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Research article

The combined effects of resource landscapes and herbivory on pollination services in agro-ecosystems

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Pollinator activity is affected by landscape-scale flower availability, and by pollinator interactions with co-occurring organisms. Of special interest are potentially detrimental effects of herbivores on the attractiveness of plants to pollinators. While insect herbivores are abundant in natural and agro-ecosystems, the combined effect of herbivory and landscape floral resources on pollinator activity and the delivery of pollination services is little studied and understood. Here we investigated the combined effects of surrounding flower cover and aphid herbivory on pollination services in agricultural landscapes. We apply a resource landscape approach for mapping the spatial distribution of floral resources across landscapes, using neighbourhood modelling and empirical data on flower availability in specific land-use types. In each of 25 Mediterranean landscapes spanning a gradient of land-use intensity ranging from natural to agricultural, we established paired patches of potted aphid-infested or aphid-free phytometer plants *Diplotaxis erucoides*. In each patch, we recorded the activity of insects visiting flowers and subsequent seed set. We also recorded the relative abundance of flowers in dominant land-use locales within a 1 km radius of each patch. Neighbourhood analyses revealed that plant–pollinator interactions in our study system are shaped by herbivory, distribution of floral resources across the landscape, and the interaction between these factors. We found a negative competitive effect of flower cover on pollinator activity and phytometer seed-set; this effect was stronger on aphid-infested than aphid-free plants. The main pollinator guilds in the study sites (wild bees, honeybees and non-bee pollinators) responded differently to these factors. Our results highlight the importance of combining a resource landscape approach with the exploration of interactions among different organisms, when mapping pollination services and identifying the scale at which pollinators respond to foraging resources.

Keywords: agroecology, ecosystem services, herbivores, land-use, Mediterranean agro-ecosystem, neighbourhood analyses, pests, wild bees

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Introduction

Understanding the factors shaping biodiversity patterns of focal ecosystem service (ES) providers, is vital for biodiversity conservation, and for managing ecosystem services. The activity of ES providers may be influenced by a variety of direct and indirect factors operating at different spatial scales, ultimately affecting plant reproductive success (Klein et al. 2007, Bommarco et al. 2013, Bartomeus et al. 2014, Dainese et al. 2019, Martin et al. 2019). Resource availability at relevant activity distances is a major factor directly shaping the overall abundance and composition of ES providers across landscapes, as well as the provision of ecosystem services, including herbivore population control and pollination (Isaacs et al. 2009, Woodard and Jha 2017, Perović et al. 2018, Albrecht et al. 2020). In addition, biotic and abiotic factors influencing plant properties may indirectly affect the activity of ES providers by altering the attractiveness of these plants (Dale and Polasky 2007, Brittain et al. 2010, van der Sluijs et al. 2013, Burkle and Runyon 2016, Liere et al. 2017). Although both direct and indirect effects have received much research attention (Roulston and Goodell 2011, Liere et al. 2017), little is known about their combined influence on the performance of ES providers. Here we report on a study of combined direct and indirect effects on the activity of pollinators and pollination services.

Bees are the main pollinator taxon in many natural and agricultural landscapes (Klein et al. 2007, Winfree et al. 2007), although recent work shows that non-bee pollinators may also provide substantial pollination services (Rader et al. 2016). Bees are central place foragers, i.e. their foraging activity is centered around their nests. Bees forage up to distances of a few kilometers, largely depending on their body size (Greenleaf et al. 2007). Pollinator guilds may therefore be differently affected by landscape characteristics. For example, large pollinator species with relatively wide foraging ranges may be more strongly affected by landscape complexity, and at larger spatial scales, than small-bodied, less mobile pollinators (Steffan-Dewenter et al. 2002). The surrounding landscape greatly affects bee abundance, diversity and species composition (Woodard and Jha 2017, Du Clos et al. 2020), as well as reproduction, survival (Bukovinszky et al. 2017, Woodard and Jha 2017) and pollination activity (Steffan-Dewenter et al. 2002, Petersen and Nault 2014). While bee species may differ in their foraging and nesting requirements, those that inhabit heterogenous landscapes often exhibit complementary habitat use, according to seasonal flowering dynamics in the different habitats (Mandelik et al. 2012, Osgathorpe et al. 2012, Mallinger et al. 2016, Bertrand et al. 2019). All bees are exclusively dependent on flowers for larval and adult nutrition (Michener 2007); the distribution of floral resources across landscapes is therefore a main factor shaping bee communities and their pollination activity (Roulston and Goodell 2011, Woodard and Jha 2017). Pollinator diversity and pollination services decline with distance to adjacent natural and semi-natural habitats (Klein et al. 2007, Ricketts et al. 2008, Garibaldi et al. 2011) and with a decrease in the proportion of natural/semi-natural habitats in the surrounding landscape (Kennedy et al. 2013, Dainese et al. 2019).

Co-flowering plants may exert facilitative or competitive effects on pollination services provided, as a consequence of sharing pollinators (Mitchell et al. 2009, Tscharntke et al. 2012, Braun and Lortie 2019). A facilitation effect can occur when patches of high flower density and/or attractiveness draw pollinators, increasing their overall density at the patch. These pollinators can then spill over to adjacent patches (Callaway 1995, Braun and Lortie 2019). Competition for pollinators among co-flowering plants may result from a dilution effect, i.e. a reduction in pollinators' rate of visitation per plant in high density floral patches, and/or due to a concentration effect, i.e. when higher density or preferable floral resources attract pollinators, thereby reducing their activity in adjacent patches (Tscharntke et al. 2012). The direction of the relationship between neighbouring floral resources depends on various landscape factors such as spatial and temporal scale (Westphal et al. 2003, Kovacs-Hostyanszki et al. 2013, Desaegher et al. 2021), stage of flowering (Grab et al. 2017), relative plant abundance (Ghazoul 2006), and pollinator guild (Holzschuh et al. 2016).

