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Community Structure of Ladybirds (Coleoptera: Coccinellidae) Across Contrasting Habitat Types in North-Central Algeria: The Role of Temporal Variation and Aphid Availability

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Abstract: This study examines ladybird (Coleoptera: Coccinellidae) communities across four contrasting habitats in North-Central Algeria (natural habitat, fruit-crop, cereal-crop, urban park), analysing how habitat, prey and seasonality shape their structure. From January to October 2025, 85 sampling events recorded 3,580 adults (23 species). Diversity was quantified using Hill numbers and iNEXT curves; community drivers and composition were analysed via GLMs and PERMANOVA. The assemblage was dominated by *Hippodamia variegata* (33.8%), *Chilocorus bipustulatus* (17.9%), *Novius cardinalis* (11.6%), and *Oenopia doublieri* (10.9%). The natural habitat showed the highest richness (20 species), agrosystems the greatest abundances (up to 86.8 ± 76.2 individuals/survey), and the urban park was species-poor (4 species, representing 2.2% of all collected individuals). Activity peaked in May-June (46.7%) and was concentrated from March to August (88%). For 10 strictly aphidophagous species (54.7% of individuals), aphid presence significantly increased abundance (IRR = 1.86; 95% CI: 1.17-2.97; p = 0.009), whereas abiotic variables had no effect. PERMANOVA revealed a significant effect of habitat type on community composition (pseudo-$F_{3,81}$ = 2.889; $p < 0.001$; R^2 = 0.243), with the urban community differing markedly in composition from the other three habitats. These results demonstrate how habitat type, prey availability and seasonality govern ladybird community dynamics in North-Central Algeria.

Key words: Aphidophagous species; Habitat type; Mediterranean region; Seasonal phenology; Species assemblages; Urban ecology

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Introduction

Beneficial insects, particularly predatory ladybirds (Coleoptera: Coccinellidae), are crucial for regulating herbivore populations and maintaining ecological balance in agricultural and natural ecosystems. Ladybirds are effective biological control agents against numerous pests, especially aphids, scale insects and other phytophagous insects (Ali-Arous et al. 2023; Ferreira et al. 2023). Their predatory efficiency can vary depending on interspecific interactions and habitat context, which influence feeding behaviour and overall fitness (Ferreira et al. 2023). Many species also feed opportunistically on other prey, pollen or nectar, allowing populations to persist when primary prey are scarce. This trophic flexibility highlights the importance of considering broader ecological interactions to understand their functional contribution to ecosystems (Gómez-Marco et al. 2015; Soares et al. 2023).

At both global and Mediterranean scales – the Mediterranean Basin being recognised as one of the world's biodiversity hotspots, owing to its exceptional species richness and endemism (Myers et al. 2000) – ladybirds play a key role in pest regulation. Their presence reduces reliance on synthetic pesticides and supports sustainable agriculture (Rusch et al. 2016; Soares et al. 2023). The region is characterised by pronounced climatic seasonality, recurrent drought, interannual variability and long histories of human land use. Environmental heterogeneity and anthropogenic pressures, including agricultural intensification, urban expansion and habitat fragmentation, shape ecosystems that are both biologically rich, and ecologically vulnerable. Predator communities respond not only to prey abundance but also to habitat heterogeneity, such as vegetation structure, floristic diversity, and spatial configuration, which together determine microhabitats, refuges and foraging opportunities.

The presence and diversity of ladybirds vary markedly among habitats. Factors influencing community composition include floristic diversity, vegetation structure, abiotic conditions and biotic interactions (Gardiner et al. 2021; Decker et al. 2026). Plant-rich and structurally complex habitats generally support higher species richness, whereas simplified or disturbed habitats favour a few dominant generalist species (Gardiner et al. 2021; Gómez-Marco et al. 2015). Urbanisation often reduces diversity and abundance due to habitat fragmentation and limited vegetation (Rocha et al. 2018; Magura et al. 2020). Conversely, agricultural habitats with high pest densities may attract large numbers of ladybirds, but usually only a few opportunistic species benefit (Grez et al. 2019; Ali-Arous et al. 2023). These patterns emphasise the need to integrate habitat complexity, prey availability and seasonal dynamics to understand predator-mediated pest control.

In Algeria, ladybirds are well represented in the humid to semi-arid Mediterranean zones of the north. A national survey reported 48 species, including 41 in northern Algeria (Saharaoui & Gourreau 1998; Lakhal et al. 2018). Despite this, their distribution among forests, agrosystems and urban areas remains poorly documented (Saharaoui et al. 2014). Moreover, little is known about how seasonal fluctuations and habitat-specific prey availability influence community composition and functional roles. No study has simultaneously compared ladybird communities in a natural habitat, fruit-crop and cereal-crop agrosystems, and an urban habitat in this region, while also assessing functional roles such as pest predation (Taranto et al. 2022; Ali-Arous et al. 2023).

In this context, we tested the following: (1) the effect of habitat type on species richness and community composition; (2) the influence of seasonality and selected abiotic variables on abundance and diversity; and (3) the relationship between prey presence (aphids and other observed prey) and ladybird abundance to evaluate functional roles. By integrating habitat and trophic context, this study reveals how ladybird communities are structured and function across contrasting Mediterranean ecosystems, providing guidance for sustainable management of agricultural and urban landscapes.

Based on the contrasting habitat types studied – natural forests, agrosystems (fruit-crop and cereal-crop fields) and urban green spaces – we hypothesise that ladybird communities will vary in both composition and abundance along this gradient of anthropogenic influence. We expect that (i) natural forests will harbour the highest species richness, including rare and specialised taxa, due to their structural complexity and diverse host plants; (ii) agrosystems will support high densities of generalist predators, with community composition dominated by a few opportunistic species responding to prey availability; and (iii) urban habitats will display simplified and homogenised assemblages, characterised by low richness and dominance of eurytopic species adapted to human-modified environments. Additionally, we predict that seasonal fluctuations and aphid presence will strongly influence local abundance, while short-term variations in abiotic conditions will play a secondary role.

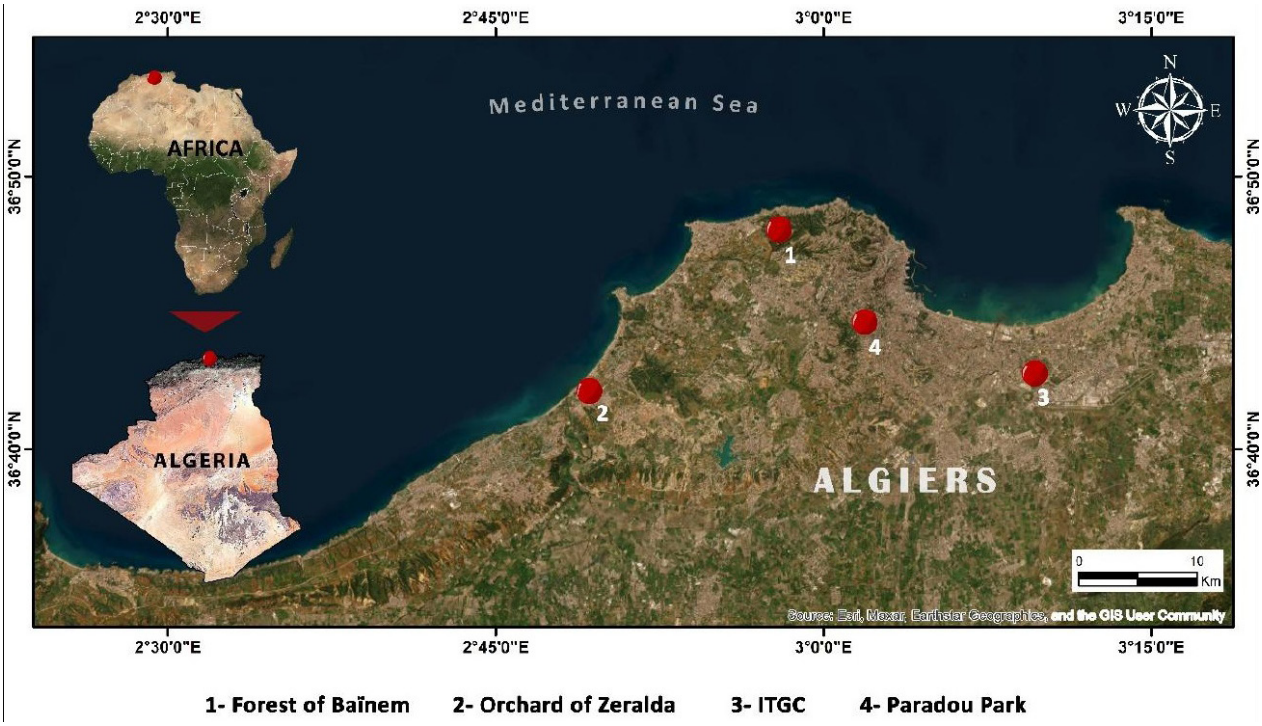

Fig. 1. Location of the study area and sampling sites

Materials and Methods

Study sites

The regional climate is Mediterranean subhumid, characterised by mild, wet winters, with precipitation concentrated between October and March, and hot, dry summers. During the study period (January–October 2025), mean daily temperatures ranged from approximately 12 °C in winter to 28 °C in summer, with occasional heat peaks, and precipitation was nearly absent during summer. These climatic conditions, combined with differences in vegetation cover and site management, provide an appropriate framework for comparing ladybird communities along a gradient from a relatively undisturbed forest habitat to a highly artificialized urban environment, with agrosystems of intermediate complexity in between (Fig. 1).

