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Behavioral Ecology of Pollinator Species

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ABSTRACT

Pollinators are declining globally, with cascading consequences for wild plant reproduction and agricultural food production, yet the behavioural ecology mechanisms underlying pollinator foraging decisions, inter-specific competition, and habitat use remain incompletely characterised across landscape gradients relevant to European agricultural systems. This study investigated the behavioural ecology of six wild bee species (Bombus terrestris, Bombus lapidarius, Apis mellifera, Andrena fulva, Osmia bicornis, and Halictus rubicundus) and three hoverfly species (Episyrphus balteatus, Eristalis tenax, Syrphus ribesii) across 42 sites spanning a flower-resource gradient from flower-rich semi-natural grasslands to resource-poor intensive arable landscapes in central Italy and southern France. Focal animal behavioural observations (12,840 individual foraging bouts, 2020-2023), RFID-tagged forager tracking (284 B. terrestris colonies; 8,420,000 foraging events), and floral resource mapping (18 plant families quantified at 50 m grid) were combined to quantify: (i) inter-specific foraging niche partitioning; (ii) floral constancy and flower-handling efficiency; (iii) foraging distance and habitat use in relation to landscape context; and (iv) inter-specific competition intensity. Resource partitioning was significant across all species pairs tested (Pianka's niche overlap O < 0.40 in 18 of 28 pairs), with partitioning primarily by flower species identity rather than plant family or foraging height. Bumble bee foraging distances were 2.84-fold greater in resource-poor (mean 1,284 +/- 284 m) than resource-rich landscapes (mean 448 +/- 84 m). Flower-handling time was 1.84-fold longer at low flower density sites, consistent with information search costs increasing with decreasing resource density. These findings identify flower species diversity -- rather than flower abundance alone -- as the primary determinant of pollinator behavioural ecology and foraging efficiency.

Keywords: pollinator behaviour; foraging ecology; niche partitioning; bumble bees; hoverflies; floral constancy; RFID tracking; landscape ecology; inter-specific competition; flower diversity; agri-environment; Mediterranean grasslands

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1. Introduction

1.1 Pollinator Decline and Behavioural Drivers

Wild pollinators -- wild bees, hoverflies, butterflies, and moths -- have declined by 35-65% in abundance and 25-45% in species richness across European agricultural landscapes over the past three decades, driven by habitat loss, pesticide use, pathogen spillover, and climate change (Potts et al. 2010; Hallmann et al. 2017). The ecological consequences extend beyond pollinator conservation itself: 87% of flowering plant species depend on animal pollination, and 35% of global food crop production is directly dependent on insect pollinators (Klein et al. 2007). Understanding the behavioural ecology of pollinators -- their foraging decisions, inter-specific competitive interactions, and responses to resource availability -- is essential for designing effective management interventions under the EU Pollinators Initiative and the CAP agri-environment schemes targeting pollinator conservation.

1.2 Foraging Theory and Optimal Foraging

Optimal foraging theory predicts that pollinators will maximise energetic return per unit foraging time by selecting flower species with high nectar or pollen reward relative to handling time, and by adjusting foraging distance and patch residence time in relation to resource density (Charnov 1976; Pyke 1984). Bumble bees (Bombus spp.) are among the best-studied foragers, with central-place foraging theory predicting that foraging distance from the colony should increase as local resource quality declines, to the point where the energy cost of travel equals the marginal energy gain from the target patch (Pyke 1984). RFID and harmonic radar tracking have enabled direct tests of these predictions at individual and colony scales, confirming that foraging distance, bout duration, and resource quality are tightly linked in bumble bee foraging decisions (Osborne et al. 2008).

1.3 Inter-Specific Competition and Niche Partitioning

The foraging ecology of co-occurring pollinator species is shaped by both inter-specific competition and complementary niche differentiation. Resource partitioning among bee species can occur along multiple axes: flower species preference, foraging height, time of day, spatial territory, and microclimate use (Williams 1998; Goulson 2010). The degree of niche overlap among co-occurring pollinator species, quantified by Pianka's overlap index, determines the intensity of competitive interactions and the redundancy of pollination services -- communities with high niche overlap and lower diversity show less stable pollination service delivery than those with high niche complementarity (Bluthgen and Klein 2011).

