RESEARCH ARTICLE

Multiscale spatial analysis of two plant–insect interactions: effects of landscape, resource distribution, and other insects

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Abstract

Context Biotic resource exploitation is a critical determinant of species' distributions. However, quantifying resource exploitation patterns through space and time can be difficult, complicating their incorporation in spatial ecology studies. Therefore, understanding the local drivers of spatial patterns of resource exploitation may contribute to better large-scale species distribution models.

Objectives We investigated (1) how the resource exploitation patterns of two trophic interactions (plant–insect) are explained by insect behaviour, resource aggregation, and potential insect-insect interactions. We also analyzed how (2) resource patch size and (3) resource accessibility in a heterogeneous landscape affected host exploitation patterns.

Methods We quantified nectar robbing by insects in the genus *Bombus* (bumblebees) and seed predation by *Brachypterolus vestitus* larvae (Antirrhinum beetle) on *Antirrhinum majus* L. (wild snapdragons) in the Pyrenees Mountains, Catalonia, Spain. We tested hypotheses about resource exploitation by integrating spatial analyses at multiple scales.

Results Both trophic interactions were aggregated, explained by the aggregation of their resource. At some scales, nectar robbing is more aggregated than the resource. Trophic interaction abundance is proportional to resource patch size, following the ideal free distribution model. Landscape features do not explain the locations exploited. Nectar robbing and seed predation occur together more often than expected.

Conclusions Our findings suggest that multiple biotic and ecological spatial factors may simultaneously affect resource exploitation at a local scale. These findings should be considered when developing agricultural projects, management plans and conservation policies.

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Abbreviations

CI	Confidence Intervals
CSR	Complete Spatial Randomness (referring to point processes)
GLM	Generalized Linear Model
HSI	Hopkins-Skellam Index

KDE	Kernel Density Estimation (referring to maps)
NLR	Null Linear Regression
PPA	Point Pattern Analysis
SCE	Simulation Confidence Envelope

Introduction

Biotic interactions are key drivers of community structure (Kéfi et al. 2012; Woodward et al. 2010) and shape species distributions on fine, local scales (Franklin & Miller 2009; Perea et al. 2021), but also at the scale of species' ranges (Wisz et al. 2013; Ortego and Knowles 2020). Despite their importance, biotic interactions are difficult and expensive to quantify thoroughly across space and time (Ovaskainen et al. 2016). Therefore, species distribution models have historically focused on abiotic factors to determine where organisms live (Graciá 2020, but see recent advances by Gargano et al. 2017 and Ortego & Knowles 2020). However, accounting for biotic interactions can greatly increase the predictive power of the distribution models (Ovaskainen et al. 2016). Joint species distribution models, for example, account for relationships between species in addition to environmental predictors (Wilkinson et al. 2021). Nevertheless, incorporating the multi-scale nature of biotic interactions poses a challenge in its application (Ovaskainen et al. 2016). Biotic interactions often result in aggregation, with a high potential impact on the distribution of populations and species. For example, individuals may be found in clusters in order to defend against biotic threats (Bertolini et al. 2019) or aggregating around beneficial species whose suitable environmental conditions are patchily distributed (Drake & Richards 2018; Hochstrasser & Peters 2004). Furthermore, if an aggregated species serve as the resource for yet another species, the host distribution can shape the distribution and size of resource-dependent populations, modify the exploitative behaviour (Goulson 2010; Matter 2000; Jácome-Flores et al. 2018) and influence coexistence with other resource-dependent species (Chesson 2000; Lancaster & Downes 2004). Specifically, plant hosts for herbivores usually aggregate in patches (Goulson 2010), where patch size can be the main limiting factor for consumer populations (Cade et al. 1999; Schooley & Wiens 2005). Therefore, the relationship between patch size and consumer abundance can be important for conservation (Matter 2000).

Three potential relationships between consumer abundance and resource patch size have been proposed. First, the *resource concentration* hypothesis suggests that consumers are disproportionately more attracted to larger patches due to an exponential increase of resources and because large patches are easier to find (Connor et al. 2000; Root 1973). Second, Schooley and Wiens (2005) coined the *undermatching* hypothesis, which suggests that populations are more abundant than expected in patches with fewer resources. Third, Fretwell and Lucas (1969) created the *ideal free distribution* model, stating that when larger patches are disproportionately more exploited, then smaller patches will become more resource-dense and attractive to exploiters. This feedback creates an even exploitation of resources that minimizes competition. Studies have found support for all three theoretical relationships (Connor et al. 2000; Kennedy & Gray 1993; Schooley & Wiens 2005), suggesting that context is important, but it is still unclear why different hypotheses hold in different systems.

Patches are not isolated but rather, are strongly influenced by their location within the landscape (Schooley & Wiens 2005). In a heterogeneous landscape, patch access could be influenced by features such as natural barriers, environmental gradients or human disturbance (Gargano et al. 2017; Verboven et al. 2014). Landscape changes that hinder access to resources may reduce insect population abundance (Gargano et al. 2017) and plant reproductive success (Verboven et al. 2014), which may lead to biodiversity loss (Knisley 2011). On the other hand, some human activities that were considered harmful for pollinators—such as agricultural and grazing practices—may have a neutral effect on bee abundance when done at low intensity (Winfree et al. 2009). Furthermore, human-modified landscapes can positively impact insect populations: garden areas and urban parks favour nesting for bumblebees, due to their greater and prolonged deposit of resources throughout the year (McFrederick & LeBuhn 2006; Osborne et al. 2007). However, research on how landscape heterogeneity and ecological gradients affect plant–insect interactions is still scarce (Gargano et al. 2017).

