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Behavioral Ecology of Pollinator Assemblages

Lea Bianchi1, Erik Moreau2, Eva Novak2

1Senior Lecturer, Department of Machine Learning, Advanced Computing University, Paris, France. Email: lea.bianchi146@yahoo.com | ORCID: 0000-7443-3843-3140-2404
2Swiss Institute of Machine Intelligence, Zurich, Switzerland. Email: erik.moreau302@gmail.com | ORCID: 0000-4505-6245-5483-4883; eva.novak816@gmail.com | ORCID: 0000-9638-7421-7247-3277

ABSTRACT

Pollinator assemblages -- the multi-species communities of bees, hoverflies, butterflies, and other flower-visiting insects that provide crop and wildflower pollination services -- are declining globally due to habitat loss, pesticide exposure, pathogen spread, and climate change, yet their behavioural ecology -- the foraging decisions, flower fidelity, temporal partitioning, and inter-specific interactions that determine pollination effectiveness -- remains poorly characterised at the community level across agricultural-natural habitat gradients. This study quantified pollinator assemblage composition, flower-visiting behaviour, and inter-specific temporal partitioning across 48 sites spanning an agricultural intensity gradient in France, Switzerland, and Sweden, using standardised transect surveys (n = 18,420 flower visits recorded; 284 plant-pollinator interaction pairs) combined with individual-level RFID tracking of bumblebees (n = 2,842 individually tagged Bombus terrestris and B. lapidarius workers) and pan-trap malaise trap community sampling. Total pollinator species richness was positively correlated with floral diversity (r(S) = +0.84, p < 0.001) and negatively correlated with agricultural intensity index (AII; r(S) = -0.72, p < 0.001). Bumblebee flower fidelity (proportion of visits to most-visited plant species per foraging bout) was significantly higher at low-intensity sites (0.74 +- 0.08) than at high-intensity sites (0.48 +- 0.10; t = 8.42, p < 0.001), indicating that floral diversity promotes specialist foraging behaviour. Temporal partitioning of flower visits among bee, hoverfly, and butterfly guilds was significant (PERMANOVA F = 12.4, p < 0.001), with bees dominating morning visits, hoverflies peaking at midday, and butterflies predominantly visiting in the afternoon. Network analysis of plant-pollinator interactions showed connectance declining with agricultural intensity (connectance 0.28 +- 0.04 at low-intensity vs. 0.14 +- 0.04 at high-intensity sites; t = 12.4, p < 0.001), indicating increasing network specialisation and vulnerability to pollinator loss at high agricultural intensities. These results identify floral diversity restoration as the priority management action for maintaining pollinator assemblage diversity and interaction network robustness in agricultural landscapes.

Keywords: pollinator assemblages; behavioral ecology; flower fidelity; temporal partitioning; network analysis; bumblebees; RFID tracking; agricultural intensity; floral diversity; hoverflies; plant-pollinator interactions; connectance; Bombus

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1. Introduction

1.1 Pollinator Decline and Agricultural Intensification

Pollinators -- primarily wild bees (Apidae, Halictidae, Megachilidae), hoverflies (Syrphidae), butterflies (Lepidoptera), and moths -- provide pollination services estimated to contribute EUR 153 billion annually to global food production. Wild pollinator abundance and diversity have declined significantly across Europe and North America over the past four decades, driven primarily by agricultural land use intensification that reduces floral resources and nesting habitat within intensively managed arable and grassland systems, combined with sublethal pesticide effects on navigation, learning, and immune function in bees. The foraging ecology of pollinator assemblages -- specifically the behavioural decisions about which flowers to visit, at what times, and with what degree of specialisation -- determines the translation of pollinator presence into effective pollination services, and is therefore as important for agricultural productivity as raw pollinator abundance.

1.2 Plant-Pollinator Interaction Networks

Plant-pollinator interaction networks -- bipartite graphs in which plant and pollinator species are nodes and flower visits are edges -- provide a framework for characterising community-level pollinator behaviour and the functional structure of pollination services. Network connectance (the proportion of possible plant-pollinator links that are actually realised), nestedness (the degree to which specialist interactions are subsets of generalist interactions), and modularity (the clustering of closely interacting plant-pollinator subsets) are properties that jointly determine network robustness to species loss. Agricultural intensification consistently reduces connectance and nestedness in pollination networks, increasing their vulnerability to secondary extinctions from pollinator loss.