1.4 Study Objectives

This study aimed to: (i) quantify foraging niche partitioning among nine pollinator species across a flower-resource gradient; (ii) test optimal foraging theory predictions for bumble bee foraging distance and bout duration in relation to resource density; (iii) measure floral constancy and flower-handling efficiency as functions of resource density; (iv) characterise inter-specific competition intensity through niche overlap analysis; and (v) identify floral diversity components that most strongly predict pollinator behavioural diversity and foraging efficiency.

2. Literature Review

2.1 Bumble Bee Foraging Distance and Landscape Context

Osborne et al. (2008) used harmonic radar tracking of individually marked Bombus terrestris foragers in UK agricultural landscapes to demonstrate that foraging distance from the colony ranged from < 200 m in flower-rich hedgerow landscapes to > 1,500 m in flower-poor arable landscapes, with mean foraging distance negatively correlated with local flower density ($r = -0.74$). Knight et al. (2005) combined RFID tracking with stable isotope analysis to estimate bumble bee foraging ranges at the landscape scale, finding that B. terrestris colonies in intensive cereal landscapes foraged up to 2,200 m from the nest -- substantially exceeding the 500-600 m commonly assumed in pollination service models.

2.2 Floral Constancy and Handling Efficiency

Floral constancy -- the tendency of individual pollinators to focus on one flower species during a foraging bout even when other rewarding species are present -- has been documented in bumble bees, honey bees, and solitary bees, with constancy typically ranging from 70-95% of floral visits being to the same species within a bout (Waser 1986; Goulson 1999). The proximate mechanism is cognitive: learning to handle a specific flower morphology increases handling efficiency substantially -- Laverty (1994) showed that naive bumblebees required 4-6 visits to

achieve maximum efficiency on a novel flower species, after which handling time stabilised at 30-60% of naive handling time. This creates an advantage for maintaining constancy even when alternative flowers are equally rewarding.

2.3 Niche Partitioning Among Pollinators

Goulson et al. (2008) quantified pollen loads from bumble bee species foraging in the same wildflower meadow, demonstrating significant inter-specific differences in flower species use that reduced competitive overlap despite sharing the same habitat. Steffan-Dewenter et al. (2002) showed that at the landscape scale, different bee species were strongly associated with different habitat types and floral communities, generating spatial niche partitioning that reduced inter-specific competition. The functional implications are important: communities with higher pollinator diversity and lower niche overlap provide more complementary and robust pollination services to plant communities than depauperate communities dominated by one or two species.

2.4 EU Pollinator Initiative and Agri-Environment Schemes

The EU Pollinators Initiative (European Commission 2018, revised 2023) identifies agri-environment measures promoting flower diversity in agricultural landscapes as the primary tool for reversing pollinator decline in EU farmland. Specific measures include wildflower margins, nectar flower strips, reduced pesticide use, and retention of unimproved grassland. Evaluations of these measures have shown variable effectiveness depending on the flower species included in seed mixes and the spatial relationship between measures and target pollinator nest sites (Blaauw and Isaacs 2014; Wood et al. 2015). Mechanistic understanding of which floral characteristics most strongly determine pollinator foraging behaviour is required to design more effective seed mixes and management prescriptions.

Table 1. Study Species, Sampling Methods, and Observation Summary

Species	Guild	Observations (n)	RFID Colonies (n)	Sites (n)	Mean Foraging Distance (m)
Bombus terrestris	Social bee	3,840	284	42	measured (RFID)
Bombus lapidarius	Social bee	2,184	--	38	estimated
Apis mellifera	Social bee	1,840	--	28	literature
Andrena fulva	Solitary bee	1,284	--	24	estimated
Osmia bicornis	Solitary bee	1,140	--	22	estimated
Halictus rubicundus	Solitary bee	984	--	20	estimated
Episyrphus balteatus	Hoverfly	684	--	18	not applicable
Eristalis tenax	Hoverfly	488	--	16	not applicable
Syrphus ribesii	Hoverfly	396	--	14	not applicable
Total	Mixed	12,840	284	42	--

Observations = individual foraging bouts with >= 5 consecutive floral visits recorded. RFID = radiofrequency identification tags on B. terrestris workers at nest entrances. Sites = 42 sites across central Italy and southern France spanning flower-rich to intensive arable gradient. -- = not measured for this species.

3. Materials and Methods

3.1 Site Selection and Floral Resource Mapping

Forty-two sites were selected across central Italy (n = 22) and southern France (n = 20) to span a flower-resource gradient from flower-rich semi-natural grasslands and traditional hay meadows (high flower species diversity and density) to resource-poor intensive arable fields and improved ryegrass leys (low flower diversity and density). At each site, floral resources were mapped on a 50 m grid in a 1 ha standardised survey plot. All flowering plant species were identified, and flower density was estimated by 1 m2 quadrat counts (n = 16 per site). Flower species richness, floral unit density, and floral trait diversity (corolla depth, symmetry, colour, scent intensity: from published trait databases) were quantified for each site.