In this study, we analyze three aspects of the fine-scale exploitation patterns of two antagonistic plant–insect interactions: seed predation by snapdragon beetle larvae and nectar robbing by bumblebees in wild snapdragons. (summarised in Table 1). First, we ask how each interaction is affected by spatial patterning of the resource and the other interaction. We predict that exploitation patterns by both beetles and bumblebees are significantly aggregated, due to the bumblebees' social nesting behaviour (Goulson 2010) and due to conspecific attraction observed in a congener beetle (MacKinnon et al. 2005). We also predict that the two plant–insect interactions are found together less often than expected due to chance because of non-trophic interactions: they may compete for a similar resource (nectar), and/or nectar robbing may negatively impact fruit development, affecting the seed predators (Stout & Goulson 2000). Second, we test the three alternative patch size-abundance hypotheses by asking whether the probability of each plant–insect interaction depends on resource patch size. Third, we ask how landscape heterogeneity such as human disturbances and natural landscape barriers affect resource exploitation. We specifically predict that low-intensity farming in the study area does not affect nectar robbing and that urban gardening and parks increase the frequency of both plant–insect interactions. We tested these predictions using spatial analysis of a large, high-resolution dataset of plant–insect interactions in a single population.

Materials and methods

Study system and site

Antirrhinum majus L. (wild snapdragon; Plantaginaceae) is a short-lived self-incompatible perennial herb (Andalo et al. 2010). Snapdragons live in rocky cliffs and disturbed areas in the French and Spanish Pyrenees Mountains (Khimoun et al. 2013). Individuals often aggregate in small persistent patches (Jaworski et al. 2016), likely due to passive seed dispersal (Andalo et al. 2010; Khimoun et al. 2013). Flowers are zygomorphic with a personate corolla, produced on terminal spikes with up to 15 simultaneously open flowers. Fruits can produce up to 400–500 seeds (Usha 1965).

Only large bumblebees (Hymenoptera) have enough strength to force their way through the flower lips to access snapdragon nectar (Guzmán et al. 2017) and pollinate snapdragons (Tastard et al. 2011, 2014). Bumblebees provide resources to their offspring by foraging on flowers in the area surrounding their nests (Goulson 2010). In our focal population, (Andalo et al. 2019) found that two of the three bumblebee species that pollinate snapdragons—*Bombus terrestris* L. and *Bombus muscorum* L.—shift their behaviour to nectar robbing across the flowering season. Specifically, they found that nearly 90% of visits produced between 05/25/2016 and 07/12/2016 were nectar robbing. Nectar robbing is the foraging behaviour in which a nectar reward is obtained without providing any benefit to the plant. Its effects on plant fitness can be neutral (Morris 1996) or detrimental, reducing the seed set (Goulson 2010; Irwin & Maloof 2002). Primary nectar robbing is defined as the first time a bumblebee robs nectar on a flower. It is easily traceable by observing the holes that bumblebees chew in the basal half of the snapdragon corolla (Andalo et al. 2019; Goulson 2010).

In our study system, we called the behaviour of feeding on flower ovules and immature seeds "seed predation". This type of feeding behaviour can have highly detrimental effects on plant fitness (Whitney & Stanton 2004). We observed larvae of *Brachypterolus vestitus* Kiesenwetter (snapdragon beetle; Coleoptera) inside 19% of sampled flowers, feeding on the ovules and possibly nectar. Often multiple individuals were found in each flower (up to 8).

Table 1 Summary of the hypotheses and spatial analyses used

spatial scale (m)	interactions	prediction: exploitation patterns are explained by…	analysis
0–120	trophic	behaviour (tendency of insects to aggregate)	point patterns
	non-trophic	the spatial pattern of the other interaction	
1 – 220	trophic	the resource patch size	quantile regression
0 – 1,500	trophic	the landscape structure	distance GLM

Adult *B. vestitus* lay their eggs inside snapdragon flower buds, where both adults and larvae feed on inner floral tissues of *A. majus* (Butler-Stoney 1988; Jelíken 2007; Wagner 1994). To identify the species, we sequenced the standard mtDNA COI barcode region from tissue of two larvae collected inside *A. majus* flowers, and six adult coleopterans collected in or on *A. majus* at our study site using standard methods (standard mtDNA COI sequences analysis performed by Brent Emerson's laboratory at CSIC and IPNA in La Laguna, Tenerife, Spain). Then we used BLAST analysis against GenBank to identify the insects (NCBI 2022). The two seed predators larvae and one adult specimen had > 99% match to *B. vestitus* (Supplementary Table 1 in Online Resource). Voucher specimens are deposited at Museo Nacional de Ciencias Naturales, Spain (larvae ID: MNCN_Ent 344,534, MNCN_Ent 344,535, adult ID: MNCN_Ent 356,420). Species in the genus *Rhinusa* are also known *Antirrhinum* seed predators, but they are present at a later stage of fruit development than when we surveyed plants (Jaworski et al. 2016).

Our study site is the Vall de Ribes, Catalonia, Spain. The study area is 3 km wide, between Planoles (42.3166N, 2.1042E) and Fornells de la Muntanya (42.3240N, 2.0472E) (Fig. 1). The site has been used in past research because it contains a flower colour cline, where yellow- and magenta-flowered *A. majus* meet and interbreed (Andalo et al. 2010; Whibley et al. 2006). Here, we ignore the effects of flower colour on plant–insect interactions because preliminary analysis indicates that nectar robbing and seed predation are not affected by flower colour (C. Baskett, unpublished data).