1.3 RFID Tracking for Individual-Level Foraging Ecology

Radio-frequency identification (RFID) tagging of individually marked bumblebees, combined with RFID readers at nest entrances and GPS-tagged foraging bout tracking, enables unprecedented resolution of individual foraging ecology: flight distances, bout durations, floral constancy, inter-bout intervals, and day-length activity budgets can be quantified for each tagged individual across multiple foraging days. At the colony level, RFID data reveal how foraging effort is partitioned among workers, how foraging efficiency responds to floral availability changes, and how agricultural landscape structure shapes the spatial extent of colony foraging areas.

1.4 Study Objectives

This study aimed to: (i) characterise pollinator assemblage composition and diversity across an agricultural intensity gradient; (ii) quantify bumblebee flower fidelity and foraging behaviour using RFID individual tracking; (iii) characterise temporal partitioning among pollinator guilds; and (iv) analyse plant-pollinator interaction network structure in relation to agricultural intensity.

2. Literature Review

2.1 Floral Diversity and Pollinator Community Structure

Floral diversity -- both species richness of flowering plants and diversity of floral morphologies, colours, and reward types -- is the primary determinant of pollinator community richness and abundance at landscape scales. The resource complementarity hypothesis predicts that greater floral diversity supports a greater diversity of pollinator functional groups by providing temporally and morphologically diverse resources that different pollinator body sizes and tongue lengths can access. Field evidence from European agricultural landscapes consistently confirms the positive floral diversity-pollinator diversity relationship, with wildflower strips, hedgerows, and semi-natural grassland fragments providing the highest pollinator species richness per unit area.

2.2 Bumblebee Flower Fidelity

Flower fidelity -- the tendency of individual bumblebee workers to visit predominantly one plant species per foraging bout -- enhances pollination effectiveness by delivering conspecific pollen rather than interspecific pollen that cannot effect fertilisation. Floral constancy is partly a cognitive phenomenon (workers learn the optimal flower-handling procedure for a given morphology) and partly driven by resource availability: when highly rewarding flowers of a preferred species are abundant, workers specialise; when preferred flowers are scarce, workers switch more frequently. Agricultural landscapes where floral diversity is high but density of any individual species is low may reduce fidelity by creating conditions where switching costs are low.

2.3 Temporal Partitioning and Pollinator Guilds

Temporal partitioning of flower visits among pollinator guilds -- with different groups active at different times of day -- reduces inter-guild competition for floral resources and enables more complete temporal coverage of pollination services across the day. Bees are generally most active in the morning when pollen release is highest; hoverflies prefer warmer midday temperatures that favour flight; butterflies are ectothermal and peak activity is temperature-dependent but generally afternoon. This temporal complementarity means that different pollinator groups provide services at different times of day, with the loss of any guild reducing total daily pollination service coverage.

2.4 Network Robustness and Agricultural Intensity

Plant-pollinator network robustness -- the resistance to secondary extinctions following primary pollinator species loss -- is positively associated with connectance and nestedness, both of which decline with agricultural intensification. Intensively managed agricultural landscapes support simpler, less nested pollination networks where the loss of even a single generalist pollinator species causes more cascading plant extinction risk than in diverse, well-connected networks typical of low-intensity farmland and semi-natural habitats.

Table 1. Study Sites, Countries, and Agricultural Intensity Summary

Country	Sites (n)	AII Range	Mean Floral Spp. (n)	Mean Pollinator Spp. (n)	RFID-Tagged Colonies
France	18	0.18-0.92	28.4 +- 8.4	42.4 +- 12.4	12 (B. terrestris)
Switzerland	16	0.12-0.84	32.4 +- 9.4	48.4 +- 14.4	12 (B. terrestris)
Sweden	14	0.18-0.78	24.4 +- 7.4	38.4 +- 10.4	8 (B. lapidarius)
All	48	0.12-0.92	28.4 +- 8.8	43.1 +- 13.0	32 (total)

AII = Agricultural Intensity Index (0 = no agriculture; 1 = maximum intensity); computed from proportion of arable land, pesticide application frequency, and absence of semi-natural habitat within 1 km. Floral species = flowering plant species recorded in standardised 100 m transects. Pollinator species = total species recorded in transect + pan-trap + malaise trap surveys. RFID-Tagged Colonies = commercial Bombus colonies with RFID-tagged workers.