The study was conducted at four sites representing distinct habitat types in the Algiers region (North-Central Algeria). Site 1 – Baïnem forest (36°48'34"N 3°00'56"E) is a natural habitat composed of Mediterranean maquis and secondary pine forest, located approximately 12 km west of Algiers (altitude 80-400 m; ≈ 500 ha). The forest is a remnant of Mediterranean coastal vegetation, dominated by dense shrubs (holm oak, mastic tree, Aleppo pine) with herbaceous clearings, and benefits from partial protection despite past wildfires and the introduction of exotic species (*Eucalyptus*) during reforestation efforts (Brakchi et al. 2025). Site 2 – Zeralda orchard (36°41'45"N 2°48'15"E) is a fruit-crop agrosystem (mixed orchard) in the western peri-urban area of Algiers, featuring mainly citrus (lemon, orange) and pomegranate trees managed as a traditional orchard with a partially maintained herbaceous layer. Site 3 – ITGC experimental plot (El Harrach) (36°42'27"N 3°11'24"E) is a cereal-crop agrosystem (*Triticum durum*) under an open-field system (~1 ha) in the Mitidja plain. Vegetation is dominated by wheat monoculture with some weeds along field margins; the site is managed with conventional agricultural practices, including tillage, annual sowing, limited irrigation, and occasional phytosanitary treatments. Site 4 – Paradou Park (Algiers) (36°44'27"N 3°01'41"E) is an urban green space (≈ 30 ha) combining landscaped and wooded areas (cypress and ash trees, oleander shrubs, lawns) within the city, subject to regular maintenance (irrigation, pruning, cleaning) and high human visitation.

Sampling strategy and data collection

Standardised sampling campaigns were conducted from January to October 2025 across the four habitat types described above. The study sites represented naturally occurring habitat patches of variable extent, ranging from approximately 1 ha in the cereal-crop agrosystem to about 500 ha in the forest. Therefore, the sampling design relied on standard-

ised survey units rather than proportional surface coverage (Legendre & Legendre 2012; Southwood & Henderson 2000; Scheiner & Gurevitch 2001), with each survey corresponding to a site × date combination as the basic unit of analysis.

A total of 85 surveys were performed (34 at site 1, 12 at site 2, 27 at site 3, and 12 at site 4), with each site visited at least once per month and twice during some spring months. Survey frequency varied according to habitat-specific constraints and phenology (e.g., more frequent visits in cereal crops during the wheat colonisation period). All surveys used the same standardised effort in terms of methods, duration and intensity, ensuring comparability among habitats, as recommended in recent insect biodiversity monitoring studies (Li et al. 2023; Gavloski et al. 2025). The number of survey rounds differed among sites because larger or more heterogeneous sites (e.g., the ~500 ha forest) required more visits to achieve comparable spatial coverage than smaller, more homogeneous sites (e.g., the ~1 ha cereal plot), and because visit frequency was further adjusted to site-specific phenology (e.g., intensified sampling in the cereal crop during the wheat-colonisation window). Rarefaction/extrapolation (iNEXT) was used to control for this imbalance in the diversity comparisons, and this caveat is taken into account when interpreting the GLM results (see Results).

Each habitat type was represented by a single site. While this design reflects the availability of sites along the studied gradient and is common in landscape-scale entomological surveys, it implies that site-level idiosyncrasies cannot be fully distinguished from habitat-type effects. Results should therefore be interpreted as indicative of habitat-type trends, and generalisation across the full range of each habitat type requires corroboration from additional sites.

Sampling was spatially stratified within each site to capture dominant vegetation types and available host plants. In large sites such as the forest, surveys were distributed across representative microhabitats (tree stands, shrub layers, clearings), whereas in smaller sites such as the cereal-crop agrosystem, surveys covered most accessible areas (Li et al. 2023).

During each survey, multiple complementary techniques were applied to sample ladybirds across all vegetation strata: herbaceous sweeping (25 double sweeps per survey), branch beating (10 beating events per survey, i.e. 10 individual host plants beaten per survey at each site, targeting representative host plants), and directed visual inspection (20 minutes). The combination of these methods maximises detection probability and community representativeness in arthropod monitoring programs (Li et al. 2023; Gavloski et al. 2025). Abiotic variables (air temperature, relative humidity, wind speed) were recorded at the beginning of each survey using a portable weather station.

Prey presence was recorded concurrently. Aphid colonies encountered on sampled plants were identified to species using morphological keys for wingless adults (Blackman & Eastop 2021), while other prey categories (scale insects, whiteflies, spider mites) were noted at the functional group level without species-level identification. Aphid colonies were scored as presence/absence per survey rather than as density or abundance, since several co-occurring aphid species and instars were frequently present on the same plant, precluding reliable quantitative counts within the standardised survey time; consequently, the aphid-presence effect reported below should be interpreted as a conservative, binary indicator of prey availability rather than a measure of prey density.

Ladybirds were sampled on 15 host-plant species across the four habitat types, comprising cultivated trees (e.g. *Citrus limon*, *Punica granatum* and *Cupressus sempervirens*, ornamental shrubs such as *Nerium oleander*, the cereal crop *Triticum durum*, and other spontaneous herbaceous and shrub species recorded at each site. The complete list of the 15 host-plant species is given in Table 3 (Results).

Laboratory identification of specimens

All adult ladybirds collected during the study were identified in the laboratory using a stereomicroscope and established taxonomic keys (Gourreau 1974; Salehi et al. 2011; Duff 2012; Derolez et al. 2014; Roy & Brown 2018; Bieńkowski 2018; Gruau & Terrasse 2025). All specimens were preserved in a reference collection for documentation and future study. Subsequent analyses focused on differences in abundance, species richness and community composition at the survey scale, allowing robust comparisons among habitat types despite differences in site area.

Data analysis

Species abundance data were summarised by habitat type. Cumulative species richness and diversity were quantified using Hill numbers ($q = 0, 1, 2$; Chao et al. 2014), where $q = 0$ corresponds to species richness, $q = 1$ to the exponential of Shannon entropy (effective number of common species), and $q = 2$ to the inverse of Simpson's concentration (effective number of dominant species). Sampling

completeness was assessed with rarefaction and extrapolation curves using iNEXT (Hsieh et al. 2016), with 95% bootstrap confidence intervals based on 200 resamples.

The effects of habitat type, aphid presence (binary: present/absent), and abiotic variables (tem-perature, relative humidity, wind speed) on aphidophagous ladybird abundance (10 strictly aphidophagous species, n = 1,958 individuals) and on local species richness (all 23 species) per survey were analysed using generalised linear models (GLMs). Due to typical overdispersion in count data, a negative binomial GLM (GLM-NB) was used for aphidophagous ladybird abundance, confirmed by a likelihood-ratio test comparing Poisson and negative binomial fits (Venables & Ripley 2002). Species richness per sur-vey (all 23 species) was analysed using a Poisson GLM. The fruit-crop agrosystem served as the reference category for habitat comparisons. Model significance was evalu-ated at $\alpha = 0.05$, and effect sizes were expressed as incidence rate ratios (IRR = exp(coefficient)).

Because the aphid–ladybird relationship is relevant only for aphidophagous species, the abundance model for the aphid effect was additionally fitted on the subset of strictly aphidophagous species. The abundance model was restricted a priori to the 10 strictly aphidophagous species because the aphid-presence predictor is ecologically meaningful only for this trophic guild; fitting it on the full community which also includes coccidiphagous, mycophagous, aleurodiphagous and acariphagous species with no expected response to aphid presence would dilute and potentially bias the estimated habitat and aphid effects.

Differences in community composition among habitats were explored using a multivariate approach. Principal component analysis (PCA) was first applied to visualise assemblage patterns, followed by a one-way PERMANOVA based on Bray-Curtis dissimilarities (9,999 permutations; Anderson 2001), with Bonferroni-corrected pairwise comparisons.

All analyses were conducted in R v. 4.4 (R Core Team 2025) using the packages vegan (Oksanen et al. 2022), iNEXT (Hsieh et al. 2016) and MASS (Venables & Ripley 2002).

Table 1. Species composition and total abundance of ladybirds collected from January to October across all study sites.

Species	Total Count	Relative abundance (%)
Hippodamia variegata (Goeze, 1777)	1209	33.8
Chilocorus bipustulatus (Linnaeus, 1758)	641	17.9
Novius cardinalis (Mulsant, 1850)	414	11.6
Oenopia doublieri Mulsant, 1846	391	10.9
Psyllobora vigintiduopunctata (Linnaeus, 1758)	182	5.1
Scymnus subvillosus (Goeze, 1777)	132	3.7
Pharoscymnus setulosus (Chevrolat, 1861)	128	3.6
Coccinella septempunctata Linnaeus, 1758	117	3.3
Rhyzobius lophanthae (Blaisdell, 1892)	79	2.2
Rhyzobius litura (Fabricius, 1787)	64	1.8
Clitostethus arcuatus (Rossi, 1794)	46	1.3
Scymnus apetzi Mulsant, 1846	35	1.0
Harmonia axyridis (Pallas, 1773)	23	0.6
Adalia decempunctata (Linnaeus, 1758)	21	0.6
Oenopia conglobata (Linnaeus, 1758)	19	0.5
Exochomus quadripustulatus (Linnaeus, 1758)	17	0.5
Exochomus ericae Crotch, 1874	13	0.4
Parexochomus nigripennis (Erichson, 1843)	12	0.3
Stethorus pusillus (Herbst, 1797)	11	0.3
Tytthaspis phalerata (Costa, 1849)	10	0.3
Harmonia quadripunctata (Pontoppidan, 1763)	9	0.3
Rhyzobius chrysomeloides (Herbst, 1793)	5	0.1
Myrrha octodecimguttata (Linnaeus, 1758)	2	0.1

Results

Species composition and overall abundance

Between January and October, a total of 3,580 ladybird individuals representing 23 species were recorded across the four habitat types. The community was strongly dominated by *Hippodamia variegata* (Goeze, 1777) (1,209 individuals, 33.8%), followed by *Chilocorus bipustulatus* (Linnaeus, 1758) (641, 17.9%), *Novius cardinalis* (Mulsant, 1850) (414, 11.6%), and *Oenopia doublieri* (Mulsant, 1846) (391, 10.9%) (Table 1). Among these dominant species, *Hippodamia variegata* (Goeze, 1777) and *Novius cardinalis* (Mulsant, 1850) occurred in all four habitats. In contrast, some rare species, such as *Myrrha octodecimguttata* (Linnaeus, 1758) and *Rhyzobius chrysomeloides* (Herbst, 1793), were observed in only a single habitat (Fig. 2).