Data collection

We quantified the prevalence of nectar robbing and seed predation, two trophic interactions (i.e., interactions based on resource exploitation) involving snapdragons. We conducted a field survey from 06/16/2020 to 07/07/2020, during the peak flowering season. We rotated haphazardly between patches all over the sampling area on a daily basis and returned
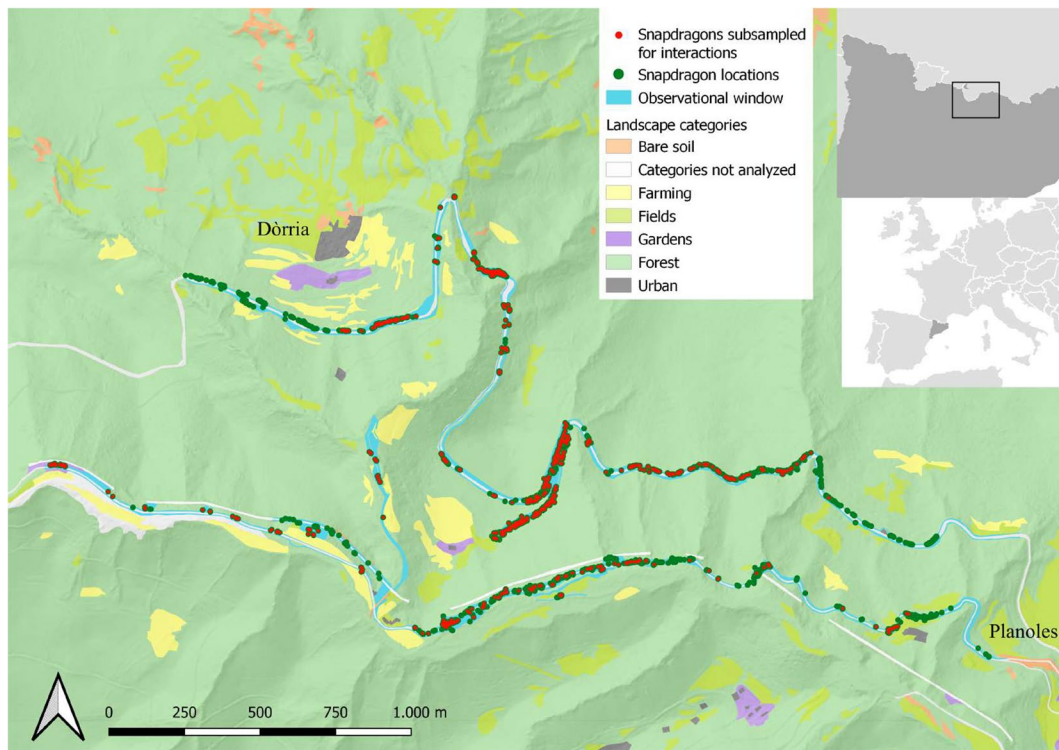

Fig. 1 Map of the study area, depicting the location of all snapdragons, the subset of snapdragons selected for plant–insect interaction analysis, the various landscape categories used, and the location of the two villages

to each patch multiple times. Censuses were taken between 9 am and 6 pm. For 944 individuals (a haphazard subset of the population, due to limited time) we collected the uppermost flower and stored it in the fridge (4ºC) for a maximum of 48 h before quantifying the trophic interactions. Primary nectar robbing sensu Goulson (2010) was indicated by a hole in the basal half of the flower corolla. Seed predation was indicated by the presence of *B. vestitus* larvae inside flowers.

In order to perform spatial analysis, we collected precise location data on the focal plants and all additional snapdragons we were able to access in the study area, for a total of 2,333 individuals. Location data (accurate to within 3.7 m at our site, Surendranadh et al. 2022) was recorded using GeoXT handheld GPS units (Trimble, Sunnydale, CA, USA). Using QGIS software (v. 3.10.14) (QGIS Development Team 2024), we manually moved the few points that were accidentally situated inside the road—due to Trimble measuring errors—to the nearest site outside it. We incorporated the point dataset inside an Observational Window (sensu Baddeley et al. 2016), which comprises the sampled area next to roads and paths where snapdragons flourish (14.86 ha), informed by 12 years of sampling snapdragons at this study site (N. Barton, unpublished data). We reprojected the spatial objects from the geographic coordinates system (EPSG: 4326) to the projected coordinates system (EPSG: 25,831) in R (v. 3.6.3) (R Core Team 2020) with the package *sf*, to facilitate working with the landscape category polygons.

Aggregation patterns

One of the functions of Point Patterns Analysis (PPA) is to visualize and quantify spatial aggregation, which can provide insight into how resources are exploited (Lancaster & Downes 2004; Rodríguez-Pérez et al. 2012) and if mechanisms of competition, exclusion or coexistence exist (Brown et al. 2011). We used first and second-order PPAs to quantify the spatial patterns of the resource (snapdragons) and both trophic interactions (seed predation and nectar robbing). The test statistics of PPA were conducted with the R package *Spatstat* (Baddeley et al. 2016).

Before performing PPAs to test our hypotheses, we tested for homogeneity of the data, a crucial first step for deciding the appropriate PPAs. The intensity of points can be constant through space—called homogeneity—or vary by an intensity function, called inhomogeneity (Baddeley et al. 2016; Law et al. 2009). We tested for homogeneity using the quadrat counting and the Kolmogorov–Smirnov techniques. The quadrat counting technique is a chi-squared test defined from Pearson goodness-of-fit sensu Baddeley et al. (2016, pp. 163–168). We decided the optimal grid to perform the quadrat counting test was 18×12 cells. Each cell had a horizontal length of 185 m and a vertical length of 130 m. This resolution reflects a trade-off between snapdragon cluster size and bias. The Kolmogorov–Smirnov technique is a measure of discrepancy between cumulative distribution functions (Perry et al. 2006) sensu Baddeley et al. (2016, pp. 184–186). Both techniques showed significant intensity differences for the snapdragons and trophic interactions (Supplementary Table 2 in Online Resource), so our subsequent analyses assumed inhomogeneous data.

To analyze if the spatial distribution of the snapdragon is determined by spatially structured features and ecological gradients we performed first-order PPA (Gimond 2021; Law et al. 2009). Additionally, we tested if the aggregation of the trophic interactions follows from the degree of aggregation of the snapdragons, which act in this case as the spatially structured features. We used the Hopkins-Skellam analysis, as recommended for inhomogeneous PPA (Baddeley et al. 2016, p. 259; Rubak 2019). Its formula is defined in Table 2a. Hopkins-Skellam index (HSI) = 1 is consistent with completely spatially randomness (CSR) pattern, HSI < 1 indicates clustering, and HSI > 1 indicates overdispersion. The Hopkins-Skellam analysis was performed using the *hopskel.test* function from *Spatstat* in R. To estimate the P-values, we proceed with a bootstrapping test. We ran 999 Monte-Carlo simulations of the Poisson null model, which is a CSR process inside the same Observational Window. The significance threshold was set at $\alpha = 0.05$. Edge correction was not used because snapdragons were distributed next to roads and could not grow inside dense forests. These actual habitat boundaries are not an artefact of sampling, so edge correction is not needed (Law et al. 2009).