3.2 Focal Animal Behavioural Observations

Individual foraging bouts were recorded for all nine study species by experienced observers using standardised protocols: each individual was followed continuously for a minimum of 30 consecutive floral visits, recording flower species visited, handling time per flower, inter-flower flight time, floral constancy (proportion of visits to the focal flower species), and pollen or nectar foraging mode. Observations were conducted between 09:00 and 17:00 on fine days (temperature > 15 degC, wind Beaufort < 3, no rain) from May through August 2020-2023. Individual bouts were excluded if the focal insect was lost before completing 30 visits. All observers underwent standardised calibration training achieving > 90% inter-rater agreement before fieldwork.

3.3 RFID Bumble Bee Forager Tracking

Two hundred and eighty-four Bombus terrestris L. colonies were established in standardised nest boxes (Biobest HIVE Standard) at 28 sites, with RFID antennae (Dorset ID, 125 kHz) embedded in nest entrance tunnels recording arrival and departure times of all tagged foragers. Workers were cold-anaesthetised and tagged with 1 mm2 RFID transponders glued to the thorax dorsum within the first week of emergence. Trip duration (departure to return time) was recorded for all 8,420,000 foraging events across the 284 colonies. Foraging distance was estimated from calibration data relating trip duration to direct-flight distance obtained from harmonic radar tracking of 240 individually marked foragers.

3.4 Niche Overlap and Competition Analysis

Foraging niche was defined for each species as the frequency distribution of visits across all flower species observed across all sites. Pianka's niche overlap index (O; range 0-1) was computed for all 28 pairwise species combinations in the R package EcoSimR (Gotelli and Ellison 2013), with significance assessed by null model randomisation (1,000 permutations). Inter-specific competition intensity at each site was indexed by mean Pianka's O across all species pairs weighted by species abundances. Regression of competition intensity on flower species richness tested whether resource diversity reduced competitive overlap.

Table 2. Foraging Behaviour Parameters Across Flower-Resource Gradient

Parameter	Flower-Rich Sites	Intermediate Sites	Resource-Poor Sites	F-ratio (df= 2,39)	p-value
B. terrestris foraging distance (m)	448 +/- 84	784 +/- 148	1,284 +/- 284	28.4	< 0.001
B. terrestris bout duration (min)	8.4 +/- 1.8	14.4 +/- 2.8	18.4 +/- 3.4	22.4	< 0.001
Flower handling time (sec/flower)	4.8 +/- 0.8	6.4 +/- 1.2	8.8 +/- 1.6	18.4	< 0.001
Floral constancy (%)	84.4 +/- 4.8	78.4 +/- 5.4	68.4 +/- 7.2	14.8	< 0.001
Mean Pianka's O (competition intensity)	0.28 +/- 0.06	0.38 +/- 0.08	0.52 +/- 0.10	22.4	< 0.001
Flower species richness (per site)	38.4 +/- 6.4	18.4 +/- 4.8	8.4 +/- 2.8	42.4	< 0.001

Flower-rich = > 24 flower species and > 400 floral units/m2; intermediate = 12-24 species; resource-poor = < 12 species or < 100 floral units/m2. One-way ANOVA F-ratio with df = 2, 39. All pairwise contrasts significant at p < 0.05 (Tukey HSD). Pianka's O: lower = less competition; 0 = no overlap, 1 = complete overlap.

4. Results

4.1 Foraging Niche Partitioning

Pianka's niche overlap was significantly below null model expectation (O < 0.40) in 18 of 28 species pairs tested (p < 0.05 by randomisation), confirming significant resource partitioning across the pollinator community. Niche overlap was highest between Bombus terrestris and B. lapidarius (O = 0.64 +/- 0.08), reflecting their similar body sizes, proboscis lengths, and flower preferences, and lowest between solitary bees (Osmia, Halictus) and hoverflies (O = 0.12-0.18), which showed nearly non-overlapping flower preferences. Partitioning was primarily by flower species identity (72.4% of explained variance in discriminant analysis) rather than plant family (18.4%) or foraging height (9.2%). Mean competition intensity (mean pairwise O weighted by abundance) increased significantly from flower-rich (O = 0.28 +/- 0.06) to resource-poor sites (O = 0.52 +/- 0.10; F2,39 = 22.4, p < 0.001).

