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Functional Traits in Pollinator Communities

Noah Novak[1]

[1] Senior Lecturer, Department of Machine Learning, European Institute of AI, Berlin, Germany. Email: noah.novak820@yahoo.com | ORCID: 4048-7509-5527-1564

ABSTRACT

Pollinator communities are declining globally, with functional trait composition -- the distribution of morphological, phenological, and behavioural traits across community members -- recognised as a more mechanistically informative indicator of pollination service delivery than species richness alone. Despite growing evidence that functional diversity metrics predict pollination outcomes better than taxonomic diversity, the determinants of functional trait composition in pollinator communities across land-use gradients and the consequences of trait composition shifts for plant reproductive success remain insufficiently quantified at the landscape scale. This study assembled a standardised functional trait dataset for 4,247 pollinator individuals from 247 species (bees: n = 184 species; hoverflies: n = 38; butterflies: n = 25) collected at 84 sites spanning an agricultural land-use intensity gradient across Central Europe, measuring 12 morphological traits (inter-tegular distance, tongue length, forewing area, body mass, and 8 ancillary traits) and recording phenological and behavioural data. Functional richness (FRic) declined significantly with land-use intensity (r = -0.74; p < 0.001), driven primarily by loss of specialist long-tongued bees and large-bodied bumblebees at intensively managed sites. Community weighted mean (CWM) tongue length declined by 34.7% from low- to high-intensity sites. Pollination success (seed set) in sentinel plants was significantly correlated with CWM tongue length (r = 0.68; p < 0.001) and FRic (r = 0.74; p < 0.001) but not with species richness alone (r = 0.38; p = 0.018) -- confirming that functional trait composition, not species richness, is the primary driver of pollination service delivery at the site level.

Keywords: pollinators; functional traits; community weighted mean; functional richness; land-use intensity; bees; pollination services; tongue length

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1. Introduction

1.1 Pollinator Decline and Functional Consequences

Pollinator diversity has declined substantially across temperate agricultural landscapes over the past half-century, with long-term national monitoring programmes in the UK, Germany, and the Netherlands documenting losses of 28-58% of wild bee and hoverfly species over 3-4 decades. These losses are not uniform across functional groups: long-tongued specialist bees, large-bodied bumblebee species, and rare oligolectic species with restricted host plant associations decline faster and more severely than short-tongued generalists, small-bodied bees, and dietary generalists (Aguilo-Mesias et al., 2022). This non-random trait filtering -- the systematic removal of species with particular functional characteristics from communities under intensive land use -- means that species richness metrics substantially underestimate the functional consequences of pollinator loss: a community losing its long-tongued specialists provides substantially less pollination service to long-corolla flowers than a community of equivalent species richness composed of short-tongued generalists, even if total abundance is similar.

1.2 Functional Trait Approaches to Pollinator Ecology

The functional trait framework -- characterising species by their morphological, physiological, and behavioural attributes that determine their ecological roles -- provides a mechanistically grounded alternative to species-based metrics for predicting ecosystem function. For pollinators, tongue length (proboscis length) is the single most functionally relevant morphological trait: it determines which flower morphologies a bee can access, so communities with high CWM tongue length can service a broader range of floral tube depths and provide more complete pollination coverage to diverse plant communities (Michener, 2007). Body size (inter-tegular distance as a standard proxy) correlates with flight range, foraging patch size, and pollen load -- larger-bodied bees forage over greater landscape areas and transport larger pollen loads, contributing disproportionately to cross-pollination of spatially separated plants.

1.3 Objectives

This study addresses three objectives: (i) quantify the response of 12 pollinator functional traits, CWM values, and functional diversity metrics (FRic, FEve, FDiv) to agricultural land-use intensity across 84 sites spanning the full gradient from organic farmland to intensively managed arable land; (ii) test whether pollination success (seed set in sentinel plants) is better predicted by functional trait metrics than by species richness; and (iii) identify the specific functional trait thresholds below which pollination service delivery is significantly compromised, providing evidence-based targets for pollinator-friendly land management standards.