Out of 944 sampled plants, we found evidence of seed predation in 175 and of nectar robbing in 685. To estimate the degree of aggregation of the interactions independently from that of the resource itself,

Table 2 Summary of the formulas used

	metric	description	formula
a	HSI	Hopkins-Skellam index*	$= \sum\limits_{i=1}^{m} d_i^2 / \sum\limits_{j=1}^{m} e_j^2$
b	$\hat{L}_{inhom}(r)$	Transformation of the K-function to the inhomogeneous L-function *	$= \sqrt{\mathbb{E}[\sum_{x_j \in X} \frac{1}{\lambda(x_j)} 1\{0 < ||u - x_j|| \leq r\}|u \in X]/\pi}$
c	$\hat{L}_{inhom,pois}(r)$	Poisson null model of the L-function *	$\equiv r$
d	$\hat{L}_{crossinhom}(r)$	Inhomogeneous L-cross function *	$= \sqrt{\lambda_j^{-1} \mathbb{E}\left[t(u, r, X^{(J)})/u\epsilon X^{(i)}\right]/\pi}$
e	$K(x;6)$	Triweight method for the Kernel Density Map †	$= \frac{35}{32}(1 - x^2)^3 1_{|x| \leq 1}$

HSI: i and j are the index of a vector of the nearest-neighbour points, d_i is the nearest-neighbour distances for m randomly sampled data points, and the empty-space distances e_j for an equal number m of randomly sampled spatial locations. $\hat{L}_{inhom}(r)$ each point x_j from the point process X is weighted depending on the function of the intensity λ that is subject to the location u on a specific radius r. $L_{inhom,pois}(r)$: $\equiv$ represents identical to $\hat{L}_{crossinhom}(r)$: $X^{(j)}$ is the sub-process of points of type j, with intensity λ_j, and $t(u, r, X)$ is the count of r-neighbours. $K(x;6)$: x in a given point and 6 is the maximum derivative of Kernel for the Triweight method.

*Baddeley et al. (2016)

†Guidoum (2015)

we proceeded to reshuffle the interaction presence—also called random labelling—across the 944 sampled plants 999 times and obtain significance with bootstrapping.

To analyze if the spatial distribution of the exploitation patterns is determined by the spatial distribution of the resource, we performed second-order PPA. Second-order analyses quantify the influence between pairs of individuals (such as exclusion or aggregation) (Gimond 2021; Law et al. 2009). The method used is the Pairwise Distances with Ripley's K-function (Baddeley et al. 2016, pp. 242–246; Dale 1999). The modification of the K-function that applies to inhomogeneous data is the Kinhom (Baddeley et al. 2016, p. 243; Law et al. 2009; Perry et al. 2006). The inhomogeneous L-function is analogous to the inhomogeneous K-function. However, we used the L-function because it stabilizes the variance and helps with visual assessment of the graph. It was computed with the Linhom function from *Spatstat* (Baddeley et al. 2016, p. 245) and it is defined in Table 2b. Then the L-function is compared with the theoretical curve of the Poisson null model, defined in Table 2c (Baddeley et al. 2016, p. 206). The intensity was estimated with the *density* function from *Spatstat* (Baddeley et al. 2016, pp. 242–246). Some judgement is needed in choosing the appropriate bandwidth to smooth the intensity (Law et al. 2009; Rubak 2019). We chose a bandwidth value of 100 m because it created a

density map large enough to not interfere with the natural aggregation processes of snapdragons and small enough to distinguish the local intensity differences. Then we proceed to bootstrap, generating 999 simulations of the Poisson null model of the L-function (Baddeley et al. 2016; Swift et al. 2017). We then created simulation confidence envelopes (SCE) with an alpha level of 0.05. If the empirical L-function lies outside the SCE, we rejected the CSR null hypothesis (Baddeley et al. 2016, pp. 390–394). When the L-function lies above the SCE, it indicates clustering, and if it is below, it suggests an overdispersed pattern (Baddeley et al. 2016, pp. 390–394). We did the simulations for all plants and each plant–insect interaction.

To determine whether seed predation and nectar robbing occur together more frequently than expected, we conducted a second-order bivariate analysis. This analysis enables us to compare the spatial relationship between two point patterns and infer biological meaning, such as coexistence or dependence (Dixon 2013). To compare bivariate data, we used the inhomogeneous L-cross function. We transformed the K-cross function to L-cross function as described in Baddeley et al. (2016, pp. 594–596) to check how many type j events are nearby the i type (Table 2d). We used the L-cross function to examine whether the non-trophic interaction is more or less aggregated than expected. The L-cross function can also compare a point pattern

with a subsample of itself with a reshuffling procedure (Baddeley et al. 2016; Fletcher & Fortin 2018). We used this feature to demonstrate that the interactions were spatially randomly sampled to avoid bias in the spatial analyses (Supplementary Fig. 1 in Online Resource), and to find the spatial patterns of trophic interactions isolating the resource effect.

Density of trophic interactions v. habitat patch size

To test whether resource exploitation depends on resource patch size, we used quantile regression analysis of interaction frequency in discrete resource patches. We defined patches with the Kernel Density Estimation (KDE) map tool in QGIS. KDE is a commonly used tool to determine hotspots—or patches in our case (Nelson & Boots 2008). No edge correction was utilised because (1) the KDE applies to the intrinsic dataset, not to the individuals that could lie outside the Observational Window and (2) we clipped the area of the KDE inside the Observational Window. We chose the Triweight method (Table 2e) because it creates sharper patches (Guidoum 2015). The KDE bandwidth estimation differs from that chosen in the second-order analyses. In this case, the objective was to create a sharp KDE to identify the patches of resources. The likelihood cross-validation bandwidth selection method, with the *bw.ppl* function from *Spatstat*, provided the optimal bandwidth for our dataset: 3.2 m. Based on our visual perception, we considered that one plant per square meter is the minimum density to create a continuous snapdragon patch for the bumblebees and adult coleopterans. Therefore, we created the KDE contour map with the QGIS tool *contour* at a density of 1 ind./m^2 and a pixel size of 0.1 m.