Spatial distribution according to habitat type

Abundance and species richness varied markedly among habitat types. Cereal-crop agrosystems accounted for the largest proportion of individuals (1,483, 41.4% of individuals), followed by fruit-crop agrosystems (1,042, 29.1%), natural habitats (978, 27.3%) and urban habitats (77, 2.2%).

Cumulative species richness was highest in natural habitats (20 species out of 23), intermediate in cereal-crop agrosystems (13 species) and fruit-crop agrosystems (9 species), and lowest in urban habitats (4 species).

At the scale of individual sampling events (habitat × host plant × date), mean ladybird abundance was highest in fruit-crop agrosystems (86.8 ± 76.2 SD individuals per sample), followed by cereal-crop agrosystems (54.9 ± 42.4 SD), natural habitats (28.8 ± 32.9 SD) and urban habitats (6.4 ± 4.8 SD) (Table 2). Mean species richness per sample showed the same trend, with fruit-crop agrosystems having the highest mean (2.6 ± 2.0 SD), followed by cereal-crop agrosystems (2.0 ± 1.1 SD), natural habitats (1.5 ± 0.7 SD), and urban habitats (1.1 ± 0.3 SD) (Table 2).

Host plants

Ladybirds were observed on 15 host plant species. The majority of individuals were collected on cultivated perennial crops. In fruit-crop agrosystems, *Citrus limon* (L.) accounted for the largest number of captures (1,012 individuals, 28.3%), followed by *Punica granatum* L. (727, 20.3%). In natural and urban habitats, *Nerium oleander* L. (440, 12.3%) and *Cupressus sempervirens* L. (377, 10.5%) were the main host plants.

In terms of cumulative species richness, *P. granatum* hosted the highest number of species (9 species), followed by *C. sempervirens* (8), *C. limon*

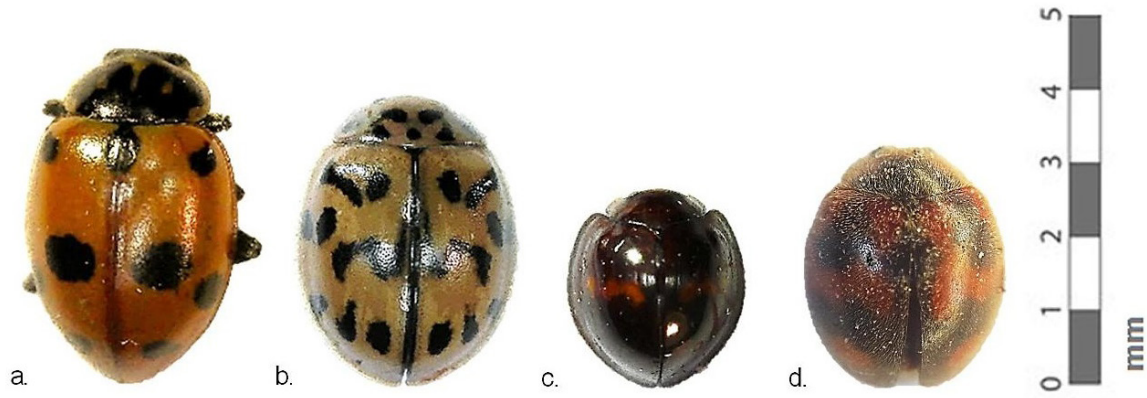

Fig. 2. Most abundant species collected during the field study by tribe. (Coccinellini tribe: a. *Hippodamia variegata* ; b. *Oenopia doublieri* ; Chilocorini tribe: c. *Chilocorus bipustulatus*; Noviini tribe: d. *Novius cardinalis*)

Table 2. Ladybird abundance and species richness according to habitat type ((1) natural habitat, (2) fruit-crop agrosystem, (3) cereal-crop agrosystem, (4) urban habitat).

Habitat Type	Number of samples	Total abundance	% of individuals	Mean abundance per sample (± SD)	Mean species richness per sample (± SD)	Cumulative species richness (N of species)
(1)	34	978	27.3	28.8 ± 32.9	1.5 ± 0.7	20
(2)	12	1042	29.1	86.8 ± 76.2	2.6 ± 2.0	9
(3)	27	1483	41.4	54.9 ± 42.4	2.0 ± 1.1	13
(4)	12	77	2.2	6.4 ± 4.8	1.1 ± 0.3	4

Table 3. List of the 15 host-plant species on which ladybirds (Coccinellidae) were sampled across the four habitat types (natural forest, fruit-crop agrosystem, cereal-crop agrosystem, urban green spaces), with associated total abundance, relative captures and cumulative species richness.

N°	Host-plant species	Family	Habitat type(s)	Total abundance (N individuals)	% of total captures	N ladybird species
1	*Citrus limon* (L.) Osbeck	Rutaceae	Fruit-crop agrosystem; Cereal-crop agrosystem	1012	28.3	6
2	*Punica granatum* L.	Lythraceae	Fruit-crop agrosystem; Cereal-crop agrosystem; Natural habitat	727	20.3	8
3	*Nerium oleander* L.	Apocynaceae	Natural habitat	440	12.3	5
4	*Cupressus sempervirens* L.	Cupressaceae	Natural habitat; Cereal-crop agrosystem; Urban habitat	377	10.5	7
5	*Triticum durum* Desf.	Poaceae	Cereal-crop agrosystem	321	9.0	2
6	*Pittosporum tobira* (Thunb.) W.T.Aiton	Pittosporaceae	Natural habitat; Urban habitat	273	7.6	5
7	Spontaneous herbaceous vegetation (“Mauvaises herbes”)	Mixed (ruderal flora)	Cereal-crop agrosystem; Urban habitat	235	6.6	3
8	*Ceratonia siliqua* L.	Fabaceae	Natural habitat	55	1.5	1
9	*Lantana camara* L.	Verbenaceae	Natural habitat	51	1.4	1
10	*Pinus halepensis* (Mill.)	Pinaceae	Natural habitat	30	0.8	2
11	*Morus nigra* L.	Moraceae	Natural habitat; Urban habitat	29	0.8	4
12	*Arbutus unedo* L.	Ericaceae	Natural habitat	14	0.4	1
13	*Prunus dulcis* (Mill.) D.A.Webb	Rosaceae	Cereal-crop agrosystem	12	0.3	1
14	*Hedera helix* L.	Araliaceae	Natural habitat	2	0.06	1
15	*Pinus canariensis* C.Sm.	Pinaceae	Natural habitat	2	0.06	1
	Total			3580	100.0	-

Note: “Spontaneous herbaceous vegetation” groups unidentified ruderal/weedy plants recorded in the field as “Mauvaises herbes”, mainly in urban and cereal-crop sites. Habitat types are listed in decreasing order of sampling frequency for each host plant. Family names follow standard botanical nomenclature (APG IV where applicable).

(6), *N. oleander* (5), and *Triticum durum* (Desf.) (2). (Table 3)

Temporal dynamics

No ladybird individuals were observed in January. The first individuals appeared in February (8, 0.2%), after which abundances increased sharply during spring, reaching peaks in May (852, 23.8%) and June (821, 22.9%). Captures subsequently declined during summer (July-August) and remained low in autumn (September-October).

Monthly species richness followed a similar trend. The number of species increased progressively from a single species in February to 18 species in June, before declining slightly towards the end of the season (10 in July, 8 in August, 9 in September, and 5 in October). No species or individuals were recorded in January (Fig. 3).