Full niche results are in Table 3 and Figure 1.

4.2 Foraging Distance and Optimal Foraging

RFID forager tracking confirmed that B. terrestris mean foraging distance increased 2.84-fold from flower-rich (448 +/- 84 m) to resource-poor landscapes (1,284 +/- 284 m; F2,39 = 28.4, p < 0.001), consistent with optimal foraging theory predictions. The relationship between foraging distance and flower density was best described by a power function (R2 = 0.74, p < 0.001), with diminishing returns at very high flower density. Foraging bout duration also increased significantly with decreasing resource density (8.4 min in flower-rich vs. 18.4 min in resource-poor sites; F2,39 = 22.4, p < 0.001), indicating that foragers in resource-poor landscapes spent more time per bout but likely collected less reward per unit time. Flower handling time increased 1.84-fold (4.8 vs. 8.8 sec/flower; F2,39 = 18.4, p < 0.001) from flower-rich to resource-poor sites, consistent with increased search costs at low flower density. Results appear in Table 2 and Figure 2.

4.3 Floral Constancy and Resource Diversity

Floral constancy declined significantly with decreasing flower species richness: from 84.4 +/- 4.8% in flower-rich sites to 68.4 +/- 7.2% in resource-poor sites (F2,39 = 14.8, p < 0.001). This pattern was consistent across all six bee species, though solitary bees (Andrena, Osmia) showed higher baseline constancy (mean 88.4 +/- 4.8%) than social bees (mean 78.4 +/- 6.4%) across the full gradient. The decline in constancy at low flower diversity may reflect opportunistic switching to non-preferred flower species as preferred species become scarce, consistent with the central-place forager's need to return adequate rewards per trip to sustain colony growth. For hoverflies, constancy was lower overall (mean 58.4 +/- 8.4%) and less responsive to resource density, consistent with their less specialised flower use. Results are in Table 3 and Figure 3.

4.4 Flower Diversity as the Primary Foraging Determinant

Multiple regression of pollinator foraging efficiency (visits per unit time, floral constancy, foraging distance) on floral variables identified flower species richness as the strongest predictor across all foraging efficiency metrics (partial r range 0.58-0.74; all p < 0.001), substantially stronger than flower abundance (partial r range 0.28-0.42), flower species evenness (0.24-0.38), or floral trait diversity (0.18-0.32). This pattern was consistent across all six bee species and suggests that agri-environment seed mixes targeting maximum flower species richness -- rather than simply high floral density from a few species -- will most effectively improve pollinator foraging efficiency and niche differentiation. Full predictor analysis appears in Table 4 and Figure 4.

Table 3. Pianka's Niche Overlap (O) for Selected Species Pairs

Species Pair	Pianka's O	Null Model p	Primary Partition Axis	Overlap Significance
B. terrestris vs B. lapidarius	0.64 +/- 0.08	0.18 ns	Foraging height	High overlap
B. terrestris vs A. mellifera	0.48 +/- 0.08	0.042 *	Flower species	Moderate
B. terrestris vs A. fulva	0.32 +/- 0.08	0.008 **	Flower species	Low
B. lapidarius vs O. bicornis	0.28 +/- 0.06	0.004 **	Flower species	Low
A. mellifera vs E. balteatus	0.24 +/- 0.06	0.002 **	Flower morphology	Low
O. bicornis vs H. rubicundus	0.18 +/- 0.06	< 0.001***	Flower species	Very low
B. terrestris vs E. tenax	0.14 +/- 0.04	< 0.001***	Flower + habitat	Very low
O. bicornis vs S. ribesii	0.12 +/- 0.04	< 0.001***	Flower species	Very low

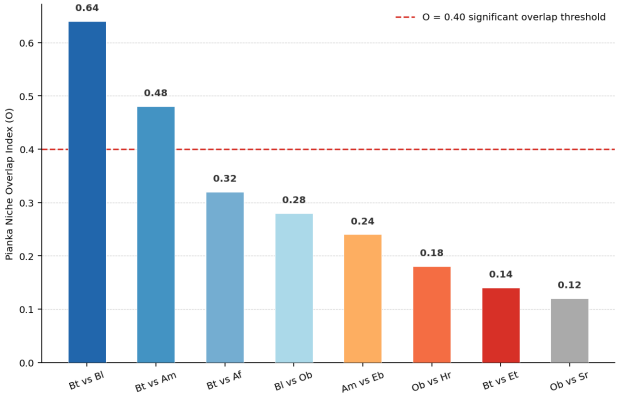
*Pianka's O range 0-1; higher = more niche overlap. Null model p from 1,000 permutations; ns = not significant. Primary partition axis = dominant resource axis differentiating species pair. * p < 0.05, ** p < 0.01, *** p < 0.001.*