The vast majority of studies on the impact of landscape composition on ES providers have been based on categorical land-use classification, primarily the percentage of natural and semi-natural habitats versus cultivated area (Garibaldi et al. 2011, Roulston and Goodell 2011, Scheper et al. 2013, Duflot et al. 2015). However, land-use classification provides only a rough, indirect assessment of the distribution of floral resources across a landscape; there is often considerable variation in floral availability and composition, as well as in other environmental properties, within land-use categories (Roulston and Goodell 2011, Duflot et al. 2015, Cole et al. 2017). The development of an alternative platform for quantitative measurement based on biologically meaningful resources, most importantly floral diversity and abundance, is thus a major challenge in assessing landscape effects on pollinators in agricultural landscapes. Resource landscape analyses characterizing spatial distribution of resources may provide such a platform for the description of landscape complexity (Nottebrock et al. 2017a). The few studies that have directly quantified surrounding floral resources and tested their effects on pollination services were conducted mostly in small experimental plots, and focused on the effects of co-flowering neighbouring plants (Lazaro et al. 2009, Hegland 2014, Bruckman and Campbell 2014, Ye et al. 2020). The effects of floral resource distribution on pollination services at the landscape scale have been little studied.

Among the indirect effects shaping the activity of pollinators across landscapes, insect herbivory may play a critical role. Herbivory by insects is a central biotic stressor of plants, often reducing overall fitness and productivity (Oerke 2006). Herbivores are known to affect basic physiological processes of their host plants, such as photosynthesis, stomatal conductance and transpiration (Shannag et al. 1998, Franzen et al. 2008, Nabity et al. 2009, Islam and Ren 2009). Herbivory may also influence various floral characteristics such as number, size and pigmentation of flowers, emission of

floral volatile compounds, and nectar and pollen production (Strauss et al. 1996, Lehtila and Strauss 1997, Krupnick et al. 1999, Mothershead and Marquis 2000, Kessler et al. 2011, Pareja et al. 2012, Barber et al. 2012, Lucas-Barbosa 2016, De Palma et al. 2016, Rusman et al. 2019). As expected, all of these herbivory-induced changes in infested plants were found to severely reduce plant detection and attractiveness to pollinators (Moreira et al. 2019), but there is also evidence for neutral (Poveda et al. 2003, Hladun and Adler 2009, Kessler and Chauta 2020, Haas and Lortie 2020) and positive (Strauss et al. 2001, Kessler and Chauta 2020, Haas and Lortie 2020) effects of herbivory on pollinators. Finally, different components of pollinator visitation behaviour such as preference, frequency and visit duration may also differ between infested and un-infested plants (Strauss et al. 1996, Lucas-Barbosa 2016, Lucas-Barbosa et al. 2016, Moreira et al. 2019). The impact of herbivory on pollinator behaviour may also have consequences for the efficiency of pollination services delivered, i.e. levels of fruit and seed set after a pollinator visit. A few studies have shown that fruit or seed set is dependent on pollination level, herbivory level and the interactions between the two (Herrera 2000, Herrera et al. 2002, Lundin et al. 2013, Munguia-Rosas et al. 2015, Ramos and Schiestl 2019). The role of landscape characteristics in pollination–herbivory interactions was not explored yet.

In this study, the combined effects of resource landscapes and herbivory on pollinator activity and pollination services delivered by various pollinator guilds were evaluated in a field experiment conducted in Mediterranean agro-ecosystems. The experiment used phytometers that were either herbivore-free or experimentally infested with aphids; these phytometers were introduced into agricultural systems for which floral resource landscapes were mapped. We conducted statistical neighbourhood analyses of the experimental data to explore how activity and pollination services of honeybees, wild bees and non-bee pollinators are affected by 1) the distribution of floral resources across the landscape, 2) herbivore presence, and 3) interactions between floral resources and herbivory. We hypothesize that 1) increased floral resources within phytometer surrounding, will enhance pollinator activity due to facilitation effect, and that this effect will vary between pollinator guilds due to differences in functional traits. Additionally, we hypothesize that 2) fewer pollinators would visit aphid-infested phytometers in response to herbivory-induced changes in flower traits that reduce their attractiveness to pollinators. In turn, this will also reduce fruit and seed set. Finally, we hypothesize that 3) there will be interactive effects of floral resource distribution and herbivory; surrounding floral resources will mitigate the expected negative effect of herbivory on pollinator activity and plant productivity.

Material and methods

Phytometer species and aphid infestation

Diplotaxis erucoides (Brassicaceae), a Mediterranean annual herb, served as our phytometer plant. The species is self-incompatible, pollinator-dependent, and dominant in the study region. *D. erucoides* grown from locally collected seeds were maintained at 20°C in a greenhouse for seven weeks. During that time, flower buds were removed to maximize vegetative growth. When plants were ca 40 cm high, we ceased removing buds and allowed the plants to flower. A week later, plants were randomly assigned to two greenhouse chambers with identical climatic conditions. Those in one chamber were kept free of aphids, while plants in the other chamber were each infested with 20 adults of *Myzus persicae* (Hemiptera: Aphididae) placed on two leaves per plant, 10–14 days prior to transport to the field. Before transport to the field, herbivore density on the infested phytometer plants were quantified by visually counting adult aphids. Infestation levels ranged from 50–150 adult aphids per plant.

Myzus persicae is a highly polyphagous herbivore and a major generalist pest of many crops around the world, including species in the families Crucifereae, Cucurbitaceae , Solanaceae and Malvaceae, as well as other cultivated, ornamental and weedy plants (Blackman and Eastop 2000). *Myzus persicae* infestation may reduce plant fitness (e.g. crop yield) by direct feeding, reduced photosynthesis caused by sooty mold colonization, and by infection with plant viruses (Blackman and Eastop 2000, Blanc et al. 2011).

Study area and experimental design

The study was conducted in the Judean Foothills, a highly fragmented Mediterranean agro-natural ecosystem in central Israel (31°36′0.00″–31°54′0.00″N, 34°42′0.00″–35° 0′0.00″E, 60–280 m a.s.l.). The study area is characterized by a mosaic of agricultural crop fields (mainly grains, sunflower, watermelon and legumes) and orchards, natural vegetation at various successional stages (herbaceous, sparse and dense shrubland), planted forests, and a few rural settlements. The area lies at the interface between a humid Mediterranean ecosystem to the north, and an arid ecosystem to the south, making it a hotspot of biodiversity (Mandelik et al. 2007), particularly of bees (Pisanty and Mandelik 2015) and plants (Weizel et al. 1978). Honeybees *Apis mellifera* are commonly kept in the region for crop pollination and honey production; wild and feral honeybees are absent due to parasitic *Varroa* mites.