Relationship with aphid presence

The sampled ladybird community comprises species with markedly different dietary regimes (Tab. 4): 10 strictly aphidophagous species representing 1,958 individuals (54.7% of the total), alongside coccidiphagous species (e.g., *Chilocorus bipustulatus*, *Novius cardinalis*), mycophagous species (*Psyllobora vigintiduopunctata*), aleurodiphagous species (*Clitostethus arcuatus*) and acariphagous species (*Stethorus*

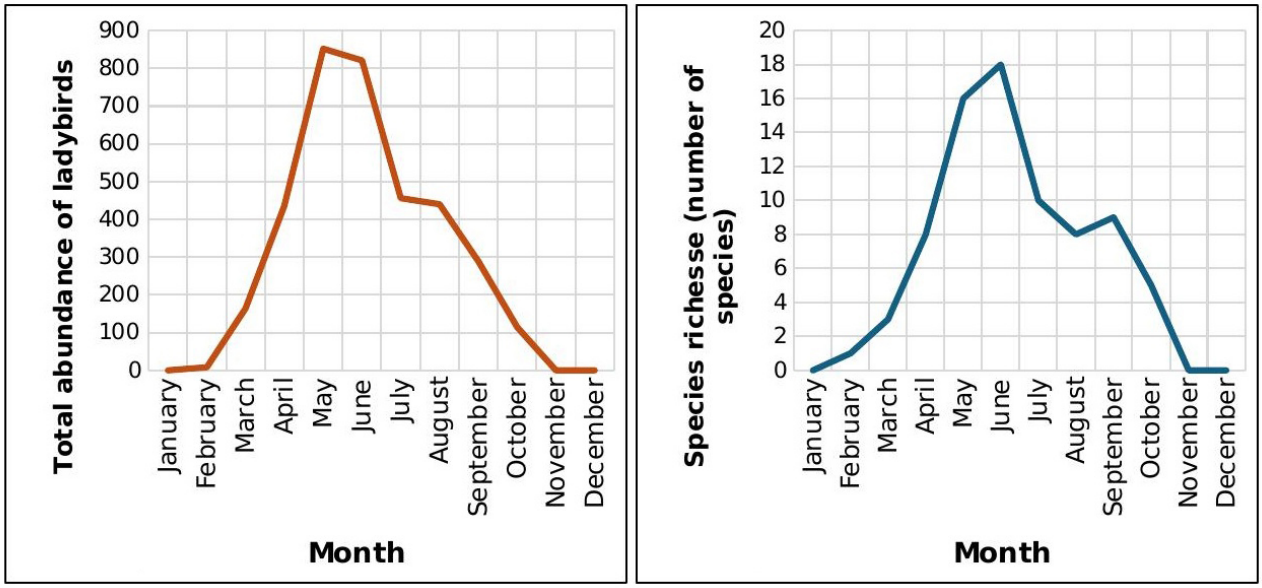

Fig. 3. Species composition of the ladybird community (total abundance per species over the entire sampling period) (left) and monthly species richness (number of ladybird species) (right).

Table 4. Dietary regimes of the 23 Coccinellidae species recorded in this study. Aphidophagous species are highlighted in bold. Sources: Hodek & Michaud (2008); Soares et al. (2023).

Species	Dietary regime	Known prey / diet
Adalia decempunctata	**Aphidophagous**	Various Aphididae
Chilocorus bipustulatus	Coccidiphagous	Diaspididae, Coccidae
Clitostethus arcuatus	Aleurodiphagous	Aleyrodidae (whiteflies)
Coccinella septempunctata	**Aphidophagous**	Various Aphididae
Exochomus ericae	Coccidiphagous	Diaspididae
Exochomus quadripustulatus	Coccidiphagous	Diaspididae, Coccidae
Harmonia axyridis	**Aphidophagous**	Various Aphididae; also other Hemiptera
Harmonia quadripunctata	**Aphidophagous**	Aphididae (conifers)
Hippodamia variegata	**Aphidophagous**	Broad range of Aphididae
Myrrha octodecimguttata	**Aphidophagous**	Aphididae (Pinaceae)
Novius cardinalis	Coccidiphagous	*Icerya purchasi* (Monophlebidae)
Oenopia conglobata	**Aphidophagous**	Various Aphididae
Oenopia doublieri	**Aphidophagous**	Various Aphididae
Parexochomus nigripennis	Coccidiphagous	Diaspididae
Pharoscymnus setulosus	Coccidiphagous	Diaspididae
Psyllobora vigintiduopunctata	Mycophagous	Erysiphales (powdery mildews)
Rhyzobius chrysomeloides	Coccidiphagous	Coccidae
Rhyzobius litura	Coccidiphagous	Coccidae
Rhyzobius lophanthae	Coccidiphagous	Diaspididae
Scymnus apetzi	**Aphidophagous**	Various Aphididae
Scymnus subvillosus	**Aphidophagous**	Various Aphididae
Stethorus pusillus	Acariphagous	Tetranychidae (spider mites)
Tytthaspis phalerata	Mycophagous	Mildews

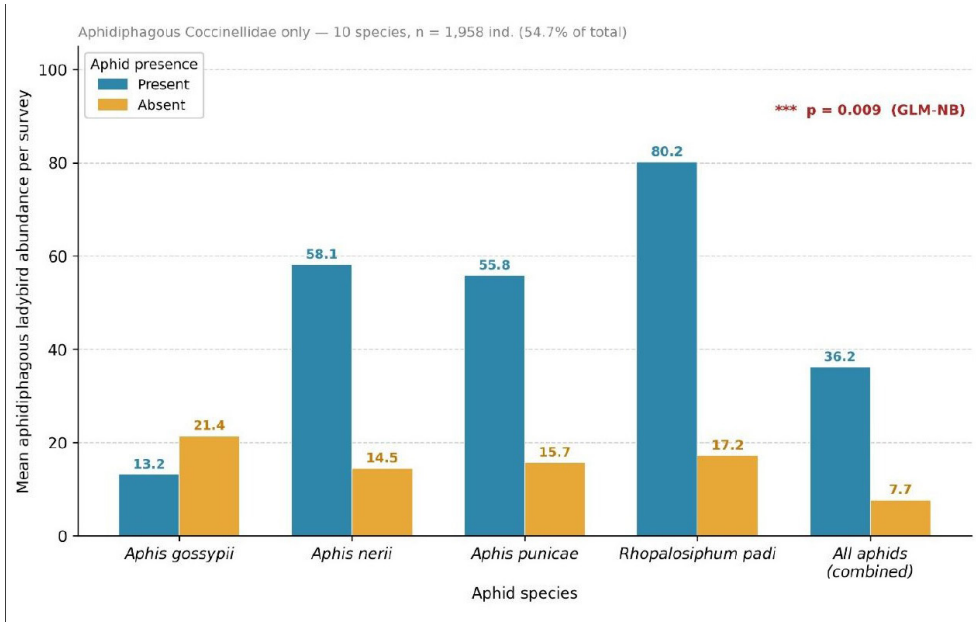

Fig. 4. Ladybird abundance per survey according to aphid presence (aphidophagous species only). Blue bars: surveys with the aphid species present; amber bars: surveys without. Values above bars indicate mean abundance. The figure is restricted to the 10 aphidophagous species (n = 1,958 individuals, 54.7% of total; see Table 4 for dietary regimes of all species). Significance of the overall aphid effect based on the GLM-NB model reported in Table 5 (coef. = 0.623; IRR = 1.86; p = 0.009).

Table 5. Results of the GLM-NB explaining aphidophagous ladybird abundance per survey (10 strictly aphidophagous species, n = 1,958 individuals) as a function of habitat type, aphid pres-ence and abiotic variables. Reference category: fruit-crop agrosystem. [1] IRR = incidence rate ratio = exp(coefficient).

Factor / variable	Coefficient	SE	Z	P	IRR[1]
Intercept	4.174	1.176	3.549	< 0.001	64.990
Habitat: cereal-crop agrosystem	-0.196	0.324	-0.605	0.545	0.822
Habitat: natural habitat	-0.927	0.319	-2.902	0.004	0.396
Habitat: urban habitat	-2.143	0.417	-5.144	< 0.001	0.117
Aphids (present)	0.623	0.238	2.622	0.009	1.864
Temperature (°C)	0.012	0.021	0.600	0.549	1.012
Humidity (%)	-0.012	0.014	-0.880	0.379	0.988
Wind (km/h)	-0.000	0.042	-0.011	0.992	1.000

pusillus). To avoid confounding this trophic diversity with the aphid–predator relationship, the following analysis was restricted to strictly aphidophagous species (highlighted rows in Table 4).

Across all 85 surveys analysed (habitat × host plant × date), at least one aphid species was detected in 56 surveys (65.9%). When considering only aphidophagous species, surveys with at least one aphid species present hosted an average of 36.2 ladybirds, compared to 7.7 in their absence – a 4.7-fold difference (Fig. 4). Species-level breakdown revealed similar patterns: mean aphidophagous ladybird abundance was 13.2 individuals per survey in the presence of *Aphis gossypii* (vs. 21.4 in its absence), 58.1 in the presence of *Aphis nerii* (vs. 14.5), 55.8 in the presence of *Aphis punicae* (vs. 15.7), and 80.2 in the presence of *Rhopalosiphum padi* (vs. 17.2).

Generalized linear models: effects of habitat type, aphid presence and abiotic variables

A negative binomial generalised linear model (GLM-NB) fitted on aphidophagous ladybird abundance per survey (Table 5; 10 strictly aphidophagous species, n = 1,958 individuals) indicated that the presence of at least one aphid species, after controlling for habitat type and abiotic variables, had a significant posi-tive effect on aphidophagous ladybird abundance (coef. = 0.623 ± 0.238; z = 2.62; p = 0.009; IRR = 1.864; 95% CI:
1.17-2.97). This means that, holding habitat type and abiotic variables constant, surveys in which

aphids were present hosted on average ~86% more aphidophagous ladybird individuals than surveys in which aphids were absent.

Habitat type exerted an additional significant effect on aphidophagous ladybird abundance. Using fruit-crop agrosystems as the reference category, cereal-crop agrosys-tems did not differ significantly (coef. = -0.196; p = 0.545; IRR = 0.82). Natural habitats showed significantly lower expected aphidophagous abundance (coef. = 0.927; p = 0.004; IRR = 0.396, i.e. ~60% fewer aphidophagous individuals per survey), while urban habitats were the least favourable (coef. = -2.143; p < 0.001; IRR = 0.117, i.e., ~88% fewer aphidophagous individuals per sur-vey).