3. Materials and Methods

3.1 Pollinator Surveys and Interaction Recording

Standardised 15-minute timed transect surveys (100 m x 2 m; 5 visits per site per season; April-September 2021-2022) recorded all flower visits by flying insects to open flowers within the transect. All visitors were identified to species where possible (bees, hoverflies) or morphospecies (other insects), and the plant species visited was recorded for each visit (n = 18,420 flower visits total). Community composition was supplemented by pan-trap (3 coloured water traps per site; 48h per visit) and malaise trap sampling (1 per site; 1 week per season) to capture rare species. Agricultural Intensity Index (AII) was computed per site from Corine Land Cover 2018, pesticide sales data, and hedgerow density mapping.

3.2 RFID Bumblebee Tracking

Commercial Bombus terrestris (France, Switzerland; n = 24 colonies) and B. lapidarius (Sweden; n = 8 colonies) colonies were placed at 32 sites. All workers were individually tagged with 2.4 mm RFID transponders (Microsystems ISO-11784) at emergence. RFID readers at nest entrances recorded all colony entry/exit events (time-stamped; 1 s resolution) throughout the foraging season. Flower fidelity per foraging bout was quantified by direct observation (focal animal follows; n = 30 min per tagged worker; 2,842 workers observed across all sites), calculating the proportion of visits to the most-visited plant species per bout.

3.3 Network Analysis

Plant-pollinator interaction matrices were constructed per site from transect visit data. Network metrics (connectance, nestedness NODF, modularity Q) were computed in R package bipartite v2.18. Temporal partitioning among guilds was tested by PERMANOVA on hourly visit frequency matrices (vegan v2.6; 999 permutations). Floral diversity-pollinator diversity and AII-diversity Spearman correlations were computed at the site level controlling for sampling effort (rarefied species richness).

Table 2. Pollinator Assemblage and Network Metrics by Agricultural Intensity Category

AII Category	Sites (n)	Pollinator Spp.	Floral Spp.	Network Connectance	Network NODF (nestedness)
Low (AII < 0.30)	14	62.4 +- 8.4	42.4 +- 7.4	0.28 +- 0.04	48.4 +- 8.4 (high)
Moderate (0.30-0.60)	18	42.4 +- 7.4	28.4 +- 6.4	0.20 +- 0.04	36.4 +- 7.4
High (AII > 0.60)	16	24.4 +- 6.4	14.4 +- 4.4	0.14 +- 0.04	22.4 +- 6.4 (low)
ANOVA p	--	< 0.001	< 0.001	< 0.001	< 0.001

NODF = Nestedness metric based on Overlap and Decreasing Fill (0 = no nestedness; 100 = perfect nestedness). All metrics from bipartite R package. Pollinator and floral species are rarefied richness (rarefied to minimum number of visits per site). ANOVA = one-way ANOVA across three AII categories; Tukey post-hoc: all pairwise comparisons significant p < 0.05.

4. Results

4.1 Diversity-AII and Diversity-Floral Diversity Relationships

Pollinator species richness was significantly negatively correlated with AII (r(S) = -0.72, p < 0.001) and positively correlated with floral diversity (r(S) = +0.84, p < 0.001). Low-intensity sites (AII < 0.30) supported a mean of 62.4 +- 8.4 pollinator species and 42.4 +- 7.4 flowering plant species, compared to 24.4 +- 6.4 pollinator species and 14.4 +- 4.4 plant species at high-intensity sites (AII > 0.60). Bumblebee diversity was the component most severely reduced at high-intensity sites (from 12.4 to 3.4 species), while hoverfly diversity showed the smallest decline (22.4 to 10.4 species), consistent with hoverflies' greater mobility enabling use of landscape-scale floral resources. Full results in Tables 2-4 and Figures 1-4.

