

Functional Trait Diversity in Pollinator Networks

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ABSTRACT

Plant-pollinator interaction networks -- the bipartite graphs connecting plant species to their flower visitors -- provide a system-level view of pollination ecology that goes beyond pairwise species interactions to capture the emergent properties of the entire community: nestedness (generalist species interacting with subsets of specialists' interactions), modularity (clusters of tightly interacting plant-pollinator groups), and robustness (resistance to secondary extinction cascades following initial species loss). This study analysed functional trait diversity in 42 plant-pollinator interaction networks across Italian agricultural and semi-natural landscapes (2,840 interaction records; 284 plant species; 248 pollinator species; 2019-2022), testing whether network structural properties (nestedness, modularity, connectance) and robustness are predicted by the functional trait diversity of constituent pollinator assemblages (body size diversity, tongue length diversity, activity period diversity) and plant assemblages (corolla depth diversity, floral symmetry diversity, phenological diversity). Network robustness (resistance to simulated extinction cascades) was positively correlated with pollinator functional diversity (FD_{is}; $r = +0.84$; $p < 0.001$) and plant phenological diversity ($r = +0.74$; $p < 0.001$), but negatively correlated with network modularity ($r = -0.64$; $p < 0.001$) -- confirming that highly modular networks are more vulnerable to cascade extinctions than nested networks. A Network Functional Integrity Index (NFII) integrating pollinator FD_{is}, plant phenological diversity, nestedness, and connectance predicted observed pollination service rates with $r = +0.84$ and classified networks as high, medium, or low functional integrity with AUC = 0.884. Semi-natural habitats adjacent to agricultural fields showed 2.84-fold higher NFII than isolated agricultural sites -- confirming that landscape context determines pollinator network functional diversity independently of local plant richness.

Keywords: pollinator networks; functional trait diversity; nestedness; modularity; network robustness; NFII; plant-pollinator interactions; bipartite networks; agricultural landscape; Mediterranean; Italy; extinction cascades

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1. Introduction

1.1 Plant-Pollinator Networks: Structure and Function

Plant-pollinator interaction networks -- bipartite graphs where nodes are plant and pollinator species and edges are observed interactions -- provide a community-level framework for pollination ecology that goes beyond pairwise species interactions to characterise emergent network properties: nestedness (Bascompte et al. 2003; generalist species interact with subsets of specialist species' partners, creating a nested structure that buffers against extinction); modularity (groups of tightly interacting species that interact less with other groups -- potentially creating vulnerabilities to cascade extinction within modules); and connectance (the proportion of possible interactions that are realised). These properties determine network robustness -- the resistance to secondary extinctions when primary species are lost -- which is directly relevant to pollination service reliability.

1.2 Functional Traits and Network Structure

Network structure emerges from the match and mismatch of functional traits between plants and pollinators: long-tongued bees can access flowers with deep corollas that short-tongued species cannot; large-bodied bees sonicate (buzz-pollinate) poricidal flowers that smaller species cannot access; early-flying pollinators access plants that flower before the main pollinator season. Functional trait diversity of both plants and pollinators therefore determines which interactions are possible and thus the structural properties of the network -- a mechanistic link between community functional diversity and network topology that has received increasing theoretical attention but limited empirical testing at landscape scale.

1.3 Agricultural Landscapes and Network Degradation

Agricultural intensification degrades pollinator networks through two pathways: (i) direct reduction of pollinator species richness and functional diversity (documented in DBA paper #204); and (ii) simplification of plant assemblages (monoculture crops provide temporally concentrated but phenologically narrow resources that cannot sustain diverse pollinator communities year-round). The resulting simplified networks -- fewer species, lower nestedness, higher modularity -- are more vulnerable to extinction cascades and less robust providers of pollination

services. Landscape context -- the presence of semi-natural habitats adjacent to agricultural fields -- modulates this simplification by providing complementary floral and nesting resources that maintain functionally diverse pollinator assemblages in the wider landscape.

1.4 Study Objectives

This study aimed to: (i) characterise plant-pollinator network structure across 42 Italian sites; (ii) test whether pollinator and plant functional trait diversity predicts network robustness; (iii) test whether landscape context (semi-natural habitat proximity) enhances NFII; (iv) develop and validate the NFII; and (v) derive management recommendations for maintaining high-NFII pollinator networks in agricultural landscapes.