Effects of habitat type and environmental variables on species richness

Species richness per survey ranged from 0 to 7 species. A Poisson generalised linear model (GLM) (Table 6) confirmed the negative effect of urban habitats: compared to fruit-crop agrosystems, urban surveys had an expected richness approximately three times lower (coef. = -1.120; p = 0.002; IRR ≈ 0.33). Natural habitats also exhibited significantly lower mean richness than fruit-crop agrosystems (coef. = -0.775; p = 0.004; IRR ≈ 0.46), whereas cereal-crop agrosystems did not differ significantly (coef. = -0.377; p = 0.126).

The binary variable indicating aphid presence/absence had no significant effect on species richness (p = 0.149), suggesting that aphid availability mainly influences the abundance of aphidophagous individuals already present rather than systematically attracting additional species. Abiotic variables (temperature, relative humidity, wind speed) showed no significant effect on either abundance or richness in any of the models (all p > 0.12; Table 5 and 6).

Effect of abiotic variables

The measured abiotic variables – air temperature, relative humidity and wind speed – did not have a significant effect on either aphidophagous ladybird abundance or species richness in the multivariate models. In the GLM-NB on aphidophagous ladybird abundance, the coefficients for tem-perature (p = 0.55), humidity (p = 0.38), and wind speed (p = 0.99) were not significant. Likewise, in the Poisson GLM on species richness, none of these variables showed significant associations with the number of species (all p > 0.20).

Table 6. Results of the Poisson GLM explaining ladybird species richness per survey as a function of habitat type, aphid presence and abiotic variables. Reference category: fruit-crop agrosystem. [1] IRR = incidence rate ratio = exp(coefficient).

Factor / variable	Coefficient	SE	Z	P	IRR[1]
Intercept	1.944	0.866	2.245	0.025	6.984
Habitat: cereal-crop agrosystem	-0.377	0.246	-1.53	0.126	0.686
Habitat: natural habitat	-0.775	0.269	-2.878	0.004	0.461
Habitat: urban habitat	-1.12	0.361	-3.104	0.002	0.326
Aphids (present)	-0.281	0.195	-1.443	0.149	0.755
Temperature (°C)	-0.006	0.012	-0.52	0.603	0.994
Humidity (%)	0.003	0.01	0.289	0.773	1.003
Wind (km/h)	-0.038	0.03	-1.257	0.209	0.963

Table 7. Hill numbers (q = 0, 1, 2) for ladybird assemblages in each habitat type and across all habitats combined.

Habitat type	q0 (species richness)	q1 (Shannon diversity)	q2 (Simpson diversity)
(1) Natural habitat – Baïnem forest	20	8.21	4.90
(2) Fruit-crop agrosystem – Zeralda orchard	9	5.07	4.19
(3) Cereal-crop agrosystem – ITGC El Harrach	13	7.07	5.23
(4) Urban habitat – Paradou Park	4	3.54	3.25
All habitats combined	**23**	**8.54**	**5.59**

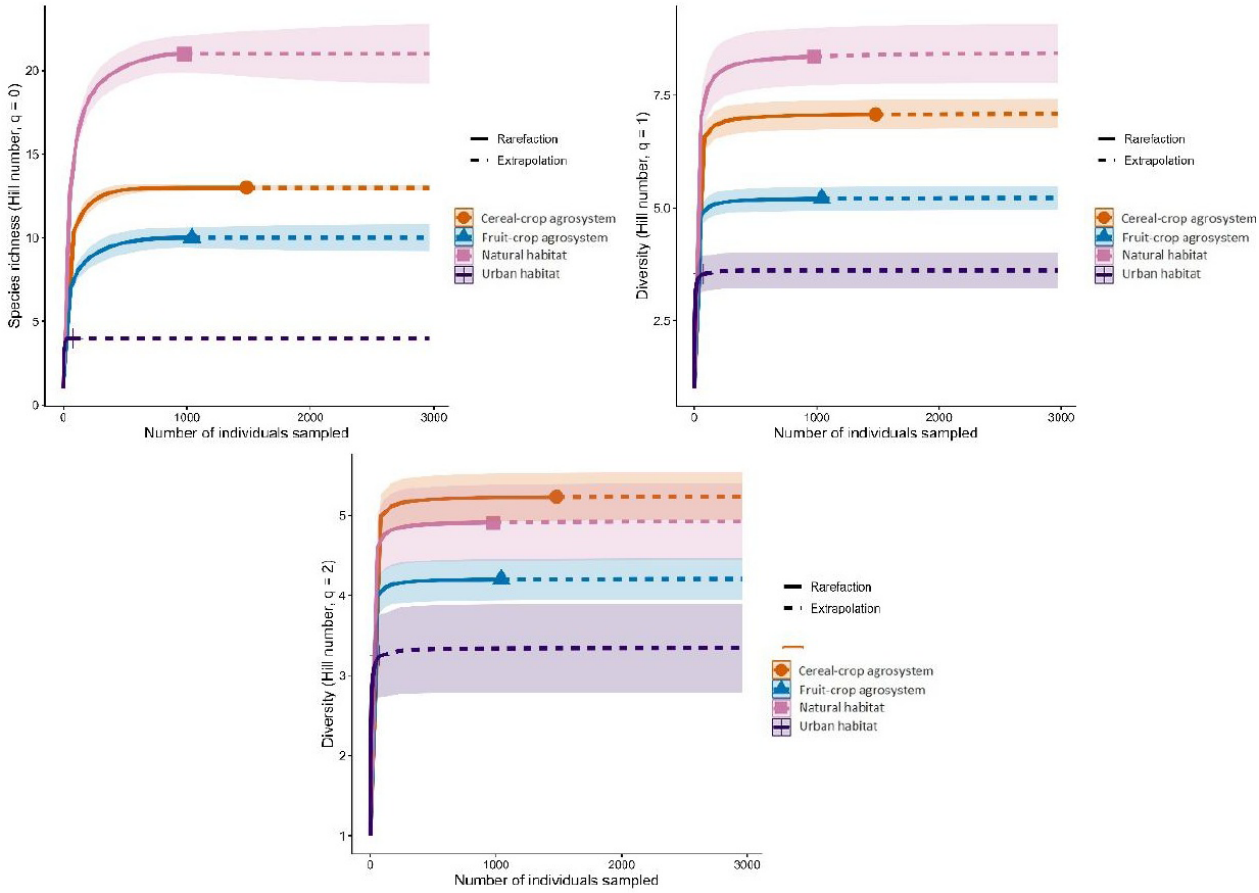

Fig. 5. Hill numbers (q = 0, 1, 2) for ladybird assemblages in four habitat types (fruit-crop agrosystem, cereal-crop agrosystem, natural habitat, urban habitat). For each habitat, q = 0 represents species richness, q = 1 the effective number of common species (Shannon diversity) and q = 2 the effective number of dominant species (Simpson diversity).

Ladybird diversity across habitats: Hill numbers for q = 0, 1 and 2

Hill numbers (Table 7; Fig. 5) and iNEXT rarefaction – extrapolation curves (Fig. 6) reveal marked differences in ladybird diversity among habitats. Natural habitats exhibited the highest species richness ($q_0 = 20$), followed by cereal-crop agrosystems (13 spp.), fruit-crop agrosystems (9 spp.) and urban habitats (4 spp.). Rarefaction – extrapolation curves indicate that sampling was essentially complete for urban and fruit-crop habitats (curves plateau), intermediate for cereal-crop agrosystems, and still increasing for the natural habitat, suggesting the presence of undetected rare species. Chao1 estimators indicate that total richness in the natural habitat could reach approximately 25 species.

Diversity indices q_1 (Shannon) and q_2 (Simpson) provide a more detailed picture of community structure. Cereal-crop agrosystems show high effective diversity ($q_1 = 7.07$; $q_2 = 5.23$), reflecting a relatively even assemblage despite moderate species richness. Fruit-crop agrosystems also exhibit a diverse structure ($q_1 = 5.07$; $q_2 = 4.19$). In natural habitats, the combination of high richness ($q_0 = 20$) and high q_1 (8.21) with a more moderate q_2 (4.90) indicates the coexistence of common species alongside numerous rare taxa. Urban habitats are characterised by low and saturated diversity ($q_1 = 3.54$; $q_2 = 3.25$), consistent with strong biotic homogenisation.

Community composition: PCA and PERMANOVA

A one-way PERMANOVA based on Bray – Curtis dissimilarities (9,999 permutations) confirmed a highly significant effect of habitat type on ladybird community composition (pseudo-$F_{3,81} = 2.889$; $p < 0.001$; $R^2 = 0.243$). The R^2 value indicates that habitat type explains approximately 24% of the total compositional variance – a robust and ecologically meaningful effect, though substantial variation (76%) remains unexplained, likely due to within-habitat temporal and microhabitat heterogeneity.

