer floral resources influences the spatial distribution of *C. carnea* during the growing season. In particular, the consumption of large amounts of pollen from woody plants early in the season (Bertrand et al., 2019) indicates that the presence of semi-natural habitats is important to support these predators. By combining information on the pollen consumed by adults (Bertrand et al., 2019; Villenave et al., 2006) and detailed information on the spatial distribution of pollen sources, pollen grains can be used as markers to quantify potential dispersal distances in agricultural landscapes (Silberbauer et al., 2010).

Here, we combine detailed information on the distribution of floral resources at the landscape scale with data on pollen types consumed by the green lacewing *C. carnea* to make inferences about the movement distances of lacewings in agricultural landscapes. We have four objectives: (i) estimate the minimal movement distances of *C. carnea* based on the nearest distances to consumed pollen sources in agricultural landscapes; (ii) evaluate how pollination mode of pollen sources (insect- vs. wind-pollinated plants) influences distances to consumed pollen sources; (iii) assess seasonal variations in the distance to consumed pollen resources; and (iv) analyse how distances to consumed pollen sources are related to landscape structure and flower availability. Since green lacewings consume pollen from several plant species, we expected that they would consume pollen from both insect- and wind-pollinated plants. However, as pollen from wind-pollinated plants can be dispersed by wind before lacewings consume it (e.g. from leaf surfaces), we expected that distance from the location of lacewing capture to insect-pollinated plants should be shorter than for wind dispersed pollen. Furthermore, since lacewings have 2–3 generations per year in the study region (Henry et al., 2002), we expected early season distances to consumed pollen (linked to post-overwintering individuals foraging on flowers) to be shorter than late-season distances (when subsequent generations are migrating for reproduction and consume more honeydew; Duelli, 2007). Finally, we expected that in complex landscapes with semi-natural habitats, distances to consumed pollen sources should be shorter than in simplified landscapes because floral resources should be available at shorter ranges.

2 | MATERIALS AND METHODS

2.1 | Lacewing sampling and pollen diet

Adult lacewings were sampled in 2019 in the Upper Rhine Valley, Rhineland-Palatinate, Germany (49.07–49.29° N, 8.09–8.34° E), in 24 landscapes (radius 0.5 km) that span a gradient of landscape composition and configuration and floral resource availability (Figure 1; see Eckerter et al., 2020 and Supporting Information for details). Landowners granted us the permission to perform fieldwork and no ethical approval was required to collect the samples. Landscape centres were at least 800 m apart (average: 1993 ± 183 m). Land-use categories (areas of forest, arable land, semi-natural habitats, urban areas) at every landscape were mapped in 2019 during insect and plant samplings. Using QGIS, measures of landscape composition (proportion of cereals, proportion of semi-natural habitats, Shannon Index of landscape and crop diversity) and configuration (edge density, calculated as the total length of edges between landscape elements divided by the total area of the landscape; and mean field size, i.e. average size of arable fields on each landscape) were calculated for each landscape (Table S1).

In the centre of each landscape, two sticky traps were placed at the edge between a herbaceous semi-natural habitat and an arable field at 1.5 m height, separated by 20 meters. Traps had two collecting surfaces facing South and North and each surface had blue, white and yellow sticky areas (see Supporting Information for more details). Traps were active for a total of 8 weeks from 1 May to 4 July. For further analyses, the sampling period was divided into early season (from 1 May to 4 June, corresponding to approximately 100–200 Growing Degree Days—GDD) and late season (from 5 June to 4 July, equivalent to 200–400 GDD). This classification was based on a previous study of *C. carnea* pollen diet, which showed a marked compositional shift between these phases (Bertrand et al., 2019). Each landscape was visited every 2 weeks and all the collected lacewings were removed from the traps using brushes with white spirit and tweezers. Each individual was stored in a separate Eppendorf tube with 70% ethanol. In the laboratory, all the lacewings belonging to the genus *Chrysoperla* were identified to the species level using morphological features when possible (San Martin, 2004; P. Duelli, personal communication).