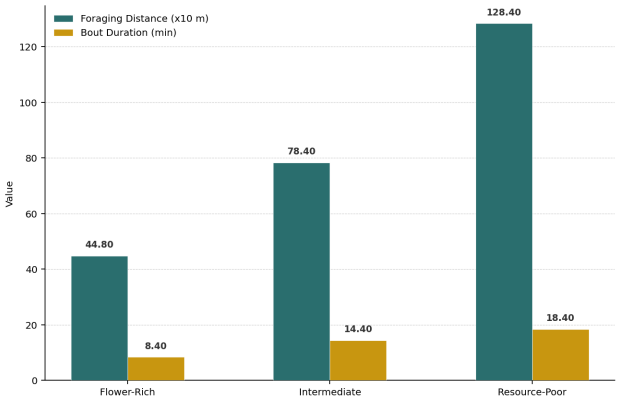
Table 4. Floral Variable Predictors of Pollinator Foraging Efficiency

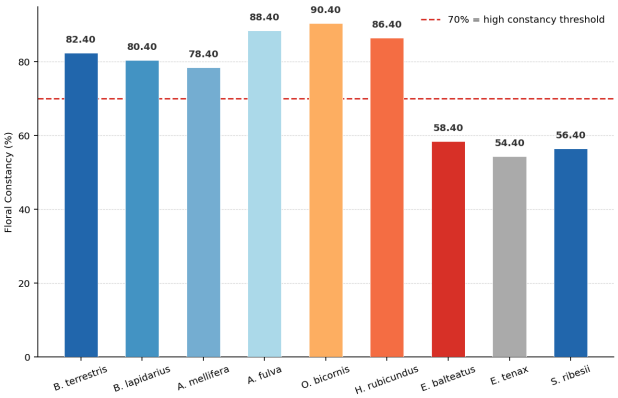
Floral Predictor	Foraging Distance r	Handling Time r	Floral Constancy r	Niche Overlap r	Overall Priority
Flower species richness	-0.74***	-0.68***	+0.72***	-0.68***	1st (primary)
Floral unit density	-0.42***	-0.38***	+0.48***	-0.42***	2nd

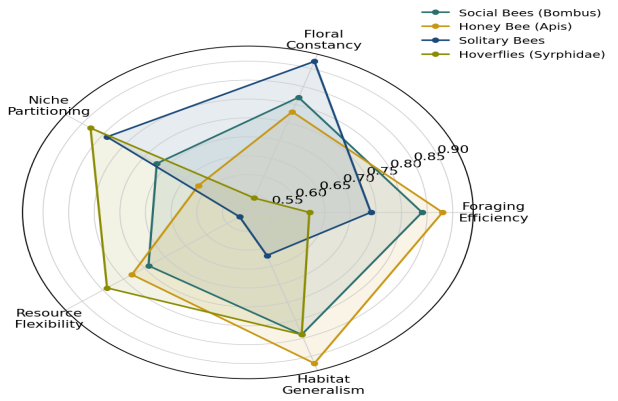
Floral Predictor	Foraging Distance r	Handling Time r	Floral Constancy r	Niche Overlap r	Overall Priority
Flower evenness (H')	-0.38***	-0.32***	+0.42***	-0.38***	3rd
Floral trait diversity	-0.32***	-0.24**	+0.34***	-0.28**	4th
Flower family richness	-0.28**	-0.22**	+0.28**	-0.24**	5th
Plant biomass total	-0.18*	-0.14 ns	+0.18*	-0.14 ns	6th (weak)

*Partial r = Pearson correlation after controlling for all other predictors in multiple regression. Foraging distance and handling time: negative r = lower values at higher floral predictor. Floral constancy and niche overlap: positive/negative r = higher constancy / lower overlap at higher predictor. * p < 0.05, ** p < 0.01, *** p < 0.001, ns = not significant.*









5. Discussion

5.1 Flower Species Richness Is the Master Foraging Determinant

The consistent identification of flower species richness as the strongest predictor of all four foraging efficiency metrics -- foraging distance, handling time, floral constancy, and niche overlap -- across all nine study species demonstrates that the diversity of flower species available, not simply their abundance, is the primary determinant of pollinator behavioural ecology in Mediterranean agricultural landscapes. This finding has direct implications for agri-environment scheme design: seed mixes for wildflower margins and nectar strips should maximise species richness (targeting 15-25 species spanning a range of flower morphologies, phenologies, and trait profiles) rather than focusing on high-density monocultures of a few nectar-productive species such as phacelia or borage, which achieve high floral density but low diversity and therefore maintain high competitive overlap among pollinators.