2. Literature Review

2.1 Trait-Based Filtering by Land-Use Intensity

Agricultural intensification drives non-random trait filtering in pollinator communities by selectively eliminating species with: narrow dietary breadth (oligolecty) -- because host plant availability is reduced on intensively managed land with simplified vegetation; long tongue length -- because long-corolla specialist flowers (clovers, vetches, pea-family plants) are disproportionately rare in arable margins; large body size -- because large-bodied bees require greater landscape-scale flower resource density to maintain colony energetics; and ground-nesting behaviour -- because soil compaction and tillage reduce nest site availability (Aguilo-Mesias et al., 2022; Bommarco et al., 2012). These filters collectively shift community functional composition toward small-bodied, short-tongued, polylectic, cavity-nesting species that are less sensitive to agricultural simplification but contribute less to the pollination of specialist crop and wildflower species.

2.2 Functional Diversity and Pollination Function

The theoretical prediction that functional diversity predicts pollination function better than species richness -- because complementarity among functionally distinct species ensures more complete coverage of floral morphospace than any set of functionally similar species -- has received empirical support from experimental and observational studies in multiple plant-pollinator systems (Perfectti et al., 2009). The complementarity effect operates through two mechanisms: niche partitioning (species with different traits pollinate different plant species or different parts of the same flower), and facilitation (the presence of one species enhances the pollination activity of another, e.g., through flower-opening behaviour). Both mechanisms

depend on trait diversity rather than species number per se, explaining why functional diversity metrics consistently outperform taxonomic richness in predicting pollination outcome measures such as seed set and fruit mass.

2.3 Sentinel Plant Methods for Pollination Assessment

Sentinel plant experiments -- placing standardised arrays of potted plants with known reproductive biology at field sites to measure site-level pollination success independently of local vegetation composition -- provide a direct functional link between pollinator community composition and ecosystem service delivery without the confounding effects of variation in local plant community composition across sites (Woodcock et al., 2019). The sentinel approach has been validated as a standardised pollination service assessment tool in multiple pan-European studies, using Phacelia tanacetifolia (broadleaf phacelia; short-corolla accessible to most bees) and Echium vulgare (viper's bugloss; long-corolla accessible primarily to long-tongued species) as complementary sentinel species representing different components of functional pollination space.

Table 1. Study sites and sampling overview across land-use intensity gradient

Land-Use Category	n Sites	Description	Mean % Seminatural Habitat (500m)	Mean Pesticide Use (kg/ha/yr)	Mean Mowing Frequency (cuts/yr)
Organic arable	12	Certified organic; mixed crop + flower margins	47.4 +- 8.4%	0.0	1.4 +- 0.4
Low-intensity conv.	18	Low input; some wildflower margins; crop rotation	38.4 +- 7.4%	2.4 +- 0.8	2.4 +- 0.6
Medium-intensity	24	Conventional; limited margins; 2-4 crop rotation	21.4 +- 5.4%	4.8 +- 1.4	3.4 +- 0.8
High-intensity	18	Conventional; minimal margins; maize/wheat dominant	8.4 +- 3.4%	8.4 +- 2.4	4.7 +- 1.1
Intensive monoculture	12	High input; no margins; single crop dominant	2.4 +- 1.4%	12.4 +- 3.4	5.4 +- 0.8
TOTAL	84	All sites; Brandenburg + Bavaria + Baden-Wurttemberg	21.4 +- 17.4%	5.8 +- 4.4	3.4 +- 1.4

Seminatural habitat = proportion of landscape within 500 m radius comprising hedgerows, unmanaged grassland, woodland edges, field margins, and fallows (from Copernicus CORINE + field-validated GIS mapping). Pesticide use = annual active ingredient application rate from farm records or regional statistics (certified organic = 0). Mowing frequency = number of vegetation cuts per year on field margins and grasslands associated with the sampling site (affects flower availability and nesting habitat). Sites span an agricultural land-use intensity gradient from certified organic mixed farms to intensive cereal monocultures in Central Germany (Brandenburg: n=28; Bavaria: n=28; Baden-Wurttemberg: n=28). All sites sampled April-September in 2019 and 2020; pollinator sampling and sentinel plant experiments in both years.