The consumed pollen by lacewings (i.e. pollen grains in the gut) were retrieved using acetolysis following the steps of Jones (2012, 2014). During this procedure, insect tissues and all pollen material with the exception of the outer pollen wall, are removed (Southworth, 1974), yielding clean pollen exines for identification. The method was previously used to study the pollen diet of lacewings and ladybeetles (Alcalá Herrera et al., 2021; Bertrand et al., 2019; Villenave et al., 2006). In short, external pollen on the bodies of lacewings were removed by rinsing them in ethanol. Each individual was placed in a centrifuge tube for acetolysis. After centrifugation, pollen pellets were diluted in 50% (v/v) glycerin and put on slides for pollen identification (Supporting Information). Pollen grains were identified using palynological keys (Beug, 2004), a photo atlas (Reille, 1992), and reference collections of the Ecosystem Analysis Group (University Kaiserslautern-Landau). Pollen were usually identified to plant species level, but for some cases to lower taxonomic levels. We further refer to 'pollen records' to describe all the different pollen types identified across all collected lacewings.

2.2 | Floral resource mapping

The major floral pollen resources for lacewings were assessed during two different sampling rounds (see Supporting Information for details). First, the cover (in m^2) of all woody plants was mapped in 2017–2018 in sampling plots of 10 × 10 m in all hedgerows and forest edges (first 10 m) of each landscape (orange dots in Figure 1d; Eckerter et al., 2020). The forest interior was not mapped since *C. carnea* is mostly active in open farmland during spring and summer (Duelli et al., 2002). The cover of each tree was estimated by measuring its crown projection area on the ground. Second, the cover (in m^2) of herbaceous flowering plants was mapped in 2019 within each landscape element containing herbaceous flowering plants. In grassy field margins, hedgerows, and forest edges, the total cover of herbaceous flowering plants was recorded (red lines in Figure 1d). In meadows and crops, the cover of flowering plants was upscaled from ten 1 m^2-subplots to the total meadow and crop area (green and yellow polygons in Figure 1d, respectively). Mapped plants were identified at species level using vegetation keys (Parolly et al., 2006; Schauer et al., 2012; Schulz, 2014). For herbaceous plants, only species that represented >5% of the pollen consumed by *C. carnea* in a previous study in the region (Bertrand et al., 2019) were sampled (Table S2). The locations of these flowering plant species were mapped and digitized to create floral resource maps in QGIS 3.18.3 (QGIS Development Team, 2021). Floral resource area (i.e. area of the landscape covered by plants consumed by lacewings), flower diversity (Shannon Index of diversity, considering the identity and area of each plant species), and early and late Flower Availability Indices (FAI) were calculated with this information (see Eckerter et al., 2020 and Supporting Information for details).