We compared the resource patch area with the number of trophic interactions detected inside. The abundance was transformed to decimal logarithm after adding 1 (Connor et al. 1997; Schooley & Wiens 2005). We then used quantile regression analysis because it supports heteroscedastic data—like ours—and is equivariant to monotonic transformations (Cade et al. 1999). We proceed as sensu Schooley and Wiens (2005), indicating the 5% regression quantile as the lower constraint, the 50% as the median and the 95% as the upper one. The slope and confidence intervals (CI) of the 95% quantile were compared with the slope of the Null Linear Regression (NLR).

We calculated the NLR slope by dividing the number of snapdragons surveyed for plant–insect interactions by the total number of snapdragons across the dataset. If the NLR is between the 5% and 95% quantile regression lines, then our data is equivalent to the *ideal free distribution* hypothesis. If the NLR is significantly above the 95% quantile, it corresponds with the *undermatching* hypothesis. When the NLR is significantly below the 5% quantile, it matches the *resource concentration* hypothesis (Schooley & Wiens 2005). Simultaneously, if the 95% quantile had a significantly greater slope (CI 95%) than the 50% quantile, then the resource patch size is the active constraint of the trophic interaction among other factors, called a *limiting-factor relationship* (Cade et al. 1999; Schooley & Wiens 2005).

Resource accessibility in a heterogeneous landscape

To assess the accessibility to resources in a heterogeneous landscape, we computed the minimum distance between the location of each trophic interaction and six landscape features. Initially, we verified the spatial autocorrelation of the point-pattern data across four scales, employing the joint count test (Stevens & Jenkins 2000) conducted with the R package *spdep*. The scales used were 5, 20, 40, and 100 nearest neighbor points. This preliminary analysis confirmed that the trophic interactions were spatially autocorrelated.

To mitigate the influence of spatial autocorrelation and ensure minimal data loss while examining the association between trophic interactions and landscape features, we implemented a thinning process (pruning) on the point spatial data, separately for seed predation and nectar robbing. We followed the procedure outlined by Assis (2020) to determine the minimum thinning required to eliminate spatial autocorrelation. First, we thinned the complete dataset to retain one individual every X meters in the surrounding area, where X ranged from 1 to 30 m in 0.5 m increments (yielding 59 subsamples). Next, we evaluated spatial autocorrelation in the subsamples at the same four spatial scales (5, 20, 40, and 100 nearest neighbor points) using the joint count test. For subsequent analysis of landscape features, unambiguously avoiding autocorrelation across multiple scales, we selected the minimum thinning interval without significant spatial autocorrelation at any of these four scales. To account for potential variation introduced by randomness in the

thinning process, we conducted bootstrapping, repeating the thinning and autocorrelation tests one hundred times. Finally, we calculated the mean of the minimum thinning distances obtained through bootstrapping. The resulting minimum thinning distance necessary to eliminate significant autocorrelation was 18.5 m for nectar robbing and 3 m for seed predation, reducing the datasets to 155 and 466 plants, respectively.

We extracted the landscape features from the soil use layer of the *Institut Cartogràfic i Geològic de Catalunya* (Cobertes del sòl. ICGC 2018) and categorized them as bare soil, fields, farming, forests, gardens and urban areas (Supplementary Table 4 in Online Resource). We computed the minimum distance between the location of the trophic interactions and the landscape features using the QGIS geoalgorithm *v.distance*. We then generated a logistic GLM to compare the presence or absence of each trophic interaction (previously thinned to eliminate spatial autocorrelation) with the minimum distance to each landscape feature, thus it is independent of plant location.

Results

Aggregation patterns

First, we quantified spatial aggregation using the HSI. We found that the resource and both trophic interactions are significantly aggregated compared to a CSR process (Table 3). The second-order analysis showed that snapdragons and the trophic interactions are above the SCE on a fine scale (Fig. 2a). However, the snapdragon aggregation dilutes after a radius of 46 m and the resource exploitation by both trophic interactions at 35 m.

Second, we asked whether each trophic interaction is as aggregated as expected, given the degree of resource aggregation. For seed predation, neither the HSI nor the L-cross function showed any deviation from the expected aggregation of the snapdragons (Table 3, Fig. 2b). For nectar robbing, the HSI was lower than its resource (more aggregated), but the difference is only marginally significant ($p = 0.065$; Table 3). Similarly, the L-cross function was within the SCE at most scales, except for the range between 0–2 m and 50–63 m, where it exceeded the SCE, and after 120 m of radius, where it fell below the SCE (Fig. 2c).

Third, we compared the spatial aggregation of the two trophic interactions to each other, that is the non-trophic interaction. The observed L-cross function peaked around 8 m, then largely exceeded the SCE until 40 m, and finally fell below the SCE at 100 m (Fig. 3). This indicates that nectar robbing and seed predation occur together more often than expected at fine scales. However, the Fig. 3 also shows a repulsion effect of the non-trophic interactions at radius above 100 m.

### Density of trophic interactions v. resource patch size

In our study area, the 2,333 surveyed snapdragons clumped in 338 patches with a mean size of 15,84 m^2. The NLR had a slope (b1) of 0.405. For seed predation, the NLR lay between the 50% and 95% quantiles, consistent with the *ideal free distribution* hypothesis. Moreover, the 95% slope is significantly greater than the 50% slope, demonstrating a limiting-factor association with habitat patch size (Supplementary Table 3 in Online Resource and Fig. 4a). For nectar robbing, the NLR is between the 5% and 50% quantiles, also consistent with an *ideal free distribution*. However, we did not detect a significant limiting-factor association: the 95% and 50% quantile slopes were not significantly different (Supplementary Table 3 in Online Resource and Fig. 4b).