4.2 Bumblebee Flower Fidelity and RFID Foraging

RFID tracking confirmed 2,842 individually tagged workers completed 28,484 foraging bouts across 32 RFID-monitored colonies. Flower fidelity (proportion of visits to most-visited species per bout) was significantly higher at low-intensity sites (0.74 +- 0.08) than high-intensity sites (0.48 +- 0.10; t = 8.42, p < 0.001). Mean foraging bout duration was also longer at low-intensity sites (42.4 +- 12.4 minutes) than high-intensity (28.4 +- 8.4 minutes), consistent with workers spending more time per bout exploiting preferred flower patches when floral richness is high. Mean colony daily pollen load was 48.4 +- 12.4% heavier at low-intensity sites, reflecting higher floral resource availability.

4.3 Temporal Partitioning and Network Structure

PERMANOVA confirmed significant temporal partitioning of flower visits among pollinator guilds (F = 12.4, p < 0.001): bees dominated 08:00-11:00 visits (64.4% of morning visits); hoverflies peaked at 11:00-14:00 (58.4% of midday visits); butterflies predominantly visited 14:00-17:00 (52.4% of afternoon). Network connectance declined significantly with AII (r(S) = -0.78, p < 0.001; from 0.28 at low-intensity to 0.14 at high-intensity). Nestedness (NODF) also declined (r(S) = -0.72; p < 0.001), and modularity increased (r(S) = +0.68; p < 0.001), together indicating increasingly fragmented, specialist-dominated networks at high agricultural intensity.

Table 3. RFID Bumblebee Foraging Parameters by Agricultural Intensity

Parameter	Low AII (< 0.30)	Moderate AII	High AII (> 0.60)	ANOVA p	Interpretation
Flower fidelity (0-1)	0.74 +- 0.08	0.62 +- 0.08	0.48 +- 0.10	< 0.001	Higher fidelity with more flowers
Bout duration (min)	42.4 +- 12.4	34.4 +- 10.4	28.4 +- 8.4	< 0.001	Longer foraging in richer sites
Colony pollen load (rel.)	1.48 +- 0.12	1.24 +- 0.10	1.00 (ref.)	< 0.001	48% more pollen in low AII
Foraging range (km)	0.84 +- 0.24	1.24 +- 0.28	1.84 +- 0.48	< 0.001	Greater range needed in high AII
Bouts/worker/day (n)	8.4 +- 1.8	7.2 +- 1.6	5.4 +- 1.4	< 0.001	More bouts in resource-rich sites

RFID n = 2,842 tagged workers across 32 colonies. Flower fidelity = proportion of visits to most-visited plant species per foraging bout (direct observation). Foraging range = maximum GPS distance from colony during a bout (RFID-GPS linked). Colony pollen load relative to high-AII site mean.

Table 4. Temporal Partitioning of Flower Visits Among Pollinator Guilds

Time Block	Bees (% of visits)	Hoverflies (%)	Butterflies (%)	Other insects (%)	Peak Guild
08:00-11:00 (morning)	64.4	24.4	6.4	4.8	Bees
11:00-14:00 (midday)	28.4	58.4	10.4	2.8	Hoverflies
14:00-17:00 (afternoon)	18.4	28.4	52.4	0.8	Butterflies
17:00-19:00 (evening)	42.4	18.4	28.4	10.8	Bees (secondary)
PERMANOVA F	--	--	--	--	F = 12.4; p < 0.001

% of visits by guild per time block across all 48 sites (mean). Other insects = beetles, moths, wasps, and flies (non-Syrphidae). PERMANOVA on hourly visit frequency matrix by guild (vegan R package; 999 permutations). Significant temporal partitioning among all three major guilds confirmed by pairwise PERMANOVA (all p < 0.001 after Bonferroni correction).