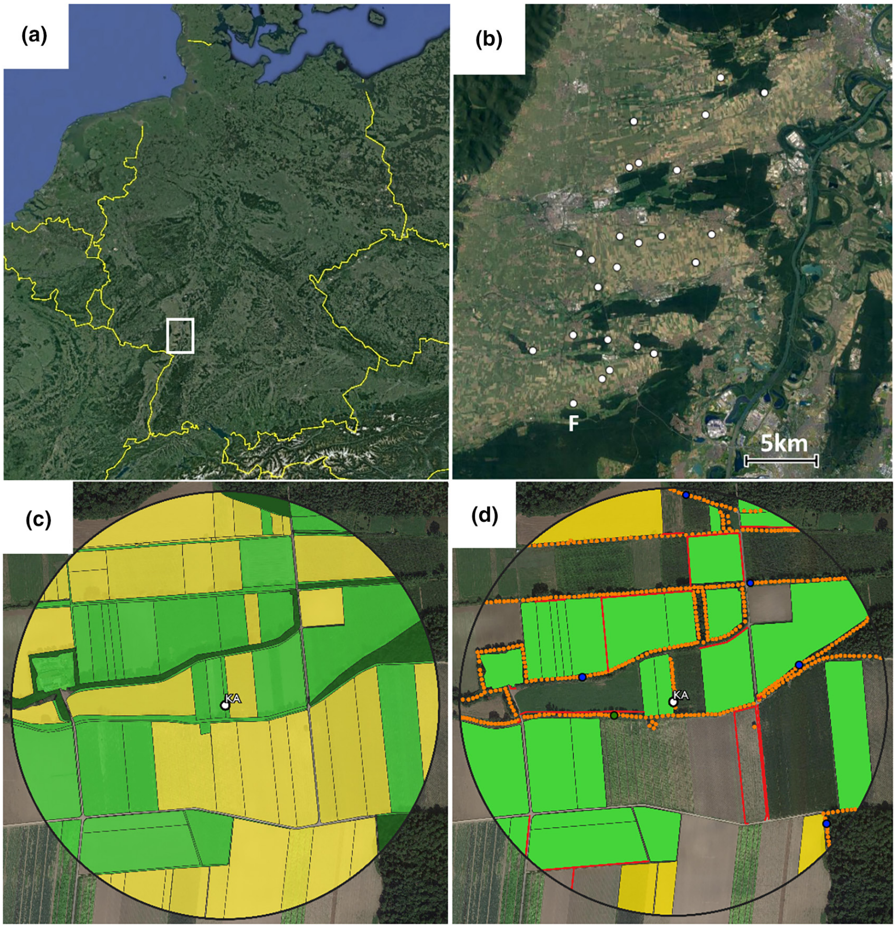

FIGURE 1 (a) Location of the study region (white rectangle) in Rheinland-Pfalz, Germany. (b) Location of 24 landscapes (500-m radius) in the study region. (c) Land use and location of sticky trap where lacewings were collected (white dot) in one of the landscapes. Arable land, woody and herbaceous seminatural habitats are indicated in yellow, dark green and light green, respectively. (d) Location of mapped floral resources in woody habitats (orange dots), grasslands (green polygons), herbaceous field margins (red lines) and flowering crops (yellow polygons). As an example, green and blue dots indicate the location of two pollen resources consumed by a lacewing collected at sampling location F. The distance between the white and blue/green dots were used to derive minimal movement distances of the lacewing and mean and median distances to consumed pollen sources.

2.3 | Floral resource distribution and movement distance estimation

To infer minimal movement distances and characterize the floral resource distribution, we measured all distances between the location of the sticky trap where a lacewing was captured and the locations of plants from which pollen detected in that lacewing could originate within that respective landscape using QGIS. Since lacewings usually ingested pollen from more than one plant species, this procedure was followed for each pollen type. This resulted in a list of distances for each pollen type that a specific lacewing individual had ingested. From this list, the minimal distance to each pollen source (distance to the nearest source of that pollen type, which represents the minimal distance a lacewing must have moved after consuming the pollen grains), and mean and median distances (average distances to all the resources of that type in the landscape, which is a measure for the resource distribution in the landscape) were calculated for each lacewing using the R package *dplyr* (Wickham et al., 2015). Furthermore, for lacewings that consumed more than one pollen type, we selected the plant species that had the highest minimal distance because this is the minimal distance that the lacewing individual must have moved. These calculations were done separately for insect- and wind-pollinated plants, but only data from insect-pollinated plants was used for addressing objectives (iii) and (iv), as we expected that these represent visits to insect-pollinated plants. For pollen from wind-pollinated plants, we cannot exclude that lacewings were taking up the pollen after being displaced by wind.

2.4 | Statistical analyses

We used linear mixed models to analyse minimal movement distances and distances to insect- or wind pollinated pollen sources (objective ii) in the early and late-season (objective iii), and to estimate the influence of landscape structure and flower availability on minimal movement distances and distances to pollen sources (objective iv). Minimal movement distance and mean and median distances to pollen resources were used as response variables. Minimal movement distance was used as a conservative measure of the estimated movement distance. Mean and median distances were included as additional measures of resource locations throughout the landscapes, where median distances were included to reduce the influence of plant locations that were very near or far from traps. Pollination mode (insect vs. wind-pollinated plants) and season (early vs. late) were the explanatory variables for objectives (ii) and (iii), respectively. For objective (iv), explanatory variables included metrics for flower availability (floral resource area, flower diversity and early and late FAI) and landscape structure (landscape and crop diversity, proportions of semi-natural habitats and cereals, edge density and mean field size), season and interactions between season and landscape metrics to account for potential differences in responses to landscape metrics across the season. Landscape ID was always used as a random variable to account for the spatial dependence of the data, whereas for mean and median distances, lacewing ID, nested within landscape, was included to account for those individuals with more than one ingested pollen type. For objectives (iii) and (iv), we worked only with pollen records of insect-pollinated plant types. Given the large number of explanatory variables for objective (iv), we used a multimodel inference approach in which we ran all the potential models including landscape metrics, season and their interactions. We then ranked all the models using their AICc-value and reported all the competitive models within a ΔAICc ≤2. In addition, we also compared the distances to all pollen sources (the full offer of pollen from every landscape) between wind and insect-pollinated plants and early and late season insect-pollinated plants to determine if the pollen offer drives the feeding choices of lacewings (see Supporting Information). The validity of the models and spatial autocorrelation were checked using the package DHARMa (Hartig, 2022). All analyses were performed using the software R (R Core Development Team, 2019) with the packages nlme (Pinheiro et al., 2012) and MuMIn (Barton, 2009). Figures were produced using the packages ggplot2 (Wickham, 2011) and ggeffects (Lüdecke, 2018).