Table 3 Hopkins-Skellam analysis for the snapdragon plants and trophic interactions. N: population size or interaction sample size. HSI significantly less than 1 indicates clustering. P-value from CSR: H$_0$ is CSR. HSI reshuffled: HSI mean of the random shuffling of trophic interactions across plants. P-value from reshuffling: H$_0$ is HSI = HSI reshuffled. Significant P-values are bolded ($\alpha = 0.05$)

actors	N	HSI	*P*-value from CSR	HSI reshuffled	*P*-value from reshuffling
resource	2,333	0.013	< 0.001	-	-
seed predators	175 (944)	0.064	< 0.001	0.090	0.550
nectar robbers	685 (944)	0.009	< 0.001	0.090	0.065

Fig. 2 The clustering function (inhomogeneous L-function) of the resources and the trophic interactions spatial patterns. **a**) Resources (in green), seed predation (in black) and nectar robbing (in orange) compared with CSR (blue). **b**) Seed predation compared with the null of reshuffled resources. **c**) Nectar robbing compared with the null of reshuffed resources. *Solid lines* represent the observed value of the L-function ($\hat{L}_{obs}(r)$); the *dashed line* represents the mean of the Monte-Carlo simulations for the CSR or reshuffling ($\hat{L}_{theo}(r)$); the *shaded area* represents the space between lower ($\hat{L}_{hi}(r)$) and upper ($\hat{L}_{lo}(r)$) critical boundary from the simulations (SCE)
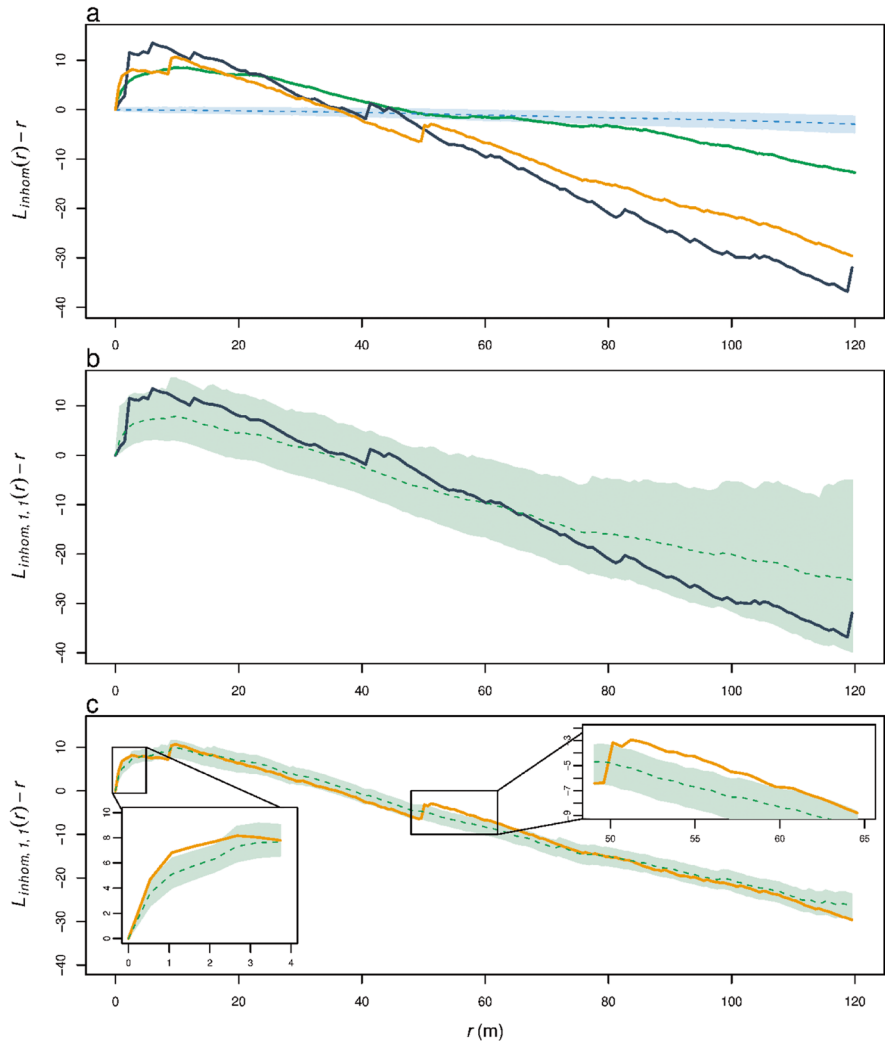
Resource accessibility in a heterogeneous landscape

The logistic GLM analysis did not detect any significant correlation between seed predation and nectar robbing frequencies and the location of any of the tested landscape features: bare soil, fields, forests, gardens and urban areas ($p > 0.1$ for all analyses). The results of the analysis are shown in Supplementary Table 5 in Online Resource.

Discussion

Biotic interactions and their strength shift when changing environmental conditions (Tikhonov et al. 2017) and the spatial scale (Ovaskainen et al.

2016). Here, we analyzed trophic and non-trophic interactions to ask how two insects exploit spatially structured resources at several spatial scales, and react to other exploiters. We integrated multiscale spatial analyses by sampling thousands of plants to quantify resource aggregation and patch size on a fine scale and by characterizing landscape heterogeneity. We found that seed predation and nectar robbing were as aggregated as the plant resource, increase proportionally with plant patch area, and are found together more often than expected at smaller scales. For a summary of the resulting findings, please refer to Table 4. Our results could be useful for building detailed spatial ecological models of resource exploitation to incorporate biotic interactions into spatial and landscape ecology,
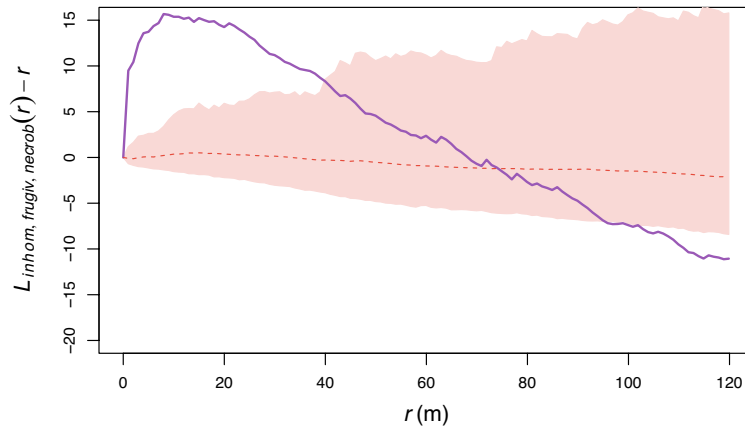
Fig. 3 The closeness function, called inhomogeneous L-cross function, of the non-trophic interaction (in purple) in a reshuffled bivariate interaction (in red). The *solid line* represents the observed value of the L-function for our data pattern ($L̂_{obs}(r)$);

the *dashed line* represents the mean of the reshuffling Monte-Carlo simulations j ($L̂_{theo}(r)$); the *shaded area* represents the space between lower ($L̂_{hi}(r)$) and upper ($L̂_{lo}(r)$) critical boundary from the simulations (SCE)