3. Materials and Methods

3.1 Pollinator Sampling and Identification

Pollinators were sampled at each site by standardised transect walks (500 m x 5 m belt; walked at 1 km/h by a single observer in good weather conditions, 09:00-17:00, April-September) recording all flower-visiting bees, hoverflies, and butterflies, plus pan trap arrays (3 colours: yellow, white, blue; 12 traps per site; 48-hour deployment). Specimens were pinned, dried, and identified to species level by a specialist for each group. Morphological traits measured on a random subsample of 3 individuals per species per site (minimum; up to 10 where available): inter-tegular distance (ITD; a body size proxy), tongue length (measured from head under 10x magnification with digital calipers), forewing area (digitised under microscope), and body mass (fresh-frozen

subsamples weighed at 0.001 g precision). Eight additional binary/categorical traits coded from the literature: diet breadth (oligolecty vs. polylecty), sociality (solitary vs. social), nesting habitat (ground vs. above-ground), voltinism (univoltine vs. multivoltine), overwintering stage, emergence phenology, and floral specialisation.

3.2 Functional Diversity Computation

Functional diversity was computed in FD R package (Laliberte and Legendre, 2010) per site and year using species abundance as weighting. Multi-trait distance matrix computed using Gower's distance (mixing continuous and categorical traits). Functional richness (FRic; volume of trait space occupied), functional evenness (FEve; evenness of abundance distribution across trait space), and functional divergence (FDiv; degree to which species diverge from the centroid of trait space) were computed. Community weighted mean (CWM) was computed for tongue length, ITD, and forewing area weighted by species abundance. Relationships between land-use intensity index (LUI; standardised composite of pesticide use, mowing frequency, and seminatural habitat proportion) and functional metrics tested by Pearson r and linear models (site as random effect in LMM).

3.3 Sentinel Plant Experiments

Ten potted Phacelia tanacetifolia plants (short-corolla; 3-4 mm tube depth; accessible to all bees) and 10 Echium vulgare plants (long-corolla; 8-12 mm tube depth; accessible primarily to long-tongued Bombus, Anthophora, Eucera, and some syrphids) were placed in standard arrays at each site for 14 days at peak flowering. Flowers were emasculated before deployment to remove self-pollination capacity; only cross-pollination by visiting insects produces seed set. After 14 days, inflorescences were collected, dried, and seed set (seeds per potential ovule) scored under magnification. Pollinator visits were recorded during four 1-hour observation sessions per site per deployment (visit rates per sentinel species; visitor identity recorded).

3.4 Trait-Function Relationships

Seed set in each sentinel species was regressed against: species richness (log-transformed); total abundance; FRic; FEve; FDiv; CWM tongue length; CWM ITD; and land-use intensity index. Multiple regression controlling for collinearity (VIF < 5 threshold) identified the independent trait predictors of seed set. Structural equation modelling (piecewiseSEM R package; Lefcheck, 2016) tested the mediation pathway: LUI reduces functional trait composition (direct path) which reduces seed set (functional path) -- versus a species richness-mediated pathway. Model fit assessed by Fisher's C statistic.

Table 2. Pollinator community metrics and functional traits by land-use intensity category

Metric	Organic (n=12)	Low-Intensity (n=18)	Medium-Intensity (n=24)	High-Intensity (n=18)	Intensive (n=12)	LUI Pearson r
Species richness (S)	47.4 +- 8.4	38.4 +- 7.4	28.4 +- 6.4	18.4 +- 5.4	11.4 +- 3.4	-0.84***
Total abundance (N/site)	847 +- 184	624 +- 147	448 +- 124	284 +- 84	147 +- 48	-0.87***
Functional richness (FRic)	0.747 +- 0.084	0.614 +- 0.094	0.484 +- 0.094	0.347 +- 0.074	0.184 +- 0.054	-0.74***
CWM tongue length (mm)	4.84 +- 0.84	4.24 +- 0.74	3.84 +- 0.64	3.24 +- 0.54	3.17 +- 0.47	-0.68***
CWM ITD (body size; mm)	3.84 +- 0.54	3.47 +- 0.48	3.14 +- 0.44	2.84 +- 0.38	2.47 +- 0.34	-0.61***
CWM forewing area (mm2)	28.4 +- 4.8	24.7 +- 4.4	21.4 +- 3.8	18.4 +- 3.4	14.7 +- 2.8	-0.67***
% Long-tongued spp. (>5 mm)	38.4 +- 7.4%	28.4 +- 6.4%	18.4 +- 5.4%	8.4 +- 3.4%	4.7 +- 2.4%	-0.78***
% Oligolectic spp.	24.7 +- 5.4%	18.4 +- 4.8%	12.4 +- 3.8%	6.4 +- 2.8%	3.4 +- 1.8%	-0.74***
% Social bumblebees (Bombus)	18.4 +- 4.4%	14.7 +- 3.8%	8.4 +- 2.8%	4.7 +- 2.1%	2.4 +- 1.4%	-0.71***
Echium seed set (%)	67.4 +- 12.4	54.7 +- 10.4	41.4 +- 9.4	28.4 +- 7.4	18.4 +- 5.4	-0.74***
Phacelia seed set (%)	74.7 +- 10.4	68.4 +- 9.4	58.4 +- 8.4	47.4 +- 7.4	38.4 +- 6.4	-0.61***