Twenty-five study sites were set up, 15 in 2017 and 10 in 2018, in agricultural fields that were vegetation-free at the time of the study, thus preventing effects by proximal plants. Sites were bordered by natural/semi-natural habitats. Sites were selected to create a gradient of landscape composition, based on the proportion of surrounding natural/semi-natural versus agricultural habitats within a 1 km radius of each site. The proportion of natural and semi-natural habitats within this radius ranged from 10 to 70% (Supporting information). A minimum distance of 500 m was maintained between plot centers. At each plot, we established two patches of 12 potted, blooming, greenhouse-grown *D. erucoides*, which served as phytometers (focal plants). Plants were placed on a 2 × 3 m yellow cloth to increase the

visibility of focal plant patches to flying insects (Fig. 1). The plants in one patch were infested with aphids (*M. persicae*); those in the second patch were aphid-free (Fig. 1). The two patches were established at a distance of 10 m from field margins and 80 m from each other. The potted plants were left in the field for three days, and watered daily. We monitored pollinator activity and quantified pollination services on the second and third days, after a day of acclimation and detection by pollinators.

Data collection

Field work was conducted for one month between early March to Early April in 2017 and 2018, coinciding with peak activity season of pollinators. Sites were sampled consecutively; each site was sampled only once. We collected the following data:

Floral resource landscapes

Based on aerial photographs and site visits, we identified six dominant land-use types in the study region: grasslands, shrublands, planted forests (mostly pines), orchards, wheat fields, and other crops, mainly clover and chickpea (Esri ArcMap, ver. 10.6.1). Where necessary, initial classifications were verified on the ground. Flower cover in each of the six land-use types was estimated visually in 96–159 randomly-placed 1m-diameter circles per land-use type, distributed across sites (15–40 circles per site); a total of 339 and 380 individual circles were sampled in 2017 and 2018, respectively. Circles were situated at least 15 m away from any adjacent land-use type; adjacent circles within the same land-use type were placed at least 10 m apart. We calculated mean flower availability for each land-use type and combined these estimates with land-use maps within a 1 km radius of each study site, to produce a spatially-explicit map of the floral resource landscape surrounding each study site.

Pollinator activity and pollination services

The frequency of pollinator visits to the phytometer plant flowers was recorded in 2017; seed-set data were collected in 2017 and 2018. To measure pollinator visit frequency, phytometer flowers in each patch were observed during two consecutive days, beginning 24 h after plants were placed in the field. At each site, the total number of flowers in the patch was counted in the early morning hours, before commencing data collection. On each day, 7–15 observation rounds of 15 min

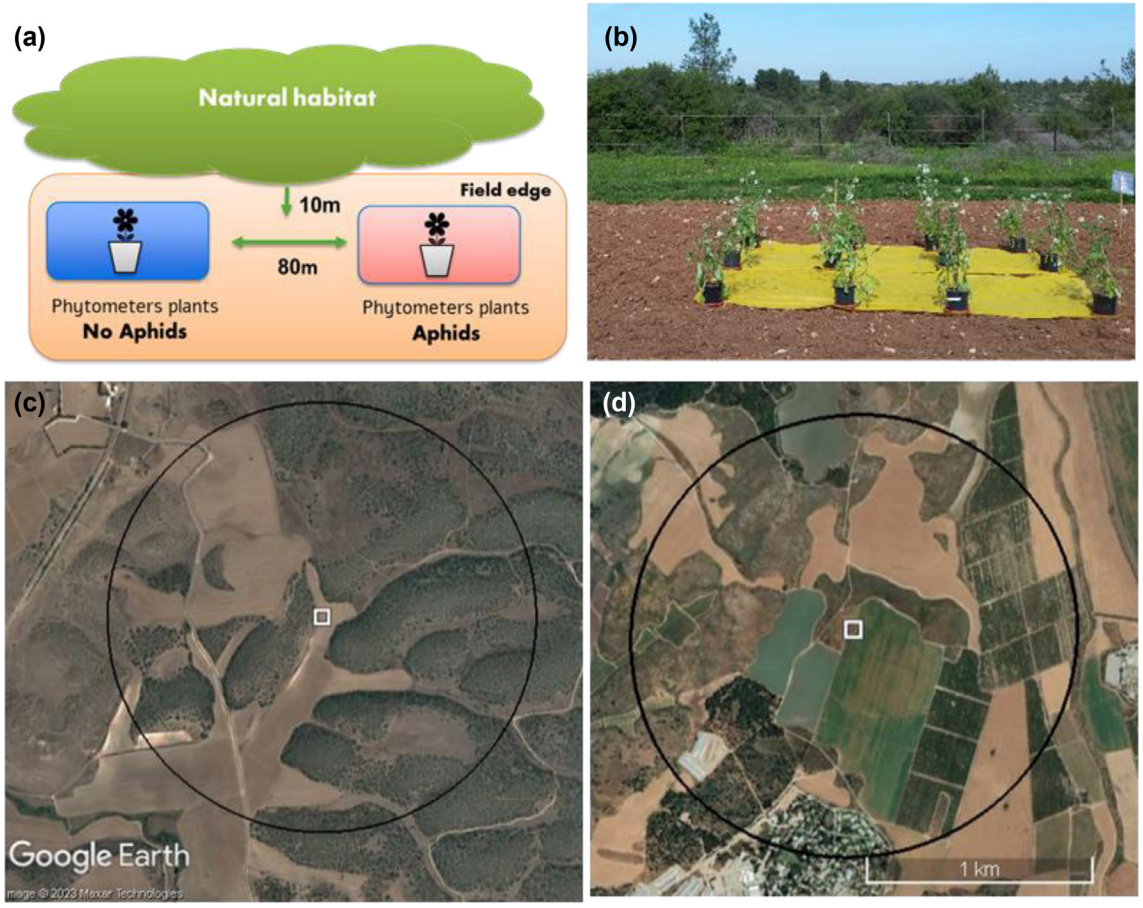


Figure 1. (A) Schematic representation of the experimental set-up of a study site comprising two adjacent phytometer patches. (B) A study site showing the surrounding landscape and a phytometer patch within a crop-free field. (C) Arial view of the 1 km radii around two sites with contrasting landscape context.