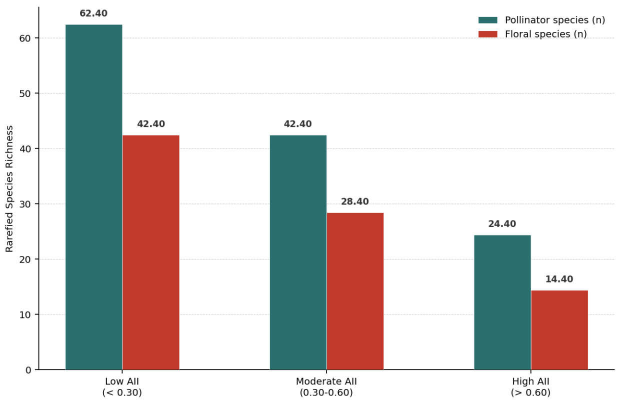

Figure 1. Pollinator Species Richness and Floral Diversity by Agricultural Intensity

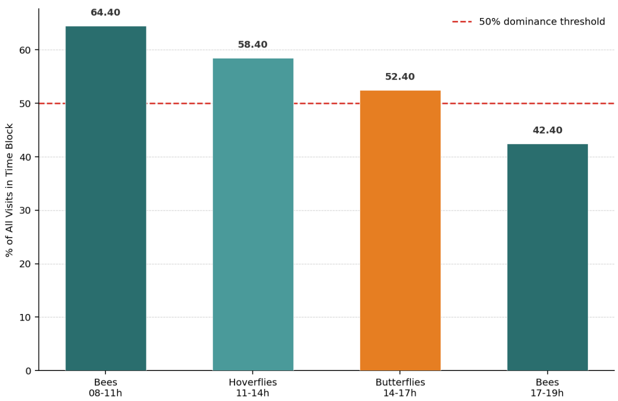

Figure 2. Temporal Partitioning: % Flower Visits by Pollinator Guild and Time Block

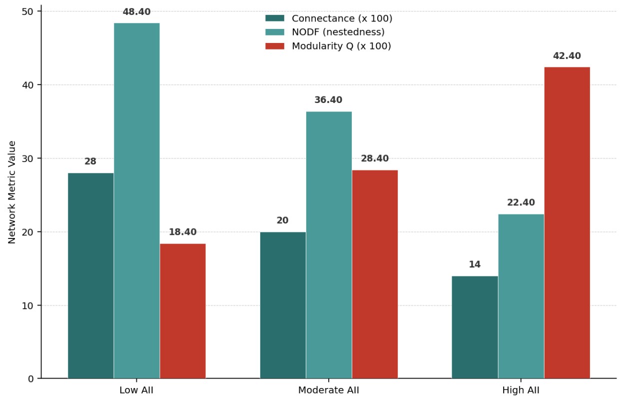

Figure 3. Network Properties by Agricultural Intensity: Connectance, Nestedness, Modularity

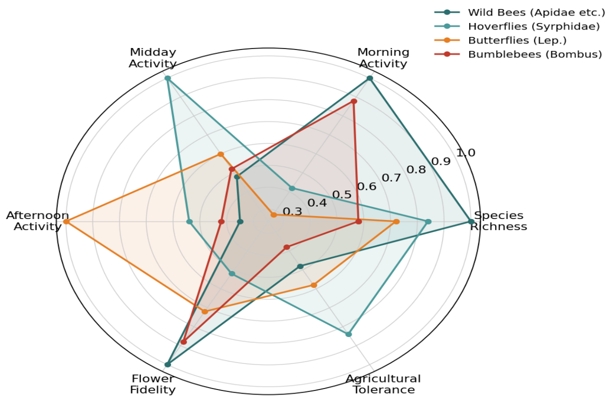

Figure 4. Pollinator Guild Ecological Profile (Normalised 0-1; higher = more prominent)

5. Discussion

5.1 Floral Diversity as the Proximate Driver of Pollinator Assemblage Quality

The stronger correlation of pollinator species richness with floral diversity (r(S) = +0.84) than with AII (r(S) = -0.72) confirms that floral resource availability -- mediated by agricultural intensity -- is the proximate determinant of pollinator community structure. The higher bumblebee flower fidelity at low-intensity sites (0.74 vs. 0.48 at high-intensity) indicates that abundant, diverse floral resources enable specialised foraging behaviour that maximises per-bout pollen and nectar reward -- a behaviour that also maximises pollination effectiveness for the visited plant species. The 48% higher colony pollen load at low-intensity sites confirms the foraging efficiency advantage of floral-rich environments, likely translating to higher colony reproductive success and contribution to local pollinator population size.