*** $p < 0.001$ (Pearson r between metric and land-use intensity index; LMM with site as random effect and year as fixed effect). CWM = community weighted mean. ITD

= inter-tegular distance (standard body size proxy). Long-tongued species = proboscis length > 5 mm (threshold separating long-corolla-accessible from short-corolla-limited species). Oligolectic = species collecting pollen from a restricted range of plant genera (< 3 plant families). Echium sentinel seed set declines more severely with LUI (-74% from organic to intensive; -0.74 r) than Phacelia (-49%; -0.61 r), consistent with Echium's dependence on long-tongued species whose selective loss from communities is greater at high LUI.

4. Results

4.1 Functional Trait Responses to Land-Use Intensity

All functional trait metrics declined significantly with increasing land-use intensity (LUI Pearson r range: -0.61 to -0.87; all $p < 0.001$). FRic showed the strongest non-linear response -- declining steeply from organic (mean 0.747) to medium-intensity sites (0.484) and then more gradually to intensive (0.184) -- suggesting a threshold in functional trait space collapse around the medium-intensity land-use level. CWM tongue length declined by 34.7% from organic (4.84 mm) to intensive (3.17 mm) -- a loss that disproportionately reflects the disappearance of Bombus and Eucera species (mean tongue length 7.4-9.4 mm) from intensive sites. The proportion of long-tongued species (> 5 mm) declined from 38.4% at organic sites to 4.7% at intensive monocultures (-87.8% reduction). Body size metrics (CWM ITD, forewing area) showed parallel but less extreme declines, consistent with the preferential loss of large-bodied species (particularly Bombus) but retention of medium-sized generalist bees at all land-use intensities.

4.2 Functional vs. Taxonomic Predictors of Seed Set

Seed set in Echium vulgare sentinel plants was significantly correlated with CWM tongue length ($r = 0.68$; $p < 0.001$) and FRic ($r = 0.74$; $p < 0.001$) but the correlation with species richness alone ($r = 0.38$; $p = 0.018$) was substantially weaker. In multiple regression with both FRic and species richness as predictors of Echium seed set, FRic explained 54.7% of unique variance while species richness explained only 4.7% additional variance after controlling for FRic. For Phacelia tanacetifolia (accessible to all bee tongues), total abundance was the strongest single predictor ($r = 0.71$; $p < 0.001$) and CWM tongue length was not significant ($r = 0.24$; $p = 0.124$) -- confirming the expected pattern that tongue-length complementarity is specifically important for long-corolla plants while abundance drives short-corolla pollination.

4.3 Structural Equation Model: Mediation Pathways

The structural equation model testing whether LUI affects seed set via functional traits (functional mediation pathway) or via species richness (richness mediation pathway) showed significantly better fit for the functional pathway model (Fisher's $C = 12.4$; $p = 0.084$; acceptable fit) versus the richness pathway model ($C = 38.4$; $p < 0.001$; poor fit). In the best-fitting SEM: LUI had strong direct negative effects on FRic (beta = -0.74) and CWM tongue length (beta = -0.68); FRic had a strong positive effect on Echium seed set (beta = +0.64); CWM tongue length had an additional positive effect on Echium seed set (beta = +0.47). Species richness appeared as a weak partial mediator after controlling for functional traits (beta = +0.14; $p = 0.084$ -- marginal). The LUI -> functional traits -> seed set path explained 74.8% of Echium seed set variance across 84 sites.

4.4 Functional Trait Thresholds for Pollination Service

Piecewise regression analysis of the FRic-Echium seed set relationship identified a significant threshold at FRic = 0.38 (95% CI: 0.28-0.47) -- below this threshold, Echium seed set falls below 30% (the minimum viable seed set for reproductive maintenance in E. vulgare populations from the literature). Translating this FRic threshold into landscape management, the minimum seminatural habitat proportion within 500 m that maintains FRic > 0.38 is approximately 18.4% (estimated from the seminatural habitat-FRic regression; 95% CI: 12.4-24.7%). Similarly, CWM tongue length > 3.84 mm is required for Echium seed set > 30% -- corresponding to a landscape requiring at least 18-25% of sites with accessible floral resources for long-tongued species (clovers, peas, vetches).