each were conducted per patch between 8:00 and 16:00 h, alternating between the aphid-infested and aphid-free patches. The observations were done on half of the plants in the patch at the time (six plants), to allow simultaneous view of all the flowers. The number of observation rounds was dependent upon weather conditions. Flower visitors were classified as honeybees, wild bees, or non-bee pollinators (mainly flies). A visit was recorded only when the visitor landed on a flower and collected nectar and/or pollen; this excluded very brief and functionally negligible visits during which visitors barely came in contact with anthers and/or stigmata. Pollinator visitation frequency was then calculated as the total number of visits per experimental patch divided by the number of flowers and observation rounds in the patch.

Floral resource assessments and pollinator observations were performed on the same day at each of the study sites, under standardized and optimal weather conditions i.e. sunny days, 16–32°C, < 2.5 m s^{-1} wind velocity. In order to check to these weather conditions, they were measured a few times during the course of each sampling day.

At the conclusion of the field experiment, we randomly selected four plants per patch in each study plot and transferred them to a net house for seed-set monitoring. Prior to transfer, 10 fresh flowers from the upper half of each plant were enclosed individually in organza bags. The remaining flowers were clipped in order to standardize fruit load per plant. Each plant was then covered with cellophane to avoid inter-plant pollen contamination during transport. In the net houses, we monitored seed set by opening mature pods and recording the number of fully developed seeds. Seed set was averaged for each combination of experimental patch and year.

Statistical analysis

We were interested in how local observations (pollinator visitation and seed set) depend on local conditions (aphid treatment) and the landscape context (floral resources). Quantifying effects of the landscape context requires estimating both the direction of landscape effects and the spatial scale over which these effects act. This can be done by evaluating the respective landscape property in concentric circles with different radii around each observation point and using the obtained scale-specific landscape properties as explanatory variables in further statistical analyses (Martin et al. 2019). However, this approach has an important limitation: it assumes that a landscape element that lies just inside the circle has the same effect on the observation as an element that is next to the observation point, whereas a landscape element that is just outside the circle has no effect at all. Simultaneously including multiple landscape properties obtained for circles of different radii is also problematic because these properties are typically collinear and because their joint inclusion markedly increases model complexity.

To overcome this problem, we developed a new, spatially continuous variant of neighbourhood models (Canham and Uriarte 2006) that estimate the effect of resource landscapes surrounding our experimental patches. Neighbourhood models were developed in plant ecology. They statistically estimate how the performance of focal plants is modified by the effects of point-like objects (e.g. other plants) in their neighbourhood, and how these neighbour effects decay with distance (Lachmuth et al. 2018). In this study, however, we were not interested in the effect of spatially discrete points but rather in the effect of spatially continuous neighbourhoods surrounding the experimental patches. We therefore developed spatially continuous neighbourhood models that describe how the effect of floral resources per unit area decays with distance from the experimental patch.

Conceptually, the total effect N of the neighbouring resource landscape (up to distance x_{max}) on flower visits and seed set in a focal patch can be described as a spatial integral in polar coordinates

$$N(\alpha) = \int_{\varphi=0}^{2\pi} \int_{x=0}^{x_{max}} \beta r(\varphi, x) f(\alpha, x) dx \, d\varphi \quad (1)$$

where $r(\varphi,x)$ is the resource quantity at angle φ and distance x from the patch, β is the local effect of this resource quantity, and f is a spatial kernel that describes how the effect decreases with distance x (Fig. 2). The strength of this distance decay is determined by kernel parameter α which measures the distance at which the effect of a location in the resource landscape drops to 50% of its maximum at distance 0 (Fig. 2; Walter et al. 2023).

This leads to

$$N(\alpha) = \beta \int_{\varphi=0}^{2\pi} \int_{x=0}^{x_{max}} r(\varphi, x) f(\alpha, x) dx \, d\varphi = \beta R(\alpha), \quad (2)$$

where $R(\alpha)$ is a distance-weighted neighbourhood resource index dependent upon kernel parameter α.

To approximate $R(\alpha)$ for a given resource landscape surrounding an experimental patch, we first divided a circle with radius $x_{max} = 1000$ m around each patch into concentric rings 10 m in width. We then used Monte Carlo integration with 10^7 randomly placed points per landscape to calculate the total quantity of resources per ring. For a given value of α, the distance-weighted neighbourhood resource index is then approximated as

$$R(\alpha) = \sum_i T_i \, f(\alpha, d_i), \quad (3)$$

where T_i is the total resource quantity in ring i, and d_i is the average of the inner and outer radii of this ring.

We used kernels of the general form

$$f(\alpha, d_i) = \exp\left(\ln \frac{1}{2} \left(\frac{d_i}{\alpha} \right)^k \right), \quad (4)$$

where k is a constant that determines kernel shape. We considered $k = 1$, 2 and 3, which yield exponential, Gaussian and