3 | RESULTS

3.1 | Lacewing diet and floral resource location

A total of 346 *Chrysoperla* individuals were collected, including *C. carnea* s. str. (46.5%), *C. lucasina* (37.3%) and *C. pallida* (13.6%), plus nine individuals that could not be identified to species level. Through acetolysis, we obtained the exines of 5753 pollen grains in a total of 585 pollen records. Out of these, we identified 41 pollen types. Pollen grains were detected in 76% of the collected individuals (79.5% of *C. carnea*, 68.2% of *C. lucasina*, 80.6% of *C. pallida*). On average, adults consumed 2.53 (±0.09) pollen types, (2.72 ± 0.14 in *C. carnea*, 2.47 ± 0.13 in *C. lucasina*, 2.08 ± 0.22 of *C. pallida*), with 57.5% of the individuals consuming two or more pollen types. 59.8% of the pollen grains were consumed in the early season and 40.2% in the late season. The most frequently consumed pollen were Rosaceae (including *Prunus*, 21.9%), Brassicaceae (10.4%), *Salix* (8.9%), Poaceae (8.3%), *Castanea* (7.3%), *Matricaria* type (Asteraceae, 7.1%), *Acer* (6.7%), *Viburnum* (5.7%), *Fraxinus* (5.3%) and Cupressaceae (3.8%; see Table S3 for the complete list of pollen types and their relative frequencies). Regarding the dispersal type of the consumed pollen, insect-pollinated plants represented 82% of the pollen grains and 66% of the pollen types.

From the 585 pollen records, 547 records (93.5%) were from plants that were mapped in the 24 landscapes. Out of these 547 records, 82% were from plants that were present in the landscape where the lacewings were collected. From the remaining 18% pollen records (which originated from plants that were not recorded in the landscape), 78% were from wind-pollinated plants. Twenty-two lacewing individuals (6.4% of all individuals) had consumed pollen from insect-pollinated plants that were mapped, but were not recorded in the landscape where the individuals were captured. Pollen that were consumed by lacewings but were not mapped included *Beta vulgaris* (Amaranthaceae), Chenopodiaceae sp., Ericaceae sp., *Galium* sp. (Rubiaceae), *Hypericum perforatum* (Hypericaceae), *Myriophyllum spicatum* (Haloragaceae), *Pisum sativum* (Fabaceae), *Scabiosa* sp. (Caprifoliaceae) and *Symphytum* sp. (Boraginaceae; see Table S4 for details).

3.2 | Distance to nearest insect- and wind-pollinated pollen sources

Minimal distances were larger for wind-pollinated than for insect-pollinated plants (Table 1; Figure 2a). Minimal distances were on average 125.3 ± 136.8 m (mean ± SD) for insect-pollinated plants and 211.7 ± 146.4 m for wind-pollinated plants (Figure 2a). Mean and median distances to consumed pollen sources were also higher for wind-pollinated plants (Figure S1). In contrast, when considering the distances to all pollen sources, wind-pollinated plants were on average closer to the landscape centres than insect-pollinated plants (Figure S2).

3.3 | Minimal movement distances: Temporal and spatial patterns

Minimal movement distance from insect-pollinated plants were shorter in the early season than in the late season (166.8 ± 132.2 vs. 199.1 ± 152.6 m; Table 1; Figure 3b), which coincided with shorter distances to all sources of pollen during the early season (Figure S1). The landscape analysis indicated that minimal movement distances may be influenced by season, proportion of arable land and semi-natural habitat, flower diversity and late-season FAI (Table 2). However, season was the only significant variable in the averaged model (Table 2) and the predictive power of the competitive models was low (marginal R^2 = 0.04–0.05; Table S5).