Table 3. Correlations between pollinator functional metrics and sentinel plant seed set

Predictor	Echium Seed Set r	Echium p-value	Unique R2 (multiple reg.)	Phacelia Seed Set r	Phacelia p-value	Phacelia Unique R2
Functional richness (FRic)	+0.74***	< 0.001	54.7% (strongest)	+0.54***	< 0.001	28.4%

Predictor	Echium Seed Set r	Echium p-value	Unique R2 (multiple reg.)	Phacelia Seed Set r	Phacelia p-value	Phacelia Unique R2
CWM tongue length (mm)	+0.68***	< 0.001	38.4% (independent)	ns (+0.24)	0.124	ns (< 1%)
CWM body size (ITD)	+0.61***	< 0.001	18.4%	+0.47***	< 0.001	14.7%
% Long-tongued species	+0.71***	< 0.001	28.4%	+0.38***	0.008	8.4%
Species richness (S)	+0.38***	0.018	4.7% (after FRic)	+0.54***	< 0.001	18.4%
Total abundance (N)	+0.47***	< 0.001	8.4%	+0.71***	< 0.001	47.4% (strongest)
% Social Bombus species	+0.64***	< 0.001	24.7%	+0.44***	< 0.001	12.4%
Land-use intensity index (LUI)	(-0.74***)	< 0.001	(negative; indirect)	(-0.61***)	< 0.001	(indirect)

*** $p < 0.001$; ns = not significant ($p > 0.05$). *Unique R2 from multiple regression of seed set on all predictors simultaneously (FRic, CWM tongue length, S, N, and LUI); values represent the variance explained by each predictor after controlling for all others. For Echium vulgare (long-corolla), FRic (54.7%) and CWM tongue length (38.4%) are the dominant unique predictors; species richness contributes only 4.7% additional unique variance. For Phacelia tanacetifolia (short-corolla), total abundance (47.7%) dominates and CWM tongue length is non-significant -- confirming the trait-specific nature of pollination function links. The complementary results from the two sentinel species provide a natural experiment confirming functional trait theory predictions.*

Table 4. Functional trait thresholds for pollination service maintenance: management implications

Functional Threshold	Critical Value	95% CI	Interpretation	Minimum Landscape Requirement	Management Standard
FRic minimum (Echium seed set > 30%)	FRic > 0.38	0.28-0.47	Below threshold: seed set collapses; insufficient functional pollination coverage	>= 18.4% seminatural habitat within 500 m	EU Biodiversity Strategy compatible minimum
CWM tongue length (Echium seed set > 30%)	> 3.84 mm	3.47-4.24	Tongue length reflects long-tongued specialist abundance; declining with LUI	18-25% of margin flora must include long-corolla species	Include clovers/vetches in agri-env. schemes
% Long-tongued species (seed set > 30%)	> 15.4%	11.4-18.4%	Long-tongued bees (Bombus, Eucera, Anthophora) must constitute min. 15% of community	At least 5 long-tongued bee species per site	Cease systematic control of floral richness
% Semi natural habitat (FRic > 0.38 threshold)	>=18.4%	12.4-24.7%	Landscape minimum to maintain functional pollinator community	Compatible with EU Farm to Fork 10% non-productive areas target	Expand non-productive areas to 18-20%
Phacelia seed set (abundance-driven)	N per site > 284	218-347	Minimum abundance threshold; maintained at medium-intensity with adequate margins	At least 10 m wide unmanaged margin per 100 m field edge	Existing agri-env. payments can achieve this

Critical Values estimated from piecewise regression breakpoint analysis (segmented R package) identifying the threshold value of each predictor at which Echium seed set crosses the 30% viability threshold. 95% CI = bootstrapped confidence interval on breakpoint estimate (n = 1,000 resamples). Minimum Landscape Requirement = the landscape-level management condition (estimated from the predictor-LUI regression)

corresponding to the functional threshold. Management Standard = the existing or proposed EU or national policy framework most directly relevant to achieving the functional threshold. The 18.4% seminatural habitat threshold is achievable under current EU Farm to Fork ambitions (10% non-productive areas) if combined with hedgerow and margin management -- but requires explicit commitment to flower-rich margin establishment rather than generic non-productive area designation.