Fig. 4 Relationship between the number of trophic interactions and the resource patch size for (**a**) seed predation and (**b**) nectar robbing. The *green dashed line* represents the NLR with $b_1 = 0.405$ and $b_0 = 0$; the *solid lines* in each graph represent the 5%, 50% and 95% regression quantiles of both seed predation and nectar robbing. Data plotted on a log–log scale
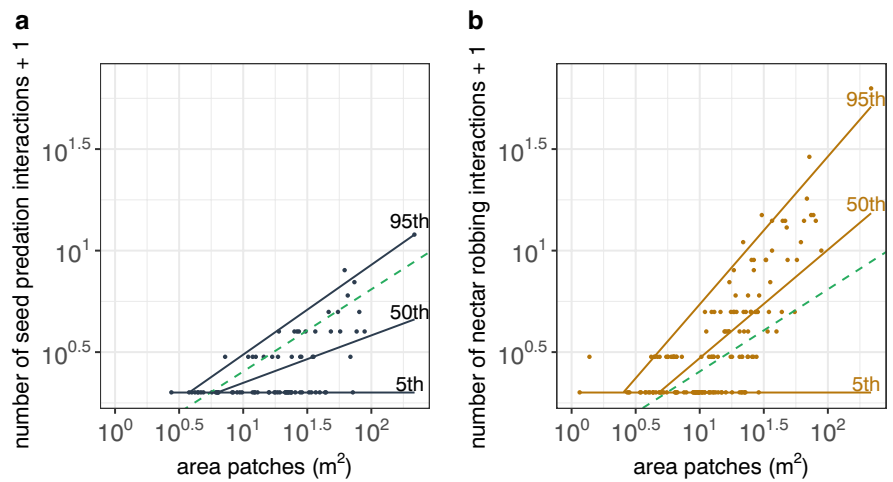
Table 4 Summary of the hypotheses addressed and results

interactions	prediction: exploitation patterns are explained by…	results	figures and tables
trophic	behaviour (tendency of insects to aggregate)	no, mainly	T. 3 and Fig. 2
non-trophic	the spatial pattern of the other interaction	yes	Figure 3
trophic	the resource patch size	ideal free distribution	Figure 4 and T. 7
trophic	the landscape structure	no	Supp. T. 5

species distribution modelling, and evolutionary ecology (Bakx et al. 2019; Ovaskainen et al. 2016).

Insects can have an aggregated distribution due to a patchy structure of their resource (Fletcher & Fortin 2018). Indeed, the first-order analysis showed that

snapdragons (the resource) are clustered (Table 3). We suggest that this is related to the preference of snapdragons to live on rocky cliffs and disturbed areas, which itself is patchily distributed (Jaworski et al. 2016). The second-order analysis also showed a

significant aggregation of snapdragons below a radius of 46 m (Fig. 2a), perhaps attributed to the species' short-distance seed dispersal mechanisms (Khimoun et al. 2013). The posterior aggregation dilution is consistent with the size of patches found in Fig. 4, while the presence of snapdragon patches exhibited significant overdispersion beyond a radius of 70 m, likely attributable to the overdispersion of suitable habitat.

We predicted that both plant–insect interactions would be significantly more aggregated than their resource due to their behaviours: social nesting in bumblebees (Goulson 2010; Kembro et al. 2019) and conspecific attraction in *Brachypterolus* beetles (MacKinnon et al. 2005). However, seed predation was as aggregated as the resource for both first- and second-order PPAs (Table 3, Fig. 2b). Despite a lack of excessive aggregation for nectar robbing overall (Table 3), our second-order analysis found an excess aggregation of nectar robbing at two ranges (0-2 m and 50-63 m), and overdispersion beyond 120 m (Fig. 2c). The excess aggregation in the 0-2 m range could be an artifact of the GPS inaccuracy in the first 3.7 m. However, it is highly unlikely that the measurement error in GPS location systematically over-aggregated points. Therefore, aggregation at this small scale could be explained due to traplining behaviour, in which bumblebees are more likely to forage on the nearby unvisited neighbour plants (Kembro et al. 2019). The excess aggregation in the 50-63 m range and the overdispersion beyond 120 m could be consequences of an interaction between foraging range and intercolony competition. Bumblebees tend to exploit resources inside a foraging range around their nest, typically within 100 m (Goulson 2010; Kembro et al. 2019). (Kembro et al. 2019; Wolf & Moritz 2008). Complementing our analysis with knowledge of bumblebee nest locations would clarify the drivers of nectar robbing aggregation patterns.

Similar to the finding that both interactions are for the most part as aggregated as the resource, we found that resource exploitation increases proportionally with patch area (Fretwell & Lucas 1969; Kennedy & Gray 1993). That is, the relationship between number of interactions and patch size fits the ideal free distribution hypothesis for both trophic interactions, with no significant pattern of under- or over-exploitation of patches depending on the patch size. An ideal