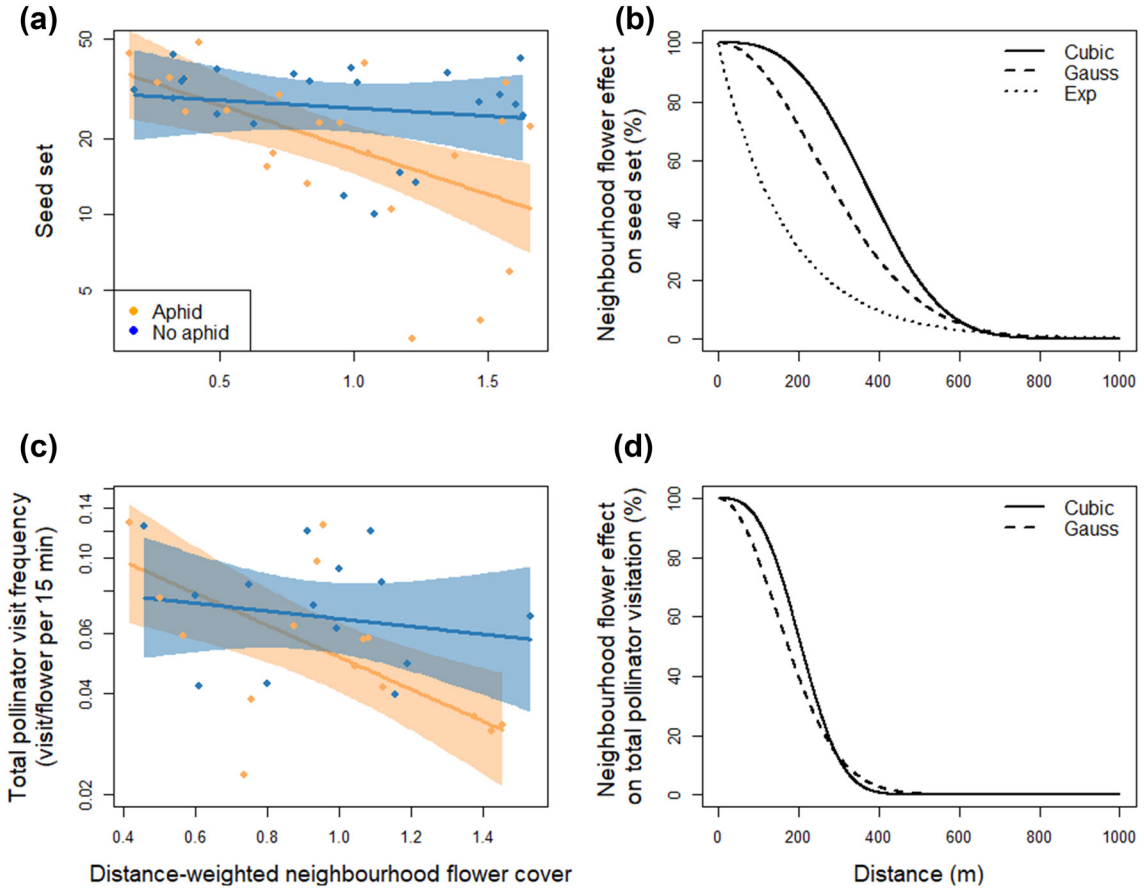


Figure 2. (a) Relationship between seed set in aphid-infested versus aphid-free *Diplotaxis erucoides* plants and distance-weighted flower cover in the neighbourhood of the experimental patches. The distance weighting of flower cover was done with the distance decay function (cubic kernel) estimated by the best neighbourhood model for seed set. y-axis has logarithmic scaling. Shaded areas are 95% confidence intervals. (b) Comparison of alternative kernels showing how the effect of neighbouring flower cover on seed set decays with distance. These kernels were estimated by alternative neighbourhood models. (c) Relationship between pollinator visitation frequency (all pollinators combined) in aphid-infested versus aphid-free plants and distance-weighted flower cover in the neighbourhood of the experimental patches (distance weighting used the cubic kernel estimated by the best neighbourhood model for visitation frequency). The y-axis has logarithmic scaling. Shaded areas are 95% confidence intervals. (d) Comparison of alternative kernels showing how the effect of neighbouring flower cover on visitation frequency (visits per flower per 15 min) decays with distance.

cubic kernels, respectively. The distance-weighting increases with an increase in k until distance α is reached, and decreases as distances exceed α (Fig. 2).

To test for interactive effects of resource landscapes and herbivory on pollinator visits and seed set, we embedded these spatially continuous neighbourhood models into linear mixed-effect models (cf. Nottebrock at al. 2017b, Walter et al. 2023). To this end, we included the neighbourhood resource index $R(\alpha)$ as a fixed-effect variable in linear mixed-effect models fitted with package lme4 (Bates et al. 2015) in R ver. 3.4.0 (www.r-project.org). Since this variable depends on the unknown distance parameter α, we used one-dimensional optimization (R optimize function) to find the value of α for which the respective linear mixed-effect model has minimal negative log-likelihood (Nottebrock et al. 2017b, Walter et al. 2023). Specifically, we optimized α within the range of 0–800 m. 95% confidence intervals of the α parameter were calculated from the likelihood-profile for this parameter (Venzon and Moolgavkar 1988). For other model parameters we calculated parametric 95% confidence intervals using package 'ciTools' (Haman and Avery 2020).

The linear mixed-effect models used log-transformed pollinator visitation frequencies and seed set as response variables. Data were pooled for each phytometer patch. The full models for each response variable included fixed effects of neighbourhood resource index, herbivory treatment (aphid-infested versus aphid-free plants), and their interaction. The models also included random effects of site and year (the latter only for seed set). For each response variable, we considered full models using exponential, Gaussian and cubic kernels (Supporting information). In addition, for each response variable and kernel type we considered simplified models that included main effects of the neighbourhood resource index and/or herbivory treatment, as well as the null model. Note that simplified models without the neighbourhood resource index can be fitted as standard linear mixed-effect models.

We compared these 15 alternative models for each response variable using the Akaike information criterion (AIC). We also used a linear mixed-effect model with a random site effect to test for effects of log-transformed pollinator activity on log-transformed 2017 seed set data.

Results

A total of 5789 flower visits were recorded during 93 h of observation. We did not observe pollinators feeding on honeydew. Seventy-one percent of all recorded visitors were wild pollinators, comprising 63% wild bees and 37% non-bee pollinators, of which 92% were flies, 6% were beetles, 1% were wasps and butterflies. Managed honeybees contributed 29% of all recorded flower visits.

Seed set

Seed set of aphid-free plants was higher than that of infested plants (likelihood-ratio test; $\chi^2_{1\,df}=5.11$, $p=0.02$). The three best models (Table 1) all included an interaction between herbivory treatment and neighbourhood resource index (distance-weighted flower cover with distance weighting determined by the spatial kernel with estimated distance parameter α Fig. 2). These models predict negative effects of neighbouring flower cover on seed set that are stronger for aphid-infested plants (Fig. 2a). The effect of surrounding flower cover on seed set decreased to 50% at distances of 380, 290 and 120 m (distance parameter α), in the best models with cubic, Gaussian and exponential kernels, respectively (Fig. 2b, Table 1). In the best model, neighbouring flower cover and herbivory treatment accounted for 28% of variance in seed set, with random effects of study site and year accounting for a further 24% (Table 1). Total pollinator activity (all visitors combined) had a positive effect on seed set of the model plants in 2017 ($\chi^2_{1\,df}=7.94$, $p < 0.01$).