TABLE 1 Model summaries for the effects of pollination mode and season on the distances to resources consumed by green lacewings.

Predictor variable	Response variable	Model components	Estimate	Standard error	*t*-value	*p*-value
Pollination mode	Minimal distances to resources	Intercept (insect-pollinated)	116.64	18.52	6.30	<0.0001
		Wind	57.19	18.89	3.03	0.0028
	Mean distances to resources	Intercept (insect-pollinated)	327.57	10.07	32.51	<0.0001
		Wind	25.65	7.50	3.42	<0.0001
	Median distances to resources	Intercept (insect-pollinated)	340.62	10.67	31.93	<0.0001
		Wind	18.40	7.45	2.47	0.0143
Season	Minimal distances to resources	Intercept (early season)	154.51	24.00	6.44	<0.0001
		Late season	52.99	24.01	2.19	0.0294
	Mean distances to resources	Intercept (early season)	314.66	12.05	26.10	<0.0001
		Late season	29.90	9.99	2.99	0.0032
	Median distances to resources	Intercept (early season)	328.17	12.64	25.94	<0.0001
		Late season	28.18	9.06	3.11	0.0022

Note: For each predictor and response variable, the estimates, standard error, *t*- and *p*-values are shown. The intercepts represent the reference levels for models evaluating pollination mode and season effects (insect-pollinated plants and early season, respectively).

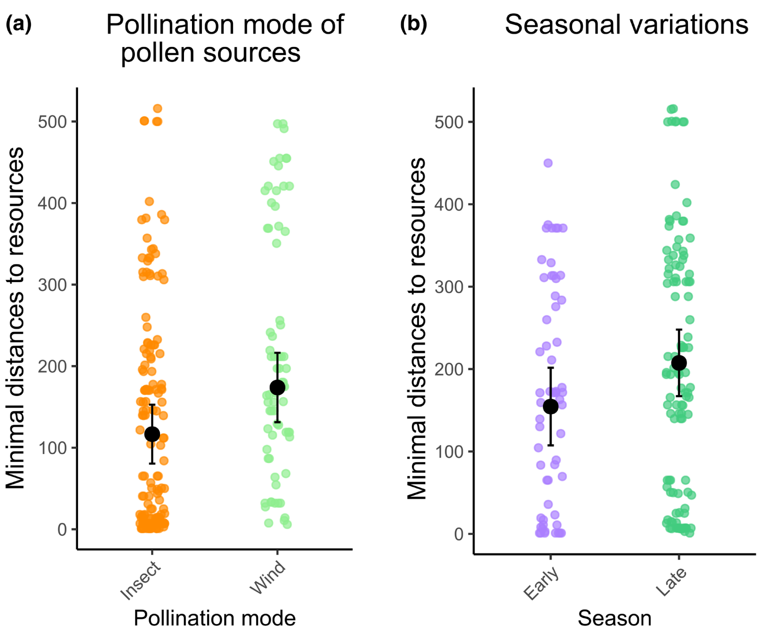

FIGURE 2 Distances from lacewing collection locations to nearest pollen sources for insect- and wind pollinated plants (a) and for the early and late season (b). Minimal distances are measured between the locations of potential sources of consumed pollen from insect (orange) and wind-pollinated plants (light green) and for insect-pollinated plants in the early and late season (b; purple and green, respectively). The estimates and 95% confidence intervals (black dot and error bars) of the linear mixed models are shown. Coloured dots represent raw data for each lacewing individual.

3.4 | Relationship between distances to consumed pollen sources and landscape variables

The landscape analysis for mean distances to resources yielded three models within ΔAICc ≤2, which included season, floral resource area in the landscape and edge density (Table 2), and had higher R^2 values when landscape variables were included (marginal R^2=0.05–0.10; Table S5). Mean distances to ingested pollen sources were higher in the late season than in the early season (Figure S3) and negatively associated with floral resource area (Figure 3a; Table 2). Only one competitive model was obtained for median distances to ingested pollen, which included season and edge density as predictors (Table 2). This model had a higher predictive power than models for minimal and mean distances to pollen sources (marginal R^2=0.17; Table S5). Median distances to resources decreased with edge density and were higher in the late season than in the early season (Figure 3b; Figure S3).