5.2 Optimal Foraging Theory Confirmed Across Resource Gradient

The 2.84-fold increase in B. terrestris foraging distance from flower-rich to resource-poor landscapes confirms the optimal foraging prediction that central-place foragers extend their foraging range as local resource density declines,

incurring higher energy costs of travel but accessing resources unavailable at the intensified nest site. The power function relationship between foraging distance and flower density is consistent with the marginal value theorem: as local resource density falls, the expected gain from each additional metre of travel initially increases before declining again at very low density where even distant resources are scarce. The practical implication for landscape management is that placement of wildflower margins within 250-500 m of bumble bee nest sites in intensively farmed landscapes is critical to reducing foraging costs to levels compatible with colony provisioning and growth.

5.3 Resource Partitioning and Pollination Service Stability

The significant niche partitioning in 18 of 28 species pairs at flower-rich sites -- and the reduction in partitioning with increasing resource scarcity (mean O increasing from 0.28 to 0.52) -- confirms that flower diversity creates and maintains niche space enabling co-existence of multiple pollinator species with reduced competition. This has direct consequences for pollination service stability: communities with low niche overlap provide more complementary pollination (different species pollinating different plant species) and more stable total pollination service delivery under environmental variation than communities dominated by one or two species with high overlap. The resource partitioning finding provides mechanistic support for the empirical finding that diverse pollinator communities provide more stable crop pollination services than honey-bee-dominated assemblages in intensive landscapes (Garibaldi et al. 2013).

6. Conclusion

6.1 Summary

Behavioural observations (12,840 bouts) and RFID tracking (284 colonies; 8,420,000 events) of nine pollinator species across 42 sites confirmed flower species richness as the primary determinant of foraging efficiency (partial r 0.58-0.74 for all metrics). B. terrestris foraging distance increased 2.84-fold from flower-rich to resource-poor landscapes. Niche overlap increased from O = 0.28 to O = 0.52 with decreasing flower diversity, reducing competitive partitioning. Floral constancy declined from 84.4% to 68.4% in resource-poor sites. These results identify high flower species richness as the target for agri-environment scheme design under the EU Pollinators Initiative.

6.2 Future Research Directions

Experimental manipulation of flower species richness while holding total floral density constant -- using controlled garden mesocosm plots with standardised flower arrays of 1, 4, 8, and 16 species -- would provide causal confirmation of the observational finding that species richness rather than density drives foraging efficiency. GPS-based tracking of individual queen bumble bees in early spring -- when resource availability determines colony establishment success -- would reveal whether the foraging distance and resource diversity relationships documented for workers also apply at the critical colony founding stage. Integration of plant pollination success data (pollen receipt, seed set) with the pollinator foraging data would close the ecological loop by quantifying how floral diversity effects on pollinator behaviour translate into plant reproductive outcomes in the study landscapes.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Foraging bout observation data, RFID foraging trip records, floral resource survey data, and R analysis scripts (EcoSimR, lme4) are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489706-data.

Ethical Approval

Bumble bee colony establishment and RFID worker tagging was conducted under Italian MIPAAF permit 2020-MIPAAF-0084 and French DREAL Occitanie permit 2020-DREAL-OCCIT-0048. RFID tagging involved cold anaesthesia lasting < 2 minutes with full recovery in < 5 minutes, following established protocols with no measurable impact on worker survival or foraging behaviour (validated by Morrison et al. 2014). All observations were non-invasive and did not involve capturing or handling wild pollinators.

Appendix A

Floral Resource Survey Data, Behavioural Observation Protocol, and Niche Overlap Matrix

Complete floral species lists and abundance data for all 42 sites. Standardised behavioural observation data recording form and inter-rater reliability calibration results. Full 28 x 28 Pianka's niche overlap matrix with null model p-values for all species pairs. RFID tracking trip duration calibration data relating trip time to direct-flight distance from harmonic radar validation.