Pollinator visitation

As for seed set, the best models for total pollinator visitation describe the interaction between herbivory treatment and neighbourhood floral resource index; they all predict negative effects of neighbouring flower cover on pollinator visitation. The negative effects are stronger for aphid-infested plants

Table 1. Best models (delta AIC < 2) showing the relationships between pollination services to focal plants (seed set and pollinator visitation) and aphid treatment (N: no aphids), neighbourhood floral resource index $R(\alpha)$, and their interaction. Models contained 'plot' and 'year' (the latter only for seed set) as random effects. The table gives the type of spatial kernel, AIC, degrees of freedom, the estimated distance parameter α, the marginal and conditional R^2 (R^2_m including only fixed and R^2c including fixed and random effects) as well as the estimated fixed effect parameters (Intercept and $R(\alpha)$ are intercept and resource effect for aphid-infested plants, Aphids N the difference in intercept and Aphids N: $R(\alpha)$ the difference in resource effect between aphid-free and aphid-infested plants).

Explanatory variables (× for main effects and interaction)	Kernel	AIC	df	Distance parameter α (m)	R^2_m	R^2_c	Intercept	Aphids N	$R(\alpha)$	Aphids N: $R(\alpha)$
Models for seed set										
Herbivory treatment × Neighboring flower effect	cubic	79.2	7	376.3	0.28	0.52	3.72	−0.29	−0.82	0.67
	gauss	79.5	7	290.5	0.28	0.51	3.71	−0.28	−0.81	0.66
	exp	80.3	7	117.6	0.27	0.49	3.69	−0.24	−0.78	0.60
Models for pollinator visitation (all guilds together)										
Herbivory treatment × Neighboring flower effect	cubic	32.1	6	207.96	0.28	0.86	−1.89	−0.56	−1.08	0.82
	gauss	32.8	6	174.94	0.27	0.85	−1.91	−0.59	−1.07	0.86
Models for honeybees										
Herbivory treatment × Neighboring flower effect	cubic	138.2	6	419.8	0.24	0.79	−12.17	5.22	5.55	−3.55
Herbivory treatment + Neighboring flower effect	cubic	138.7	5	418.8	0.23	0.76	−10.98	1.76	4.28	
Herbivory treatment × Neighboring flower effect	gauss	139.0	6	139.0	0.22	0.78	−11.82	5.14	5.15	−3.44
Herbivory treatment + Neighboring flower effect	gauss	139.1	5	332.3	0.21	0.76	−10.72	1.79	3.18	
Herbivory treatment × Neighboring flower effect	exp	140.2	6	132.2	0.18	0.78	−11.10	4.92	4.36	−3.15
Models for wild bees										
Herbivory treatment × Neighboring flower effect	exp	71.8	6	382.3	0.10	0.84	−3.52	−2.40	−0.13	2.33
Herbivory treatment × Neighboring flower effect	gauss	72.9	6	400.0	0.06	0.85	−2.90	−2.15	−0.78	2.08
Models for non−bees pollinators										
Herbivory treatment + Neighboring flower effect	cubic	65.2	5	304.3	0.17	0.46	−3.60	0.09	−1.10	
Herbivory treatment + Neighboring flower effect	gauss	65.5	5	263.9	0.15	0.47	−3.62	0.09	−1.08	
Herbivory treatment × Neighboring flower effect	cubic	66.88	6	298.4	0.17	0.46	−3.44	−0.35	−1.28	0.45

than for aphid-free plants (95% CI [−1.71, −0.45], Table 1, Fig. 2c). The effect of surrounding flower cover on pollinator visitation frequency decreased to 50% at distances of 208 and 175 m in the best models with cubic and Gaussian kernels, respectively (Fig. 2d, Table 1). In the best model, neighbour flower cover and herbivory treatment accounted for 28% of variance in pollinator visitation, with random effects of study site and year accounting for a further 58% (Table 1).

We next tested whether pollinator functional groups responded differently to surrounding flower cover and herbivory. While honeybee visit frequency was higher on aphid-free plants than on infested plants ($\chi^2_{1\ df}=9.53$, $p < 0.01$, Fig. 3), wild pollinators (bees and non-bees) did not show such a preference (wild bees – ($\chi^2_{1\ df}=0.13$, $p=0.72$; non-bee pollinators – ($\chi^2_{1\ df}=0.04$, $p=0.84$, Fig. 3).

Neighbourhood modeling for pollinator visitation revealed differing trends among the different pollinator groups (Table 1, Fig. 4). The best model for honeybees predicted a positive effect of neighbouring flower cover on their activity (Fig. 4a, Table 1), while a negative effect is predicted for non-bee pollinators (Fig. 4c, Table 1). The best model for wild bees included an interaction between herbivory treatment and neighbourhood floral resource index; visitation of the aphid-free plants was positively affected by neighbour flower cover, and visitation of the infested plants did not show a clear response (Fig. 4b). The three pollinator types did not differ clearly in the spatial scales at which their visitation responded to neighbouring flower cover, as indicated by largely overlapping 95% confidence intervals for kernel parameter α (Fig. 5).

Discussion

In this study, we used phytometer plants in agricultural landscapes and applied a resource landscape approach, to explore the effect of herbivory and the distribution of floral resources on pollination services. Pollinator activity and pollination services were found to be affected by these factors and by the interaction between them; neighbouring flower cover had a negative effect on total pollinator activity and seed set, and this negative effect was more pronounced for aphid-infested plants (Table 1, Fig. 2). We further found that different pollinator guilds in the system – managed honeybees, wild bees and non-bee pollinators – responded differently to surrounding flower cover) and herbivory (Table 1, Fig. 3–4). To the best of our knowledge, this study is the first to examine these complex plant–herbivore–pollinator interactions across resource landscapes.