4 | DISCUSSION

Here, we inferred minimal movement distances of lacewings based on their pollen consumption and the location of plants in the landscape that could have provided these pollen. The highest minimal distance to an insect-pollinated plant that a lacewing consumed represents the minimal movement distance of that lacewing within

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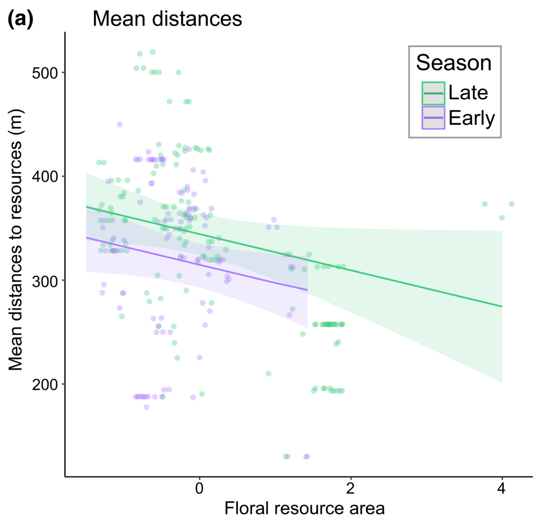

FIGURE 3 Landscape and seasonal effects on mean (a) and median distances to resources (b). Distances between sampling location of lacewings and locations of consumed pollen resources in the surrounding landscape were estimated for insect-pollinated plants. Regression lines and 95% confidence intervals of the linear mixed models are shown. Dots represent raw data for each pollen record (purple for early and green for late season).

TABLE 2 Averaged models for the influence of season, flower availability and landscape structure on the distances to consumed pollen resources by green lacewings.

Response variable	Predictor variables	Estimates	Adjusted SE	*z* value	*p*-value
Minimal distances to resources	Intercept (early season)	154.63	24.07	6.37	<0.0001
	Late season (1)	53.24	24.12	2.19	**0.0286**
	Arable land (0.20)	−14.98	16.07	0.88	0.38
	Late FAI (0.17)	15.73	21.09	0.70	0.48
	Semi-natural habitat (0.14)	6.14	15.07	0.38	0.70
	Flower diversity (0.13)	−6.91	18.57	0.35	0.73
Mean distances to resources	Intercept (early season)	314.06	11.45	27.20	<0.0001
	Late season (1)	30.21	10.00	2.99	**0.002**
	Floral resource area (0.53)	−18.57	8.86	1.98	**0.04**
	Edge density (0.20)	−11.34	9.04	1.18	0.24
Median distance to resources	Intercept (early season)	328.92	11.55	28.47	<0.0001
	Late season (1)	27.17	9.02	3.04	**0.003**
	Edge density (1)	−21.34	9.09	−2.34	**0.03**

Note: Each model represents the conditional average of all the models within a ΔAICc ≤2 (see Supporting Information for AICc values of competitive models). For each model, the response variables are listed and the parameter estimates, adjusted standard errors, *z* and *p*-values are shown. The importance of each independent variable (sum of model weights including that variable) is shown in parentheses. Significant estimates are highlighted in bold. The intercepts represent the reference level of season in both models (early season).

the time during which ingested pollen is detectable in the gut (González, Bianchi, Wizorek, et al., 2022). Our results indicate that lacewings consume mostly pollen that are available in the surrounding landscape, with shorter distances to insect-pollinated than wind-dispersed pollen sources and with shorter distances in the early season than in the late season. Still, 6.4% of the captured lacewings contained pollen that were mapped, but not recorded in the respective landscape, suggesting that lacewings have moved more than 500 m after consuming that pollen. In addition, landscapes with high flower availability and edge density were associated with shorter distances to pollen sources, demonstrating that lacewings have to bridge shorter distances between pollen feeding and oviposition in crops in such landscapes. This underlines the value of semi-natural habitats for the pest-suppressive potential of agricultural landscapes (Martin et al., 2019).