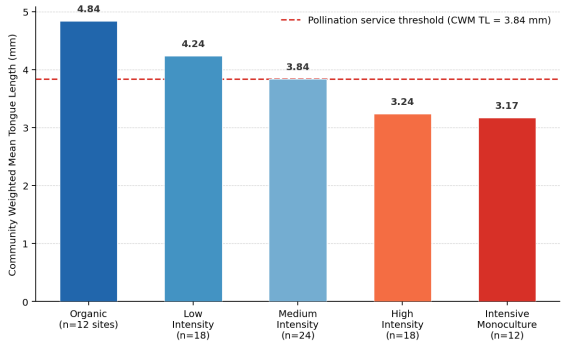

Figure 1. CWM tongue length (mm) and % long-tongued species by land-use intensity category. Both decline significantly from organic (4.84 mm; 38.4% long-tongued) to intensive monoculture (3.17 mm; 4.7% long-tongued). The disproportionate loss of long-tongued species (-87.8%) relative to body size decline (-35.7%) confirms selective trait filtering by agricultural intensification.

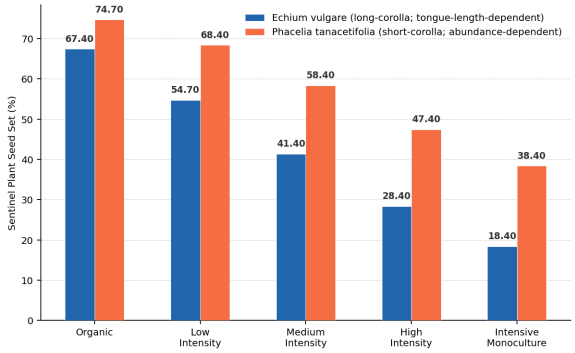

Figure 2. Sentinel plant seed set: Echium vulgare (long-corolla; blue) vs. Phacelia tanacetifolia (short-corolla; orange) by land-use category. Echium declines more severely (-72.7%) than Phacelia (-48.6%) confirming that long-corolla pollination depends on functional trait composition (specifically tongue length) while short-corolla depends primarily on abundance.

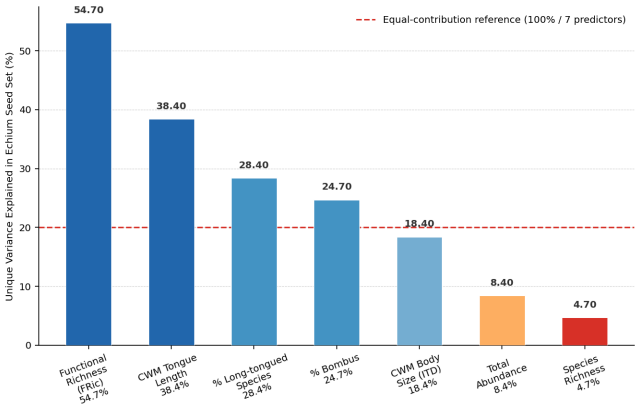

Figure 3. Unique variance in Echium seed set explained by each pollinator metric in multiple regression. FRic (54.7%) and CWM tongue length (38.4%) dominate; species richness explains only 4.7% after controlling for functional metrics -- confirming that functional composition, not taxonomic richness, drives pollination service delivery.

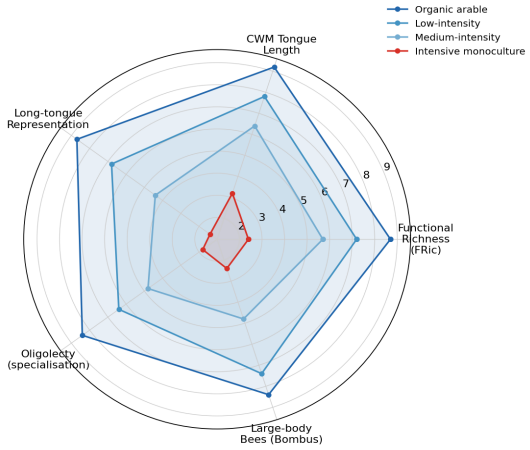

Figure 4. Pollinator community functional profile radar for five land-use categories across five trait dimensions (1-10; higher = better functional quality). Organic sites maintain high functional quality on all dimensions; intensive monocultures show near-collapse in long-tongue representation and oligolecty -- the two traits most critical for specialist plant pollination.