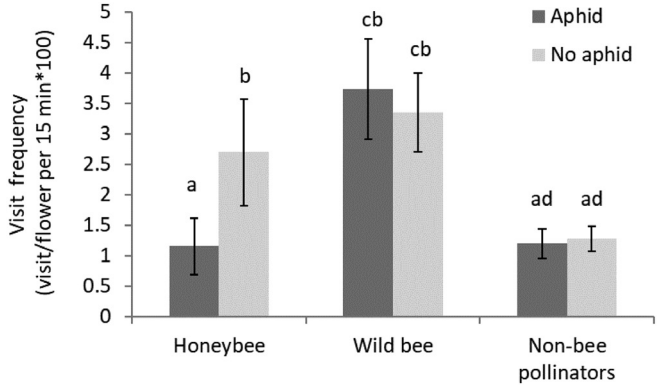


Figure 3. Flower visitation rate (mean ± SE) of the different pollinator functional groups on aphid-infested and aphid-free *Diplotaxis erucoides*. Bars with a shared letter do not differ statistically (post hoc multiple comparison test by least-squares means; $p < 0.05$).

Effects of resource landscapes and herbivory on overall pollinator activity and pollination services

In our study system, an increase in surrounding flower cover had negative effects on total pollinator activity and seed set of phytometer plants, which likely results from competition for pollinators causing pollen limitation. While this suggestion is supported by the positive effect of visitation on seed set, a supplementary pollination treatment would be needed to unequivocally demonstrate pollen limitation (Lachmuth et al. 2018). The negative effect of flower cover may indicate competition for pollination services between our focal plants and surrounding flowers, as a result of a dilution and/or concentration effects. Both of these effects have been shown to occur in agricultural and natural ecosystems, between both crop and wild plants (Ghazoul 2006, Holzschuh et al. 2011, 2016, Evans et al. 2017, Grab et al. 2017, Xie et al. 2019). Dilution and concentration effects should therefore be integrated into the assessments of pollination service distribution across heterogeneous landscapes.

Interestingly, the negative competitive effect of surrounding flower cover on pollinator activity and seed set was much stronger on aphid-infested plants. Plant–pollinator interactions were thus shaped by an interactive effect of resource landscape and herbivory. Aphid herbivory may amplify the effect of competition with neighbouring flowering plants by decreasing the relative attractiveness of aphid-infested plants to pollinators. Plant attractiveness may be reduced by changes in visual and/or chemical properties of the flowers, and by decreasing the quantity and/or quality of floral rewards associated with herbivory (Moreira et al. 2019). In addition, the flowers of heavily infested plants may be less accessible to pollinators due to the large numbers of aphids covering their surface (Shapira et al. unpubl.). Aphid-infested plants may suffer a further reduction of seed set as a result of direct stress exerted by aphid herbivory (Haas and Lortie 2020).

Three equivalent models fit the spatial scale of the effect of neighbouring floral resources on the delivery of pollination services (seed set) to our phytometer plants (Fig. 2b). These models differ in their distance kernel function, and thus in their overall shape, but they all show a rapid decrease in the effect of neighbourhood flower cover on pollination services with distance extending up to 120–380 m. These results may reflect the high flower density in different natural and semi-natural patches in our fragmented heterogeneous study system. In such systems, pollinators, even relatively long-distance

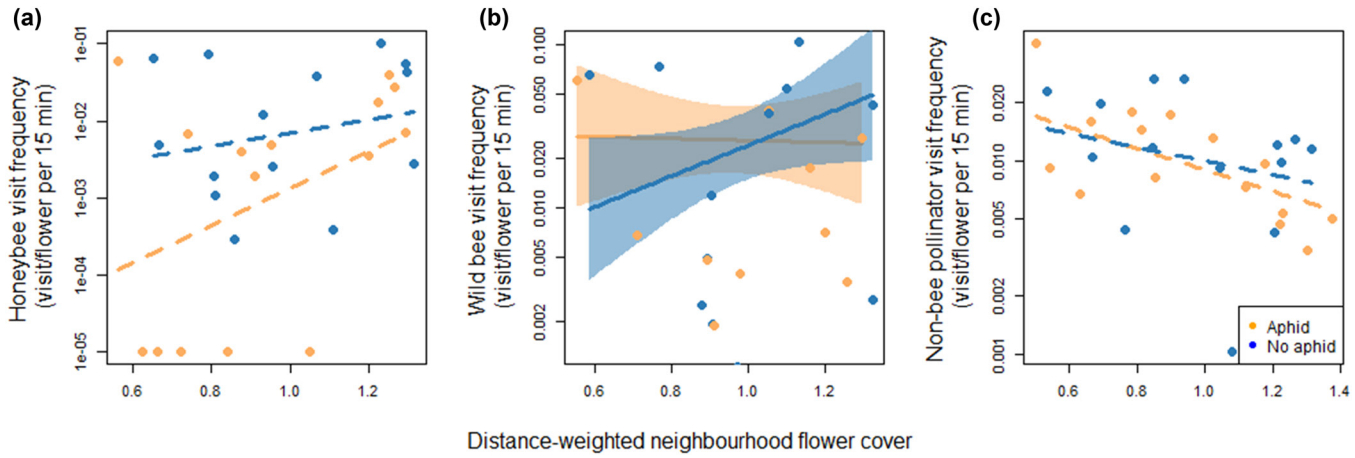


Figure 4. Predicted effects of surrounding flower cover on visitation by (a) honeybees (b) wild bees, and (c) non-bee pollinators on aphid-infested and aphid-free *Diplotaxis erucoides*. Neighbourhood flower indices and prediction lines were obtained from the best model for the visitation frequency of each pollinator type. Predicted model effects are represented as solid lines and dashed lines for significant and non-significant aphid treatment × neighbourhood floral resource index interaction, respectively. The y-axis has logarithmic scaling. Dots represent observed data. Shaded areas in (B) are the 95% confidence intervals.

flyers such as honeybees, may show short foraging distances. Moreover, the bee fauna in our study region is comprised mostly of small-bodied species (Pisanty et al. 2016) that have relatively short flying distances (Greenleaf et al. 2007).