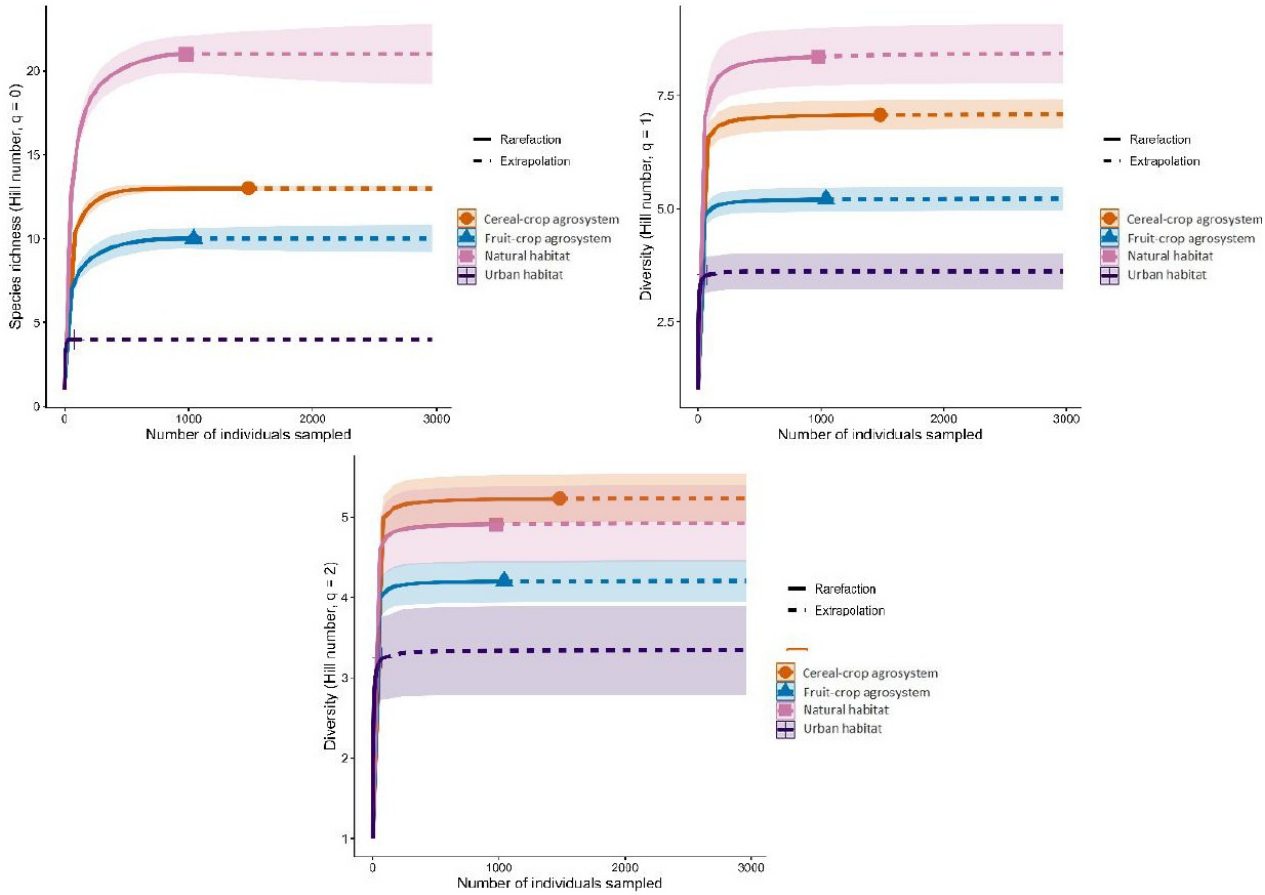

Fig. 6. Diversity of ladybird assemblages across habitat types: iNEXT rarefaction curves for Hill numbers (q = 0, 1, 2)

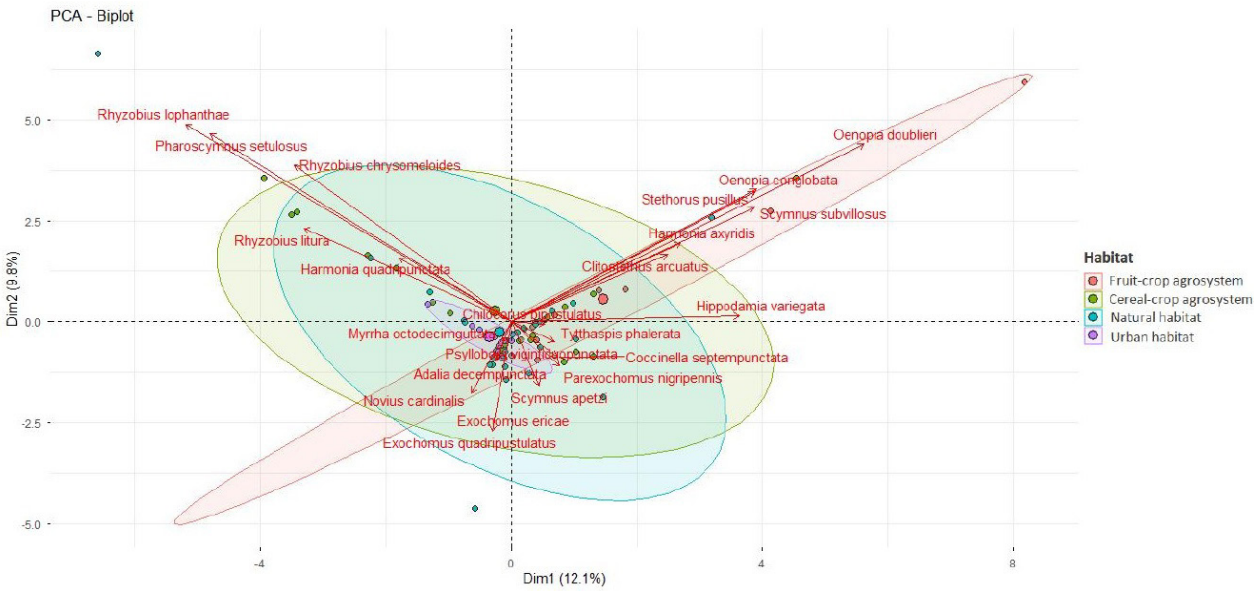

Fig. 7. Principal Component Analysis (PCA) of ladybird assemblages (biplot). Points represent surveys, coloured according to habitat type; arrows indicate species (variables). Ellipses show the dispersion of surveys by habitat (confidence level as defined in the software). Dim1 = 12.1% and Dim2 = 9.8% of the total inertia.

Bonferroni-corrected pairwise comparisons showed that the urban habitat was significantly distinct from all other habitats (all $p < 0.05$), whereas the natural habitat, fruit-crop agrosystem and cereal-crop agrosystem did not differ significantly from one another. A preliminary PCA (Fig. 7) visually confirmed this pattern, although the first two axes explained only 21.9% of total inertia (Dim1 = 12.1%; Dim2 = 9.8%), reflecting the inherent complexity of species assemblages and supporting the use of PERMANOVA as the primary inference tool.

Discussion

Habitat gradient and community structuring

Our results reveal a clear structuring of Coccinellidae assemblages along a gradient of anthropogenic disturbance, from the semi-natural Baïnem forest to the highly artificialized Paradou Park. This gradient aligns with environmental filtering theory: structurally and floristically heterogeneous habitats allow species with diverse ecological traits to coexist, whereas simplified or disturbed environments favour a limited number of tolerant, eurytopic taxa (Grez et al. 2013; Gómez-Marco et al. 2015; Rocha et al. 2018).

The natural habitat harboured the highest diversity ($q_0 = 20$), including taxa apparently restricted to this site, such as *Myrrha octodecimguttata* – a conifer-associated aphid predator (Holecová et al. 2018) – confirming the role of semi-natural habitats as reservoirs of specialised biodiversity. Vertical stratification, diverse host plants, litter layers and clearings create a mosaic of trophic and spatial niches that sustain both common and rare species.

Our dominant assemblage (*Hippodamia variegata, Chilocorus bipustulatus, Oenopia doublieri* and *Novius cardinalis*) differs from the four species most frequently reported as dominant in earlier Algerian surveys focused on agricultural habitats – *Coccinella algerica* (now synonymised with *C. septempunctata*; Romanowski et al. 2020), *Coccinella undecimpunctata, Hippodamia variegata* and *Scymnus subvillosus* (Lakhal et al. 2018; Saharaoui 2000). This divergence likely reflects the broader habitat gradient sampled here – including a natural habitat and an urban park in addition to the two agrosystem types on which earlier studies focused – rather than a shift in the regional species pool.

Although the natural habitat harboured the highest cumulative species richness (20 species), its per-survey abundance was significantly lower than that of fruit-crop agrosystems, likely reflecting differences in prey density and vegetation structure: forests provide a wider array of microhabitats and rare taxa, whereas agrosystems concentrate large numbers of a few opportunistic species around locally abundant prey.

In contrast, urbanization acts as a strong homogenising force. PERMANOVA results indicate that the urban habitat is the only assemblage significantly distinct from all others, highlighting urbanization – rather than the natural-to-agricultural gradient per se – as the primary driver of community dissimilarity (Rocha et al. 2018; Magura et al. 2020). Habitat fragmentation, dominance of impermeable surfaces, pollution and intensive horticultural maintenance restrict ecological niches to a small number of eurytopic species. This process of biotic homogenisation is particularly concerning in rapidly urbanizing North African coastal regions (Decker et al. 2026), where urban green spaces may increasingly function as isolated ecological islands.

The low abundance of *Harmonia axyridis* (Pallas, 1773) – the harlequin ladybird – representing only 0.6% of total captures, is noteworthy. Although this invasive species has restructured native communities in parts of Europe and North America (Grez et al., 2013; Sloggett, 2021), its limited presence in our sites suggests that local assemblages currently retain structural integrity. Nevertheless, its presence warrants continued monitoring, as future population growth could lead to competition or intraguild predation with native species – processes that have been documented in North African countries neighbouring Algeria.