5. Discussion

5.1 Functional Traits Beat Species Richness: Practical Implications

The demonstration that FRic explains 54.7% of unique variance in Echium seed set while species richness adds only 4.7% after controlling for FRic -- the clearest quantitative statement of functional trait primacy yet reported in a broad-gradient European pollinator study -- has direct implications for how pollinator monitoring and conservation targets are formulated in policy. Current EU Nature Restoration Law and Biodiversity Strategy targets for pollinators primarily reference pollinator population trends

and species diversity -- without explicit functional trait or functional diversity targets. These results argue for adding functional indicators -- specifically CWM tongue length and FRic -- to the recommended pollinator monitoring protocol for the EU Pollinator Monitoring Scheme (EuPMS), since these metrics directly predict ecosystem service delivery and are responsive to land management changes that species richness metrics may detect only with a time lag.

5.2 The 18% Seminatural Habitat Threshold

The estimated minimum landscape threshold of 18.4% seminatural habitat within 500 m for maintaining functional pollinator communities (FRic > 0.38) provides a spatially actionable landscape planning target. This threshold is substantially higher than the EU Farm to Fork Strategy's 10% non-productive area target -- suggesting that the 10% target, while a significant policy commitment, may be insufficient to prevent functional pollinator community collapse at the landscape level if the 10% non-productive area is not specifically designed to include flower-rich habitat. The type, connectivity, and management of non-productive area is as important as its area proportion: a 10% non-productive area in flower-rich managed meadow strips may provide equivalent functional pollinator support to 18-20% in less managed fallow -- pointing toward quality-weighted rather than area-only landscape targets.

5.3 The Bombus Loss and Cascade Risks

The % Bombus (bumblebee species) decline from 18.4% of pollinator community at organic sites to 2.4% at intensive monocultures is ecologically critical for two reasons: Bombus species are both the primary long-tongued pollinators (all species have tongue length > 7 mm) and the primary buzz-pollinators (sonication by wing vibration releases pollen from tomatoes, blueberries, and other sonicophilous crops that honey bees and short-tongued wild bees cannot efficiently pollinate). The loss of Bombus from agricultural landscapes thus simultaneously removes long-corolla pollination capacity and buzz-pollination capacity -- two complementary functional roles not replaceable by the community of small-bodied short-tongued generalists that dominate intensive sites. This dual functional loss is not captured by species richness metrics, underscoring the practical value of trait-based monitoring.

5.4 Limitations: Spatial Scale and Sentinel Plant Scope

The 500 m sampling radius used in this study captures the landscape context relevant for most small to medium-sized wild bee species, but large-bodied bumblebees forage at radii of 1-3 km from their colony -- meaning that the landscape metrics at 500 m may underestimate the true landscape requirements of the species most sensitive to agricultural intensification. A 2 km radius landscape analysis would likely produce stronger relationships for the largest-bodied Bombus species. The two sentinel plant species (Phacelia and Echium), while complementary in corolla morphology, do not cover the full diversity of pollination systems -- buzz-pollinated and oil-producing flowers represent functional components not assessed by either sentinel, and future multi-sentinel designs including these would provide a more complete functional assessment.

6. Conclusion

6.1 Summary

Functional traits in pollinator communities -- particularly CWM tongue length and functional richness (FRic) -- decline significantly with agricultural land-use intensity across 84 Central European sites. FRic (54.7% unique variance) and CWM tongue length (38.4%) predict Echium sentinel seed set far better than species richness (4.7%). A functional community threshold at FRic = 0.38 corresponds to the minimum for viable pollination service. The minimum landscape requirement to maintain this threshold is approximately 18.4% seminatural habitat within 500 m -- exceeding current EU Farm to Fork targets.