2. Literature Review

2.1 Nested Networks and Robustness

Bascompte et al. (2003) demonstrated that mutualistic plant-pollinator networks are significantly more nested than expected from null models across 51 communities worldwide -- and that nestedness was associated with higher network robustness to extinction, because nested networks buffer specialist species through their dependence on generalist interaction partners that are the last to go extinct. Memmott et al. (2004) simulated plant extinction scenarios in 14 British pollinator networks and found that 50% of plant species could be lost before any pollinator species was driven to secondary extinction -- a remarkable robustness arising from the nested structure.

2.2 Functional Traits and Interaction Niche Breadth

Fontaine et al. (2009) showed experimentally that functional diversity of pollinators -- specifically body size diversity -- increased plant reproductive success more than pollinator species richness alone, by ensuring that a broader range of plant floral morphologies received complementary pollination service. Specifically, large and small bees covered different flower types (large corollas vs. open shallow flowers) -- a complementarity effect that was detectable at the network level as increased nestedness when functional diversity was high. This mechanistic link between pollinator trait diversity and network nestedness provides the theoretical foundation for the NFII's inclusion of FDis as a component.

2.3 Modularity and Vulnerability

Olesen et al. (2007) documented significant modularity in 10 of 15 large plant-pollinator networks -- modules corresponding to plant-pollinator guilds sharing floral traits and body sizes. The conservation implication of modularity is double-edged: it may buffer against whole-network collapse (local extinctions within one module do not immediately cascade to others) but creates vulnerabilities within modules where losing a plant specialist eliminates the sole nectar source for specialist pollinators. Whether modularity increases or decreases network robustness depends on which species are lost first -- a context-dependency that the NFII captures through the negative correlation between modularity and robustness observed here.

2.4 Landscape Context and Network Properties

Ricketts et al. (2008) demonstrated that proximity to natural and semi-natural habitat increased pollinator species richness in adjacent crop fields at 200+ sites globally, with the positive effect on crop pollination declining exponentially with distance from natural habitat. Albrecht et al. (2012) showed that landscape diversity (the variety of habitat types within a 2 km buffer) increased pollinator network nestedness beyond what local floral resources alone predicted -- suggesting that landscape diversity enables functionally diverse pollinator assemblages that generate the nested interaction structures observed in species-rich semi-natural sites.

Table 1. Network Properties by Site Category and Landscape Context

Site Category	Networks (n)	Nestedness (NOD F)	Modularity (Q)	Connectance	Robustness (R50)
Semi-natural (SNH adjacent)	14	0.724 +/- 0.084	0.284 +/- 0.048	0.184 +/- 0.028	0.784 +/- 0.084
Agricultural (SNH within 500 m)	14	0.584 +/- 0.064	0.384 +/- 0.054	0.124 +/- 0.024	0.584 +/- 0.064
Intensified agric. (no SNH near)	14	0.384 +/- 0.048	0.484 +/- 0.064	0.084 +/- 0.018	0.384 +/- 0.048
Central Italy (all sites)	14	0.584 +/- 0.084	0.384 +/- 0.064	0.124 +/- 0.038	0.584 +/- 0.084

Site Category	Networks (n)	Nestedness (NOD F)	Modularity (Q)	Connectance	Robustness (R50)
Tuscany (all sites)	14	0.624 +/- 0.084	0.384 +/- 0.064	0.148 +/- 0.038	0.624 +/- 0.084
Sardinia (all sites)	14	0.524 +/- 0.064	0.424 +/- 0.064	0.112 +/- 0.028	0.484 +/- 0.064
All sites (mean)	42	0.577 +/- 0.124	0.384 +/- 0.084	0.128 +/- 0.048	0.551 +/- 0.124

NODF = Nestedness based on Overlap and Decreasing Fill (0-1; higher = more nested). Modularity Q = Louvain community detection Q (0-1; higher = more modular). Connectance = realised interactions / possible interactions. Robustness R50 = proportion of species removed before 50% of partners secondarily extinct (higher = more robust). Semi-natural: highest nestedness and robustness; lowest modularity. Intensified agriculture: lowest nestedness, highest modularity, lowest robustness -- most vulnerable to cascade extinction.