It is important to note that each habitat type in this study is represented by a single geographic site, which precludes full statistical separation of habitat-type effects from site-specific factors. The observed patterns are consistent with broader literature and ecological expectations, but replication across multiple sites per habitat type would strengthen causal inference. Future studies should include at least two to three sites per habitat type to formally test habitat-type effects in an ANOVA-type framework.

Agrosystems: intermediate richness and functional dominance

The two agrosystems displayed intermediate species richness but were characterised by strongly dominated community structures. *Hippodamia variegata* alone accounted for 33.8% of total captures and was present in all four habitats, confirming its ecological plasticity and opportunistic strategy (Saharaoui & Gourreau, 1998). Its dominance reflects traits typical of r-selected predators: high fecundity, rapid de-

velopment, trophic generalism and strong dispersal capacity, enabling rapid colonisation of aphid outbreaks (Hodek et al. 2012).

In the Zeralda orchard, *H. variegata*, *Coccinella septempunctata* and *Oenopia doublieri* were abundant on aphid-infested citrus and pomegranate trees, suggesting their potential for natural pest suppression when pesticide pressure is low. Similarly, in the wheat field, *H. variegata* and *O. doublieri* were well represented, likely contributing to reductions in cereal-crop aphid (*Rhopalosiphum padi*) occurrences after May (Taranto et al. 2022; Soares et al. 2023). In orchards, *Chilocorus bipustulatus* and *Novius cardinalis* were also abundant, indicating trophic diversification linked to the presence of scale insects and Monophlebidae (Gómez-Marco et al. 2015). More broadly, the fact that fruit and ornamental trees (*Punica granatum, Cupressus sempervirens, Citrus limon*) supported the highest cumulative species richness among host plants is consistent with the structural complexity and prey diversity typically associated with perennial hosts (Gómez-Marco et al. 2015) and further underscores the major role of fruit and ornamental trees as key substrates sustaining ladybird diversity in this system.

Agricultural disturbances – ploughing, harvesting, mowing and phytosanitary treatments – remain key structuring forces, interrupting life cycles and destroying refuges, thereby filtering out less resilient species (Rusch et al. 2016; Soares et al. 2023). Field observations confirmed temporary declines in ladybird numbers following insecticide applications in the orchard. Nonetheless, when chemical pressure is moderate and habitat elements such as field margins are preserved, agrosystems can sustain substantial predatory activity and contribute meaningfully to biological control (Gardiner et al. 2021).

Seasonal dynamics and bottom-up regulation

Ladybird phenology followed a marked Mediterranean seasonal pattern consistent with the region's climate (Lionello & Scarascia, 2018). The complete absence of individuals in January reflects winter diapause and low aphid availability under cool conditions (Sloggett, 2021). Populations increased sharply from March, peaking in May–June when spring aphid outbreaks on cereals and fruit trees coincide with optimal reproductive conditions for ladybirds.

Statistical models confirmed a significant positive effect of aphid presence on aphidophagous ladybird abundance (IRR = 1.86; p = 0.009), providing empirical evidence of bottom-up regulation: prey availability is the primary proximate driver of predator dynamics at the survey scale. The aggregation of adults in aphid-infested plots is consistent with chemically mediated prey detection – via plant volatiles or honeydew – and numerical response mechanisms (Li et al., 2024). Dominant aphidophagous species – particularly *H. variegata*, *C. septempunctata* and *O. doublieri* – respond rapidly to aphid outbreaks, concentrating reproductive effort where resources are abundant.

Instantaneous abiotic variables (temperature, humidity, wind speed) showed no significant independent effect on either abundance or richness. At the temporal and spatial scales considered here, habitat structure and trophic availability appear to outweigh short-term microclimatic variation in determining ladybird distribution patterns (Gardiner et al., 2021).

Landscape complementarity and functional resilience

At the landscape scale, complementarity between semi-natural habitats and agrosystems emerges as a key mechanism for maintaining both regional diversity and functional integrity of predatory guilds. Natural habitats act as reservoirs of specialised and low-density species, while cultivated systems support high densities of generalist predators capable of delivering effective pest regulation. The combined habitat mosaic increases overall regional richness (23 species observed; ~25 estimated) and stabilises ecosystem services across seasons (Hsieh et al., 2016; Rusch et al., 2016).

Management implications and perspectives

While management recommendations were not directly tested in this study, the observed patterns suggest several avenues for agroecological management, consistent with the broader literature. Preserving semi-natural habitats adjacent to crops may enhance recolonisation processes and sustain predator reservoirs. In orchards and cereal systems, reducing insecticide applications – particularly during peak spring reproductive periods – while maintaining grassy strips, hedgerows and floral resources could support ladybird persistence outside aphid outbreaks.

In urban environments, increasing vegetation complexity, planting diverse trees and shrubs, reducing impervious surfaces, and moderating pesticide use could mitigate biotic homogenisation and improve ecological connectivity for beneficial arthropods (Rocha et al., 2018; Magura et al., 2020; Sockhill et al., 2025).

Expanding monitoring across broader spatial and temporal scales, integrating functional trait analyses, and replicating the study design across multiple sites per habitat type would further clarify

how agricultural intensification, urban expansion and climate change interact to influence aphid–predator trophic networks in North Africa (Taranto et al., 2022; Soares et al., 2023).

Conclusion

This comparative study of Coccinellidae across four contrasting habitats in North-Central Algeria indicates that habitat type is associated with marked differences in taxonomic diversity and in the structure of predatory guilds. Semi-natural forests act as biodiversity reservoirs, supporting rare and specialised species, while agrosystems sustained abundant generalist predators whose numbers tracked aphid presence, consistent with a potential contribution to pest regulation, although actual pest-suppression outcomes were not measured in this study. Highly artificial urban habitats, in contrast, promote simplified and homogenised assemblages, reflecting strong biotic homogenisation associated with urbanization (Rocha et al., 2018; Magura et al., 2020).

Ladybird diversity and ecological function are closely linked to habitat complexity and prey availability. The combination of structural heterogeneity, diverse host plants and trophic resources in forests and agrosystems sustains both rare and common species, enabling stable predator populations across seasons. The observed positive effect of aphid presence on aphidophagous species abundance further confirms the importance of bottom-up regulation in shaping local community dynamics (Li et al., 2024). Maintaining landscape-scale heterogeneity is associated with higher regional species richness (~23 species observed; Chao1 estimate ~25) and may help support ecosystem services, consistent with findings in Mediterranean systems (Hsieh et al., 2016; Rusch et al., 2016).

By documenting these patterns, this study strengthens regional knowledge of ladybird assemblages and their trophic interactions, providing an empirical basis for the role of native predatory insects in regulating pest populations. Conserving and restoring habitat complexity across forests, farms and urban green spaces thus represents a biodiversity objective that may also contribute to sustaining functioning agroecosystems, though this latter link was not directly tested here (Gardiner et al., 2021; Rusch et al., 2016; Soares et al., 2023).

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References

Ali-Arous S., Meziane M. & Djelouah K. 2023. Interactions between wild flora, crops, aphids (Hemiptera, Aphididae) and their natural enemies in citrus orchards. – J. Insect Biodivers. Syst. 9 (1): 17-32. https://doi.org/10.52547/jibs.9.1.17

Anderson M. J. 2001. A new method for non-parametric multivariate analysis of variance. – Austral Ecol. 26: 32-46. https://doi.org/10.1046/j.1442-9993.2001.01070.x

Bieńkowski A. O. 2018. Key for Identification of the Ladybirds (Coleoptera: Coccinellidae) of European Russia and the Russian Caucasus. Pensoft Publishers, Sofia: 233-260. https://doi.org/10.11646/zootaxa.4472.2.2

Blackman R. L. & Eastop V. F. 2021. Aphids on the World's Plants: An Online Identification and Information Guide. URL: http://www. aphidsonworldsplants. info (last accessed 13 April 2026). http://www.aphidsonworldsplants.info/

Brakchi L., Djerrad Z., Terfi S., Debieb A., Adi N., Bouti L. & Kaci M. 2025. Ecodendrometric characterization of Aleppo pine (*Pinus halepensis* Mll.) stands in the Baïnem Forest (Algeria). – Appl. Ecol. Environ. Res. 23 (3): 5499-5520. https://doi.org/10.15666/aeer/2303_54995520.

Chao A., Chiu C.-H. & Jost L. 2014. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. – Annu. Rev. Ecol. Evol. Syst. 45: 297-324. https://doi.org/10.1146/annurev-ecolsys-120213-091540

Decker O., Uhler J., Redlich S., Chao A., Kortmann M., Steffan-Dewenter I., Tobisch C., Ewald J., Englmeier J., Fricke U., Ganuza C., Haensel M., Bozicevic V., Morinière J., Zhang J. & Müller J., 2026. Distance-decay reveals contrasting effects of land-use types on arthropod community homogenisation. – Nature Communications 17: 763. https://doi.org/10.1038/s41467-025-67612-9.