While the far majority of the recorded pollen could have been consumed within 500 m from the location where lacewings were captured, 6.4% of the lacewings contained pollen from plants further away. This resembles movement patterns found for foraging ladybeetles and parasitoids using mark and (re)capture experiments, with many more short-distance than long-distance movements (Bianchi et al., 2009; van der Werf et al., 2000). Foraging lacewings typically fly at heights below two meters (Duelli, 1980b) and these flights are likely to mainly comprise short distances. For instance, mark and (re)capture studies found that lacewings tended to move up to 62 m between strips of alfalfa (Hagler et al., 2020) and moved short distances (below 100 m) between hedgerows and neighbouring orchards (Lefebvre et al., 2017). With 183 m on average, the minimal movement distances recorded in our study were substantially higher, although there were also cases where plants that may have provided pollen were found just a few meters from the trap. A dominance of short distance movement events can explain why some studies have found higher lacewing densities and oviposition activity near flower-rich field margins (e.g. Ndakidemi et al., 2022; Pfister et al., 2017). Since long-distance flights usually take place at higher heights (Chapman et al., 2006; Duelli, 1980b), our sticky traps probably captured mainly individuals during short-distance foraging movement. The relative high estimates of movement distances in our study compared to artificial marker studies suggest that natural markers (such as pollen) may help to overcome the bias caused by the difficulty to recapture artificially marked insects over long distances.

The collected lacewings fed on pollen originating from flowering trees (e.g. *Prunus* spp.), herbs (e.g. *Brassica* spp.) and grasses, confirming their generalist feeding habits (Bertrand et al., 2019; Villenave et al., 2005, 2006). In some cases we found that lacewings fed on pollen from plant species that were previously not considered as a food source for *Chrysoperla* spp., such as *Beta vulgaris* and *Galium* sp. (Bertrand et al., 2019; Villenave et al., 2006). In agreement with our prediction, distances to consumed insect-pollinated plants were on average shorter than to wind-pollinated plants, although wind-pollinated plants were on average closer to the landscape centres. This finding indicates that lacewings actively visited insect-pollinated plants and confirms the suitability of the use of pollen grains as a natural marker. The larger distances to wind-pollinated plants could reflect feeding on wind dispersed pollen from leaf surfaces when lacewings search for other food sources, such as honeydew (Lundgren, 2009). However, the higher amount of insect-dispersed than wind-dispersed pollen in the guts of lacewings (82% vs. 18%, respectively) indicates that pollen feeding on flowers is the main mode of pollen foraging.

In line with our hypotheses, minimal movement distances of lacewings were shorter early in the growing season than in the late season. We can explain this finding in two ways. First, the abundance of flowering plants is higher in the early than in the late season, resulting in shorter distances between the location of lacewings and the nearest pollen providing flowering plant. Second, lacewings may show different types of movement during the early and late growing season. In the early season, lacewings tend to exhibit directed flights from overwintering sites to nearby feeding sites. Later in the season, newly emerged adults engage in longer-distance pre-ovipository flights (Duelli, 1980b), so a larger fraction of the populations can be represented by migrant individuals. Variation in plant flowering times is well documented and has been shown to strongly influence movement patterns and resource consumption in other insect groups, such as pollinators (Peterson & Roitberg, 2016; Walther-Hellwig & Frankl, 2000). In addition to temporal changes, mean and median distances to sources of consumed pollen by lacewings were negatively associated with flower availability and edge density. This confirms that lacewings need to bridge longer distances between flowering resources and crop fields in simplified landscapes (Thomine et al., 2023). These results are also in agreement with reports of relatively high lacewing abundance in cultivated habitats and semi-natural habitat located in small-scale heterogenous landscapes (González, Bianchi, Eckerter, et al., 2022; Serée et al., 2020; Thomine et al., 2023).