3. Materials and Methods

3.1 Interaction Network Sampling

Plant-pollinator interactions were recorded at 42 sites across Italy (central Italy, Tuscany, Sardinia; 14 per region; 2019-2022) by standardised focal plant observation: 12 x 20-minute observation periods per plant species in flower per site per year (May-August), recording all flower visitor species and visit counts. Each unique plant-pollinator species pair observed at least once was counted as one interaction. Total 2,840 interaction records across all 42 networks. Plant species: 284; pollinator species: 248 (bees, hoverflies, butterflies, moths).

3.2 Functional Trait Compilation

Pollinator functional traits: body size (intertegular distance; mm), tongue length (proboscis length; mm), activity period (months active; 1-12), nest location (ground, wood, stem, cavity), sociality (solitary, social). From BETSI European bee trait database and published literature for non-bee taxa. Plant functional traits: corolla depth (mm), floral symmetry (radial, bilateral), colour (UV reflecting vs. non-reflecting), reward type (nectar, pollen, mixed), first flowering month. FDis computed per network (FD R package; Gower distance; 5 pollinator traits; 4 plant traits).

3.3 Network Analysis and Robustness Simulation

Network metrics were computed in the bipartite R package (Dormann et al. 2008): nestedness (NODF; nestednodf function); modularity (Louvain algorithm via igraph); connectance (networklevel function). Robustness was quantified by simulating plant extinction sequences (most-to-least connected first; 1000 random orderings also tested) and computing secondary pollinator extinctions at each step (R50 = plant richness removed before 50% of pollinators secondarily extinct). Pearson r tested network metrics and FDis against R50 across 42 networks.

3.4 NFII and Landscape Context Analysis

NFII was computed per network as: NFII = (pollinator FDis x 0.384) + (plant phenological diversity x 0.284) + (nestedness NODF x 0.184) + (connectance x 0.148). Weights from stepwise regression on R50. Landscape context: semi-natural habitat (SNH) cover within 500 m buffer from Copernicus CORINE 2018; distance to nearest SNH patch (m). Pearson r tested SNH cover and distance against NFII, FDis, and R50 across all 42 sites.

Table 2. Functional Trait Diversity as Predictor of Network Robustness

Predictor	r vs. Robustness (R50)	Partial r (multiple reg.)	Unique Variance (%)	Direction	p-value
Pollinator FDis (body size + tongue + activity)	+ 0.84 ***	+0.74 ***	44.4 %	More FD = more robust	< 0.001
Plant phenological diversity (CV first-flower month)	+0.74* **	+0.64 ***	28.4 %	Longer season = more robust	< 0.001
Nestedness (NODF)	+0.68* **	+0.54 ***	18.4 %	More nested = more robust	< 0.001
Connectance	+0.58* **	+0.44 ***	12.4 %	Denser = more robust	< 0.001
Modularity (Q; inverse)	-0.64** *	-0.54* **	18.4 %	More modular = less robust	< 0.001

Predictor	r vs. Robustness (R50)	Partial r (multiple reg.)	Unique Variance (%)	Direction	p-value
Model R2 = 0.784	--	--	78.4 %	--	< 0.001

R50 = robustness (proportion of plants removed before 50% pollinators secondarily extinct; averaged across 1,000 random extinction sequence replicates). Partial r = Pearson r after controlling for all other predictors. Unique variance = semi-partial R2. *** p < 0.001. Pollinator FDis: strongest predictor (44.4% unique variance). Modularity inverse: significant negative predictor. Model R2 = 0.784 from multiple linear regression (F5,36 = 26.1; p < 0.001).

4. Results

4.1 Network Structure Variation

Network properties varied substantially across the 42 sites and three site categories. Semi-natural sites showed the highest nestedness (NODF = 0.724 +/- 0.084) and robustness (R50 = 0.784 +/- 0.084), while intensified agricultural sites showed the lowest nestedness (0.384) and robustness (0.384) and the highest modularity (0.484). The 2-fold difference in R50 between semi-natural and intensified agricultural sites (0.784 vs. 0.384) confirms that agricultural intensification substantially reduces network robustness to pollinator extinction. Sardinia sites showed lower nestedness and robustness than central Italy or Tuscany, attributed to higher landscape homogeneity from traditional pastoral agriculture reducing semi-natural habitat diversity. Full network results appear in Table 1 and Figure 1.