Derolez B., Orczyk N. & Declercq S. 2014. Clé d'identification des coccinelles du Nord-Pas-de-Calais, version 4.2. Groupe Ornithologique et Naturaliste du Nord-Pas-de-Calais, Lille, 85 p. https://gon. bibli. fr/scan/2014_v4_2_cle_coccinelles_NPdC.pdf

Duff A. G. (ed.) 2012. Checklist of Beetles of the British Isles, 2nd ed.\u2014 Pemberley Books, Iver, 164 pp. ISBN: 978-0-9573357-0-7

Ferreira J. O., Silva-Torres C. S. A., Carmo E. B. S., Laumann R. A., Borges M. & Blassioli Moraes M. C. 2023. Do interactions among ladybeetles affect their fitness and predatory behavior? – J. Insect Behav. 35: 195-212. DOI: 10. 1007/s10905-022-09810-7

Gardiner M. M., O'Rourke M. E., Fox T. B. & Landis D. A. 2021. Community science data suggest that urbanization and forest habitat loss threaten aphidophagous native lady beetles. – Ecol. Evol. 11 (4): 1583-1594. https://doi.org/10.1002/ece3.7229

Gavloski A. J. A., Dewaard J. R., Steinke D. & Fryxell J. M. 2025. Sampling requirements for standardized insect biodiversity monitoring vary with abundance. – FACETS 10: 1-16. https://doi.org/10.1139/facets-2024-0007

Gómez-Marco F., Jacas J. A., Urbaneja A. & Tena A. 2015. Ground cover management in citrus affects the biological control of aphids. Acta Horticulturae 1065: 1125-1128. https://doi.org/10.17660/actahortic.2015.1065.141

Gourreau J. M. 1974. Systématique de la tribu des Scymnini (Coccinellidae). – Ann. Zool. Écol. Anim. n o H. S. 1974, INRA, édit., 149, rue de Grenelle, 75341 Paris 1 vol. relié, pp 224.

Grez A. A., Rand T. A., Zaviezo T. & Castillo-Serey F. 2013. Land use intensification differentially benefits alien over native predators in agricultural landscape mosaics. – Divers. Distrib. 19 (7): 749-759. https://doi.org/10.1111/ddi.12027

Grez A. A., Zaviezo T. & Roy H. E. 2019. The impact of urbanization on ladybird communities. In Roy H. E. & Brown P. M. J. (Eds.): The Role of Coccinellids in Urban Ecosystems. Wiley-Blackwell, Hoboken, pp. 127-149.

Gruau K. & Terrasse G. 2025. Clé illustrée des Scymnini et Stethorini (Coccinellidae) de la moitié Nord de la France. – Harmonia 31: 1-24.

Hodek I. & Michaud J. P. 2008. Why is Coccinella septempunctata so successful? (A review). – Eur. J. Entomol. 105 (1): 1-12. https://doi.org/10.14411/eje.2008.001

Hodek I., Van Emden H. F. & Honěk A. 2012. Ecology and Behaviour of the Ladybird Beetles (Coccinellidae). Wiley-Blackwell, Chichester, 600 pp. ISBN: 978-1-4051-9661-8

Holecová M., Zach P., Hollá, K., Šebestová, M., Klesniaková, M., Šestáková, A., Honěk, A., Nedvěd, O., Parák, M., Martinková, Z., Holec, J., Viglášová, S., Brown, P. M. J., Roy, H. E., & Kulfan, J. 2018. Overwintering of ladybirds (Coleoptera: Coccinellidae) on Scots pine in Central Europe. European Journal of Entomology, 115, 658-667. https://doi.org/10.14411/eje.2018.065

Hsieh T. C., Ma K. H. & Chao A. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). – Methods Ecol. Evol. 7 (12): 1451-1456. https://doi.org/10.1111/2041-210X.12613

Lakhal M. A., Ghezali D., Nedvěd O. & Doumandji S. 2018. Checklist of ladybirds of Algeria with two new recorded species (Coleoptera, Coccinellidae). – ZooKeys 774: 41-52. https://doi.org/10.3897/zookeys.774.23895

Legendre P. & Legendre L. 2012. Numerical Ecology, 3rd English ed. – Developments in Environmental Modelling 24. Elsevier, Amsterdam, 1006 pp. ISBN: 978-0-444-53868-0

Li C., Yu J., Mao R., Kang K., Xu L. & Wu M. 2024. Functional and numerical responses of Harmonia axyridis (Coleoptera: Coccinellidae) to Rhopalosiphum nymphaeae (Hemiptera: Aphididae). – Insects 15 (9): 633-645. https://doi.org/10.3390/insects15090633

Li M., Lei T., Wang G., Zhang D., Liu H. & Zhang Z. 2023. Monitoring insect biodiversity and comparison of sampling strategies using metabarcoding. – Ecol. Evol. 13 (4): e10031, 14 pp. https://doi.org/10.1002/ece3.10031

Lionello P. & Scarascia L. 2018. The relation between climate change in the Mediterranean region and global warming. – Reg. Environ. Change 18 (5): 1481-1493. https://doi.org/10.org/10.1007/s10113-018-1290-1

Magura T., Ferrante M. & Lövei GL. 2020. Only habitat specialists become smaller with advancing urbanization. – Glob. Ecol. Biogeogr. 29 (11): 1978-1987. https://doi.org/10.1111/geb. 13168

Myers N., Mittermeier R. A., Mittermeier C. G., Da Fonseca G. A. B. & Kent J. 2000. Biodiversity hotspots for conservation priorities. – Nature 403: 853-858. https://doi.org/10.1038/35002501

Oksanen J., Simpson G. L., Blanchet F. G., Kindt R., Legendre P., Minchin P. R., O'Hara R. B., Solymos P., Stevens M. H. H., Szoecs E. & Wagner H. 2022. vegan: Community Ecology Package. R package version 2. 6-2. URL: https://CRAN.R-project.org/package=vegan

R Core Team 2025. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. URL: https://www.R-project.org/. https://doi.org/10.32614/r.manuals

Rocha E. A. & Fellowes M. D. E. 2018. Does urbanization explain differences in interactions between an insect herbivore and its natural enemies and mutualists? – Urban Ecosyst. 21 (3): 405-417. https://doi.org/10.1007/s11252-017-0727-5

Romanowski J., Ceryngier P., Větrovec J., Piotrowska M. & Szawaryn K. 2020. Endemics versus newcomers: the ladybird beetle (Coleoptera: Coccinellidae) fauna of Gran Canaria. – Insects 11 (10): 641, 24 pp. https://doi.org/10.3390/insects11090641

Roy H. E. & Brown P. M. J. 2018. Field Guide to the Ladybirds of Britain and Ireland. Illustrated by R. Lewington. \u2014 Bloomsbury, London, 160 pp. ISBN: 978-1-4729-2280-2

Rusch A., Bommarco R. & Eklund H. 2016. Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. – Agriculture, Ecosystems & Environment. 221. 198-204pp. https://doi.org/10.1016/j.agee.2016.01.039

Saharaoui L. & Gourreau J. M. 1998. Les coccinelles d'Algérie: inventaire préliminaire et régime alimentaire (Coleoptera, Coccinellidae). – Bull. Soc. Entomol. Fr. 103 (3): 213-224. https://doi.org/10.3406/bsef.1998.17418

Saharaoui L., Hemptinne J.-L. & Magro A. 2014. Biogéographie des coccinelles (Coleoptera: Coccinellidae) d'Algérie. – Entomologie Faunistique – Faunistic Entomology 67: 147-164.

Saharaoui M. 2000. Contribution à l'étude des coccinelles (Coleoptera, Coccinellidae) d'Algérie. – Rev. Écol. Biol. Sol 37 (4): 221-239.

Salehi T., Pashaei Rad SH., Mehrnejad M. R. & Shokri M. R. 2011. Ladybirds associated with pistachio trees in part of Kerman province, Iran (Coleoptera: Coccinellidae). \u2014 Iran. J. Anim. Biosyst. 7 (2): 157\u2013169.

Scheiner S. M. & Gurevitch J. 2001. Design and Analysis of Ecological Experiments, 2nd ed. – Oxford University Press, New York, 415 pp. https://doi.org/10.1093/oso/9780195131871.001.0001

Sloggett J. J. 2021. Aphidophagous ladybirds (Coleoptera: Coccinellidae) and climate change: A review. – Insect Conserv. Divers. 14 (2): 193-206. https://doi.org/10.1111/icad. 12527

Soares A. O., Haelewaters D., Ameixa O. M. C. C., Borges I., Brown P. M. J., Cardoso P., De Groot M. D., Evans E. W., Grez A. A., Hochkirch A., Holecová M., Honěk A., Kulfan J., Lillebø A. I., Martinková Z., Michaud J. P., Nedvěd O., Omkar, Roy H. E., Saxena S., Shandilya A., Sentis A., Skuhrovec J., Viglášová S., Zach P., Zaviezo T. & Losey J. E. 2023. A roadmap for ladybird conservation and recovery. – Conserv. Biol. 37 (1): e13965. https://doi.org/10.1111/cobi.13965

Sockhill N. J., Lin B. B., Berthon K., Thomas F., Fuller R. A. & Bekessy S. 2025. Designing urban garden beds: native vegetation creates healthy habitats for arthropods in Melbourne, Australia. – Urban Ecosystems. https://doi.org/10.1007/s11252-025-01751-1.

Southwood T. R. E. & Henderson P. A. 2000. Ecological Methods, 3rd ed. – Blackwell Science, Oxford, 575 pp. ISBN : 978-0-632-05477-0

Taranto L., Rodrigues I., Santos A. P., Villa M. & Pereira J. A. 2022. Response of the Coccinellidae community within sustainable vineyards to the surrounding landscape. – Agronomy 12 (9): 2140, 16 pp. https://doi.org/10.3390/agronomy12092140

Venables W. N. & Ripley B. D. 2002. Modern Applied Statistics with S, 4th ed. Springer, New York, 495 pp. https://doi.org/10.1007/b97626

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