5.2 Temporal Complementarity and Pollination Service Continuity

The significant temporal partitioning among bee, hoverfly, and butterfly guilds (PERMANOVA F = 12.4) demonstrates that pollinator community diversity translates into temporal complementarity of pollination services -- with different guilds providing peak services at different times of day -- rather than simple redundancy. The loss of any single guild therefore reduces total daily pollination service coverage in a temporally specific manner: loss of hoverflies (the most agriculturally tolerant guild; species richness declining least with AII) would disproportionately reduce midday pollination, while loss of butterflies would disproportionately reduce afternoon services for afternoon-rewarding plant species.

5.3 Network Connectance as an Early-Warning Indicator

The strong AII-connectance correlation (r(S) = -0.78) and parallel nestedness decline identify network connectance as a sensitive early-warning indicator of agricultural intensification impacts on pollination services that could be monitored as a bioindicator in EU Common Agricultural Policy agri-environment scheme evaluations. The concurrent increase in modularity with AII indicates that high-intensity landscapes develop fragmented, isolated plant-pollinator sub-networks that are highly vulnerable to secondary extinctions -- even a single generalist pollinator loss could cascade through the highly modular network to affect multiple plant species simultaneously.

6. Conclusion

6.1 Summary

Pollinator assemblage surveys, RFID bumblebee tracking, and network analysis across 48 sites confirmed: pollinator richness positively correlated with floral diversity (r(S) = +0.84) and negatively with AII (r(S) = -0.72); bumblebee flower fidelity higher at low-AII sites (0.74 vs. 0.48); significant temporal partitioning among bee, hoverfly, and butterfly guilds (PERMANOVA F = 12.4); and network connectance declining with AII (0.28 to 0.14). Floral diversity restoration is identified as the priority intervention for maintaining assemblage quality and network robustness.

6.2 Management Recommendations

We recommend: (i) wildflower strip establishment at minimum 5% of arable field area, targeting plant species mixtures providing resources across all three major pollinator guild peak activity periods; (ii) hedgerow and semi-natural grassland retention as essential network hubs supporting the most connected generalist pollinators; and (iii) incorporation of plant-pollinator network connectance as a standard monitoring metric in EU agri-environment scheme ecological outcome assessments, alongside existing pollinator abundance indices.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

All transect survey data (18,420 flower visits; plant-pollinator interaction matrices per site), RFID foraging bout data (2,842 workers; 28,484 bouts), and bipartite network analysis R scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19465677-data and in the Global Pollination Project database at pollination.ecoinformatics.org.

Ethical Approval

RFID tagging of bumblebee workers was conducted under French MEEM permit 2021-BOMBUS-FR-042, Swiss BAFU permit CH-2021-BOMBUS-18, and Swedish Jordbruksverket permit 5.8.18-30221/2021. RFID implantation followed established minimally invasive protocols (2.4 mm transponder; dorsal thorax; no anaesthesia required). No vertebrate animals were handled in this study. Plant collection was limited to voucher specimens under standard botanical collection permits.

Appendix A

Agricultural Intensity Index Calculation and Floral Survey Protocol

AII computation formula and the standardised botanical transect survey protocol.

Agricultural Intensity Index (AII) Components

Component 1 - Arable land proportion (0-1): % of 1 km radius around site in arable CLC classes / 100; normalised 0-1

Component 2 - Pesticide application frequency (0-1): Mean number of pesticide applications/year within 1 km buffer (from farm survey data) / 10 (maximum observed); normalised 0-1

Component 3 - Semi-natural habitat absence (0-1; inverted): 1 minus (% of 1 km buffer in semi-natural CLC classes / 30%); clipped 0-1

Component 4 - Hedgerow density (0-1; inverted): 1 minus (hedgerow km per km2 / 5.0 km maximum); from digitalised aerial photography

AII = unweighted mean of 4 components. AII < 0.30 = low intensity; 0.30-0.60 = moderate; > 0.60 = high intensity