Response of different pollinator guilds to resource landscapes and herbivory

Different pollinator guilds responded differently to aphid herbivory (Fig. 3); while herbivory had no effect on the visitation frequency of wild pollinators (bees and non-bees), honeybees visited aphid-free plants significantly more often. This result may be attributed to differences in life history traits

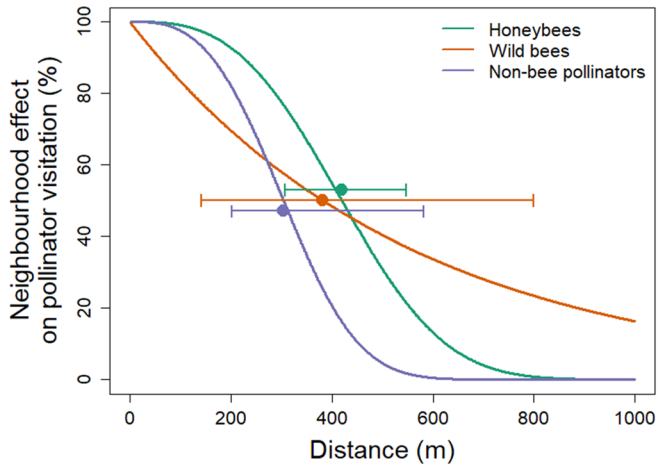


Figure 5. Distance-dependent neighbourhood effects of flower cover on flower visitation in focal plants by honeybees, wild bees and non-bee pollinators as estimated by the best neighbourhood model for each pollinator group (Table 1). See the Supporting information for all best models. Points indicate the distance α at which the neighbourhood effect drops to 50% of its maximal value, horizontal bars are the 95% confidence intervals of α.

such as level of sociality and group foraging, as well as morphological and physiological characteristics such as body size and flight ability (Pisanty and Mandelik 2015, Pisanty et al. 2016). As a eusocial organism with highly developed communication among nest-mates, honeybee foragers are likely to transfer information concerning differences between two adjacent floral patches (infested and un-infested) to their colonies, thus affecting collective foraging patterns in favor of the more attractive and rewarding patches. As most of the wild bees in this region are solitary, as are the non-bee visitors to the phytometer plants, they exhibited no collective information transfer that would affect their foraging preferences. Therefore, the stronger negative effect of surrounding flower cover on visitation and seed set of the infested plants (Fig. 2a, c) is likely to be mediated primarily by the foraging preferences of honeybees. Hoffmeister et al. (2016) also reported differences between honeybees and wild bees in their preferences for infested versus un-infested plants, but they reported patterns which differed from ours, and varied between plant species. This suggests that plant–pollinator–herbivore interactions and their effect on foraging choices of pollinators are context dependent (Karp et al. 2018), and may vary considerably among pollinator communities of different functional composition. As a result of honeybees' preference for aphid-free plants, infested plants were more dependent on wild pollinators for pollination. Hence, a cross-taxon perspective is needed for the management of pollination services, so that interactive and indirect effects of other organisms inhabiting the ecosystem are considered.

Further differences among pollinator guilds were revealed in the effect of surrounding flower cover on visitation activity (Fig. 4). First, non-bee pollinators (mainly flies) responded negatively to the surrounding flower plants, whereas honeybees and wild bees responded positively, with the exception of wild bees on infested plants. These differences may be attributed to different resources required for bee and non-bee

pollinators, especially floral and non-floral (e.g. prey, decaying organic matters), respectively (Rader et al. 2020). Secondly, only wild bees exhibited an interactive effect between aphid herbivory and surrounding flower cover. Namely, the enhancement effect of floral landscapes on wild bee visitation was limited to the non-infested patches. It seems that the wild bees were more responsive to changes (likely, reduction) in floral quality or the attractiveness of aphid-harboring plants, compared to the surrounding bloom.

Differences among pollinator guilds might be reflected by the spatial scale and shape of kernels characterizing their response to resource landscapes (Fig. 5). For instance, the solitary foraging behaviour of wild bees could make their kernels more fat-tailed than that of group-foraging honeybees. However, the broadly overlapping confidence intervals of the spatial scales of kernels (Fig. 5) show that our study had limited statistical power to detect such differences. Moreover, it should be noted that foraging activity is also affected by the distribution, quality and composition of nesting resources. While quantifying the availability of nesting resources was beyond the scope of the current study, the suggested link between the foraging behaviour of animals, and kernels describing their response to resource landscapes, merits further studies with an increased sample size (cf. Walter et al. 2023).

Conclusions

Assessment of pollination services should be based on both a resource landscape approach and integration of potential interactions among dominant co-occurring organisms. We were able to identify the scale at which pollinators respond to resource landscapes, and discern pollinator foraging behaviour patterns by quantifying resource distribution and applying neighbourhood modeling. We found that spatial scales of effects were limited (mostly < 1000 m), thus demonstrating the importance of local vegetation management for pollination services. Furthermore, exploring the combined and interactive effects among resource landscape, pollinators and herbivores enabled us to understand the direction and the extent of floral resource distribution's influence on the provision of pollination services. Importantly, different pollinator guilds were affected differently by resource landscapes and herbivory, highlighting the need for integrating a life-history approach to the study of pollination service delivery. Our results highlight possible mechanisms underlying interactions among pollinators, herbivores and foraging resource landscapes in natural and agroecosystems. Drawing more generalized conclusions and making management recommendations based on our study system is premature; further research is needed of other landscapes and plants, both wild and agricultural crops.

Finally, the resource landscape approach applied here should be expanded in future work to address additional focal resources of pollinators, such as the availability and quality of nesting sites. More so, flower cover (relative abundance) is only a rough measure of actual resource availability, as different flower species may vary considerably in the overall amount and properties of pollen and nectar they provide. Additional gauges that better reflect actual distribution of forage resources in different land-cover types will likely enhance the accuracy of the resource landscape approach. Ultimately, a combined forage and nesting resource landscape approach may further advance our ability to accurately map and analyze the role of resources in shaping pollinator activity and pollination services.

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Data availability statement

Data are available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.n8pk0p33t (Shapira et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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