free distribution is often found for bumblebee foraging patterns, but the mechanism is not necessarily as simple as random patch selection (Goulson 2010). Larger patches are more easily spotted or more likely to be encountered, but this is balanced by two factors. First, as stated in the ideal free distribution hypothesis, larger patches tend to be overexploited, and individuals can learn to avoid them. Second, there is a tendency to visit a higher proportion of flowers in small patches, where bumblebees are better able to memorize and avoid previously visited flowers than in large patches (Goulson 2010; Ohashi & Yahara 1999). In addition to our patch size relationship findings, we detected a limiting-factor relationship of patch size for seed predators, but not for bumblebees. We hypothesize that seed predation might be limited by the patch size because plants are both resource and habitat for the coleopteran larvae. The congener *B. pulicarius* is attracted by conspecifics and selectively feeds on flowers of *Linaria vulgaris* (morphologically similar to snapdragons, and also in Plantaginaceae) with a higher density of ramets (Egan & Irwin 2008; MacKinnon et al. 2005). If this behaviour were extrapolated to *B. vestitus*, the preference of adult individuals to eat and to lay their offspring in large snapdragon patches and their attraction to the presence of other beetle individuals (perhaps as mates) may lead to limitation of beetle density by patch size. Schooley and Wiens (2005) found a similar limiting-factor relationship for a Hemiptera species with a life cycle similar to our focal seed predator (larvae live and feed on a patchily distributed cactus). However, we caution that the limiting factor result could be driven by false negatives of seed predation if larvae were too small during sampling, and a scarcity of large patches (Fig. 4). Nonetheless, we have certainly demonstrated that both trophic interactions increase proportionally with patch size. These findings have relevance for conservation decision-making for organisms that rely on patchily-distributed habitat or resources.

Landscape heterogeneity, such as distance from forest edge or human disturbance, can cause significant effects on plant–insect interactions (Gargano et al. 2017; Totland 2001; Winfree et al. 2009). However, we did not find any significant effects of landscape features on plant–insect interaction frequency. Our results are in accordance with the findings of Swift et al. (2017), where the nesting clustering

behaviour of the shorebird Hudsonian Godwit remained independent of the habitat and landscape characteristics. We hypothesize three possible (non-exclusive) explanations for the lack of association between plant–insect interactions and landscape features. First, variation in foraging behaviour may be driven more strongly by resource spatial structure than landscape features. Second, variation in landscape features may be on too large of a scale to affect resource use. Both bumblebees and *Brachypterolus* beetles are flying species in their adult life cycle and appear to be making decisions at a scale range of meters and tens of meters—as previously discussed in the last two paragraphs. However, the landscape structure is at a scale of an order of magnitude higher, where for the points with interactions, the mean of the farthest landscape feature was approximately 560 m for each interaction. Third, the lack of patterns at landscape scales could be a consequence of the potential dilution of effects resulting from both interactions occurring at community scales. This is due to the fact that both pollinators and seed predators interact with other species within the community. Together, these results do not support our hypothesis that a heterogeneous landscape affects the patterns of resource exploitation. However, these findings imply that we can isolate the behaviour and biotic interactions of the species from the structure of the surrounding landscape.

In addition to analyzing the spatial patterns of the trophic interactions in relation to their resource and landscape context, we asked whether there are any signals of non-trophic interaction between the bumblebees and beetles. We found a repulsion effect on the non-trophic interaction on radius above 100 m (Fig. 3). This phenomenon could be explained by bumblebees and adult coleoptera not choosing the same patches at large scales (perhaps due to landscape features we could not detect). However, at small scales when they choose the same patches they tend to choose the same flowers. That is, contrary to our prediction of competitive exclusion at fine scale, we found nectar robbing and seed predation to be closer than expected on a radius below 40 m. The steep initial slope is explained by the finding of both interactions inside 120 out of 944 sampled plants (69% of plants with seed predation and 18% of plants with nectar robbing). First, the lack of evidence for competition could be

explained by resource partitioning, because the two insects exploit different resources. Second, it could be explained by temporal partitioning. We found that nectar robbing is more frequent early in the season and seed predation later (Supplementary Fig. 2 in Online Resource). Beyond simply a lack of competition, however, we observed a more aggregated pattern than expected (Fig. 3). One possible explanation is that the species have a commensal relationship (Hochstrasser & Peters 2004), where egg-laying coleopterans utilize the nectar robbing holes to access the flower's interior. A more likely explanation is that both insects are attracted to similar floral and plant traits (Rodríguez-Rodríguez et al. 2017). Further study is needed; as Carl Sagan said, "Extraordinary claims require extraordinary evidence".

Conclusions and future directions

Despite the importance of biotic interactions for structuring organisms' spatial distributions, they are more challenging to quantify than the abiotic environment, and have thus been only infrequently analyzed in a spatially explicit context (Ovaskainen et al. 2016; Wilkinson et al. 2021). Here, we collected a large spatial dataset on two antagonistic plant–insect interactions and their plant host and analyzed their distribution on multiple spatial scales. We found that plant aggregation impacted the resource exploitation patterns of plant–insect interactions. In addition, we demonstrated an ideal free distribution of exploitation for both species. Finally, we found an intriguing pattern of overlap in nectar robbing and seed predation. Our results could be useful for scaling up to multiple populations in order to integrate biotic interactions into species distribution modelling where resource exploitation cannot be measured on so fine of a scale. Future work in the system could simultaneously consider temporal and spatial dynamics of insect behavior, resource exploitation (Cressie & Wikle 2015; Gabriel & Diggle 2009) and resource availability, such as effects of flowering synchrony (Jácome-Flores et al. 2018). A multivariate analysis at the community level can also be considered in the future (as in Perea et al. 2021). Finally, further analysis could compare whether plant traits or plant spatial structure is more predictive of biotic interaction frequency.

Data availability (data transparency)

The datasets generated and analysed during the current study will be deposited to the ISTA Research Explorer repository upon manuscript acceptance. Voucher specimens of insects are deposited in the *Museo Nacional de Ciencias Naturales*, Spain.

Code availability (software application or custom code)

The majority of analyses were conducted in R. Project code is available, upon prior request, in the following Github repository: https://github.com/Guill emPocull/Spatial_Ecology_Antirrhinum_majus. Upon manuscript acceptance, the scripts used to generate the final published results will also be deposited to the ISTA Research Explorer repository. QGIS software was used without coding.

Authors' contributions   All authors interpreted results and critically reviewed the manuscript. G. Pocull performed data collection, statistical and GIS analysis, and manuscript writing. N. Barton contributed to statistical analysis. C. Baskett contributed to study design, manuscript writing and editing.

Declarations

Competing interests   The authors declare no competing interests.

Consent to participate (include appropriate statements)   The research did not involve human participants.

Consent for publication (include appropriate statements)   The authors approve the version to be published.

Conflicts of interest   The authors have no conflicts of interest to declare that are relevant to the content of this article.

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