Our study used spatially-explicit information on flowering plant locations to infer minimal insect movement distances in a highly replicated landscape design. However, the methodology has some limitations which need to be considered for interpreting the results. First, as relatively generalist feeders, adult lacewings consume numerous common pollen resources, which has most likely led to the high number of potential plants that could have been the sources of the ingested pollen in the landscapes. Thus, inferred minimal movement distances describe only the lower limit of lacewing movement and are a very conservative estimate because they assume that the lacewings fed pollen on the nearest plant from the trap and moved in a straight line from the plant to the trap. Other methods to track insect movement, such as protein (Hagler et al., 2020; Lefebvre et al., 2017) or fluorescent marking (Guiller et al., 2016; Huais et al., 2022), or using a single pollen source (i.e. a flower strip with only one flowering plant species; Wratten et al., 2003) may provide more precise estimations of movement distances. However, marking methods can influence insect behaviour (Hagler & Jackson, 2001) and may suffer from limited recapture and sampling locations (Osborne et al., 2002). Second, studies collecting lacewings flying at high altitudes (Chapman et al., 2006) and using flight mills (Liu et al., 2011) estimated that lacewings can move several kilometres using wind currents during pre-ovipository flights. However, we sampled lacewings on sticky traps at 1.5 m, which likely mainly captured foraging lacewings (Duelli, 1980b) and not migrating lacewings that fly at higher distances. Therefore, our estimates are only representative for foraging lacewings and we assume that the chosen 500 m radius is useful to study lacewings in the agricultural landscapes, as observed the positive associations between lacewing abundance and the proportion of semi-natural habitats (Serée et al., 2020), edge density (Thomine et al., 2023) or flower availability (González, Bianchi, Eckerter, et al., 2022). Third, an important aspect of movement is time. The half-life of pollen grains in lacewing guts is in the order of 3–5 days, but the chance to detect a consumed plant species after 2 weeks in the laboratory is still >50% (González, Bianchi, Wizorek, et al., 2022). Unfortunately, this creates a large uncertainty with respect to the timescale in which the movements have taken place. Other potential natural markers, such as prey DNA, are detectable for shorter time periods (Chen et al., 2000; Harper et al., 2005). Prey species with low mobility and high host plant specificity could thus give a more precise estimate of predator movement, such as the nettle- or walnut-specific aphid species detected in ladybirds by Ammann et al. (2020). However, the shorter detectability period of prey DNA will likely come at the cost of lower detection frequencies.

5 | CONCLUSIONS

We found that lacewings consumed pollen from a wide variety of insect-pollinated plant species, whereby 6.4% of the captured individuals had fed from pollen outside the 500 m landscape radius. Despite that wind-pollinated plants were on average closer to the traps, distances to consumed insect-pollinated resources were shorter, suggesting that lacewings actively foraged for nearby pollen providing flowers. Longer distances to consumed pollen sources later in the season reflect the general decline in floral resource availability from spring towards summer. Our study revealed that minimal movement distances exceeded 160 m for the majority of lacewings, which is substantially more than reported by artificial marker studies. This suggests that artificial marker studies underestimate movement distances because of the difficulty to recapture marked insects over long distances, and underlines the high potential of using pollen as natural marker for animal movement studies. DNA-based tracking of consumed pollen and drone-based mapping of floral resources could facilitate and further improve this research avenue.

Given the strong reliance of lacewings on pollen from nearby insect pollinated woody plants, the integration of native shrubs and trees such as *Prunus*, *Salix* and *Castanea* should benefit lacewing populations and pest suppression potential in agricultural landscapes. Especially, enhancing the availability of late-flowering species can reduce the dispersal distances in periods of particularly low flower offer (Rundlöf et al., 2014). Doing this in the form of hedgerows or agroforestry systems would lead to only minimal reduction in production areas, and provide additional benefits such as biodiversity conservation.

AUTHOR CONTRIBUTIONS

Ezequiel González, Felix J. J. A. Bianchi and Martin H. Entling designed the study; Philipp W. Eckerter performed field sampling, Ezequiel González performed laboratory and statistical analysis and wrote the first draft of the manuscript; all authors contributed to the manuscript and agreed on the final version.

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CONFLICT OF INTEREST STATEMENT

We declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.d51c5b0b2 (González 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.

Table S1: Proportions of land-use categories in each of the studied landscapes.

Table S2: List of the mapped pollen types within forest edges (i.e. the first 10 m inside forests) inside the nine landscapes which contained forests.

Table S3: List of mapped pollen types to estimate flower availability measures and pollen consumed by the green lacewing *C. carnea* and their availability in SW Germany.

Table S4: List of unmapped pollen types consumed by the green lacewing *C. carnea* in SW Germany.

Table S5: Best models for the influence of season, flower availability and landscape structure on the distances to consumed pollen resources by green lacewings.

Figure S1: Estimates of distances between sampling location of lacewings and locations of pollen resources in the surrounding landscape.

Figure S2: Variation of distance to pollen sources among plants with differing pollination modes (A) and early and late season resources (B).

Figure S3: Estimates of distances between sampling location of lacewings and potential locations of pollen resources in the surrounding landscape.

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