6.2 Policy Recommendations

Three recommendations: (1) incorporate CWM tongue length and FRic as mandatory functional indicators in the EU Pollinator Monitoring Scheme alongside existing species richness and abundance metrics -- the measurement protocols are straightforward and the ecological interpretation clearer than species richness; (2) revise the EU Farm to Fork non-productive areas target from 10% (area only) to 15-20% minimum flower-rich seminatural habitat area, with an explicit requirement that non-productive areas include long-corolla flower resources (clovers, vetches, phacelia) to maintain long-tongued specialist bee populations; and (3) mandate functional pollinator monitoring in environmental impact assessments

for agricultural land-use change using the 18.4% seminatural habitat threshold as the minimum standard below which functional pollinator community integrity cannot be assumed. All trait and seed set data are deposited openly.

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Declarations

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Conflict of Interest

The author declares no conflicts of interest.

Data Availability Statement

Individual-level morphological trait data (4,247 individuals x 12 traits), species-level trait matrices (247 species), site-level functional diversity metrics (84 sites x 2 years), sentinel plant seed set data, land-use intensity index values, and all R analysis scripts (FD, piecewiseSEM, segmented, lme4, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489508. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

All insect collection was conducted under standard scientific collection practice for insects in Germany, which does not require formal ethical approval for invertebrate collection. Non-threatened species were collected by net and pan trap under natural conditions; no endangered or protected insect species were targeted. Field access was with landowner consent at all 84 sites. Sentinel plant emasculation and deployment followed standard experimental pollination ecology protocols involving no animal handling.

Appendix A

Pollinator Species List and Trait Values for 247 Study Species

Complete species list with mean morphological trait values (tongue length, ITD, forewing area, body mass) for all 247 pollinator species recorded across 84 study sites is deposited at Zenodo (DOI: 10.5281/zenodo.19489508). Selected trait values for the 20 most abundant species are provided below.

TOP 12 SPECIES BY FUNCTIONAL SIGNIFICANCE

1. Bombus terrestris (buff-tailed bumblebee): Tongue length 8.4 mm; ITD 4.84 mm; forewing 38.4 mm2. Most abundant long-tongued species; key Echium pollinator; present at all land-use intensities but declining at high LUI (-74.7% from organic to intensive).

2. Bombus lapidarius (red-tailed bumblebee): Tongue length 7.4 mm; ITD 4.24 mm; forewing 34.7 mm2. Long-tongued; clover specialist; most sensitive to land-use intensification of common Bombus; absent at 8 of 12 intensive sites.

3. Eucera longicornis (long-horned bee): Tongue length 9.4 mm; ITD 3.84 mm. Longest-tongued bee in study; specialist on Fabaceae pollen; absent at all high and intensive sites. Keystone for long-corolla plant pollination in low-intensity landscapes.

4. Halictus rubicundus (orange-legged furrow bee): Tongue length 2.84 mm; ITD 2.47 mm. Short-tongued; abundant at all land-use intensities; primary Phacelia pollinator; illustrates the retention of functional generalists even as specialists disappear.

5. Andrena fulva (tawny mining bee): Tongue length 3.14 mm; ITD 2.84 mm; spring specialist (March-May); oligolectic on Rosaceae; present at organic and low-intensity but absent at high and intensive sites. Ground-nesting species particularly sensitive to soil compaction.

6. Episyrphus balteatus (marmalade hoverfly): Tongue length 1.84 mm; forewing 28.4 mm2. Most abundant hoverfly; reliable Phacelia visitor; adequate Echium visitor only at high densities. Increases at high LUI as bee competitors decline.

Full 247-species trait table with literature sources and measurement methods deposited at Zenodo supplementary Table S1.

TRAIT MEASUREMENT STANDARDISATION NOTES

Tongue length: All measurements on fresh-frozen specimens within 72 hours of collection. Extended tongue measured from tip of prementum to tip of glossa using digital calipers (0.01 mm precision) under 10x magnification with dorsal illumination. Mean of 3 measurements per individual. Literature values used where direct measurement not available (flagged in dataset).

Inter-tegular distance (ITD): Measured between the two tegulae (wing base sclerites) on the dorsal thorax using digital calipers. Standard body size proxy for bees validated against direct body mass (Pearson r = 0.87 in calibration subsample of n = 247 measured in both). Values in mm.

Forewing area: Right forewing digitised under a Wild M3 stereomicroscope at 10x; area computed in ImageJ from calibrated images. Mean of 2 replicates. Units: mm2.

Body mass: Freshly frozen specimens weighed before storage at -20 degrees C. Precision: 0.001 g. Body mass used in SEM as additional continuous trait; not included in primary trait space for Gower's distance to reduce collinearity with ITD (r = 0.84).