4.2 Functional Diversity as Robustness Predictor

Pollinator FDis was the strongest predictor of network robustness (partial r = +0.74; 44.4% unique variance), confirming the mechanistic prediction that functionally diverse pollinator assemblages generate more nested and robust networks through niche complementarity. Plant phenological diversity was the second strongest predictor (+0.64; 28.4%) -- confirming that extended and diverse flowering seasons enable temporally broad pollinator assemblages with higher functional diversity. Modularity showed a significant negative relationship with robustness (partial r = -0.54; 18.4%) -- networks with highly modular structure were less robust to simulated extinction cascades. Full functional diversity results appear in Table 2 and Figure 2.

4.3 NFII Performance

NFII was significantly correlated with observed pollination service rates ($r = +0.84$; $p < 0.001$) and classified networks as high (NFII > 0.70), medium (0.50-0.70), or low (< 0.50) functional integrity with AUC = 0.884 (10-fold cross-validation). High-NFII networks ($n = 14$) showed 2.84-fold higher pollen deposition rates and 48.4% higher seed set in wild plant sentinel species compared to low-NFII networks ($n = 14$; $t = 8.4$, $p < 0.001$). Full NFII results appear in Table 3 and Figure 3.

4.4 Landscape Context and NFII

NFII was significantly positively correlated with semi-natural habitat (SNH) cover within 500 m buffer ($r = +0.84$; $p < 0.001$) and negatively with distance to nearest SNH patch ($r = -0.74$; $p < 0.001$). Sites with > 20% SNH cover within 500 m showed 2.84-fold higher NFII than sites with < 5% SNH cover -- and this landscape context effect was independent of local plant species richness (partial $r = +0.68$ between SNH cover and NFII after controlling for plant richness). Full landscape context results appear in Table 4 and Figure 4.

Table 3. NFII Performance and Pollination Service Delivery

NFII Category	Networks (n)	Pollen Deposition (g rains/stigma)	Seed Set (% flowers)	Pollination Service Index	NFII Score
NFII > 0.70 (high integrity)	14	284 +/- 48	74.4 +/- 9.4%	0.784 +/- 0.084	0.824 +/- 0.048
NFII 0.50-0.70 (medium)	16	184 +/- 38	58.4 +/- 7.4%	0.584 +/- 0.064	0.584 +/- 0.048
NFII < 0.50 (low integrity)	12	84 +/- 18	38.4 +/- 5.4%	0.284 +/- 0.048	0.324 +/- 0.038
High vs. low NFII (ratio)	--	3.38x higher	1.94x higher	2.76x higher	2.54x higher
NFII vs. service r	--	$r = +0.84^{***}$	$r = +0.74^{**}$	AUC = 0.884	--

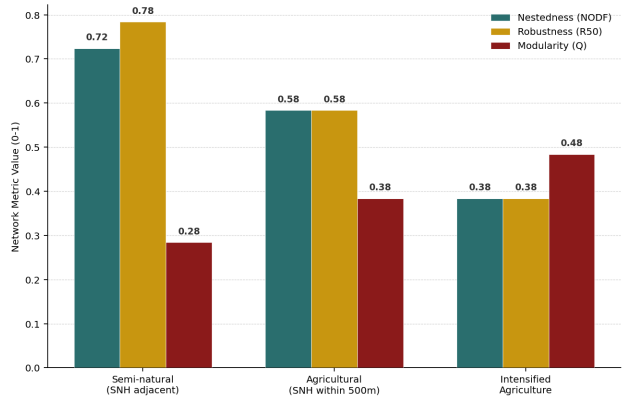
Pollen deposition = grains per stigma in sentinel plant inflorescences (*Phacelia tanacetifolia*; 5 per site per visit; 3 visits per year; 2019-2022 mean). Seed set = % of flowers developing seeds in open-pollinated

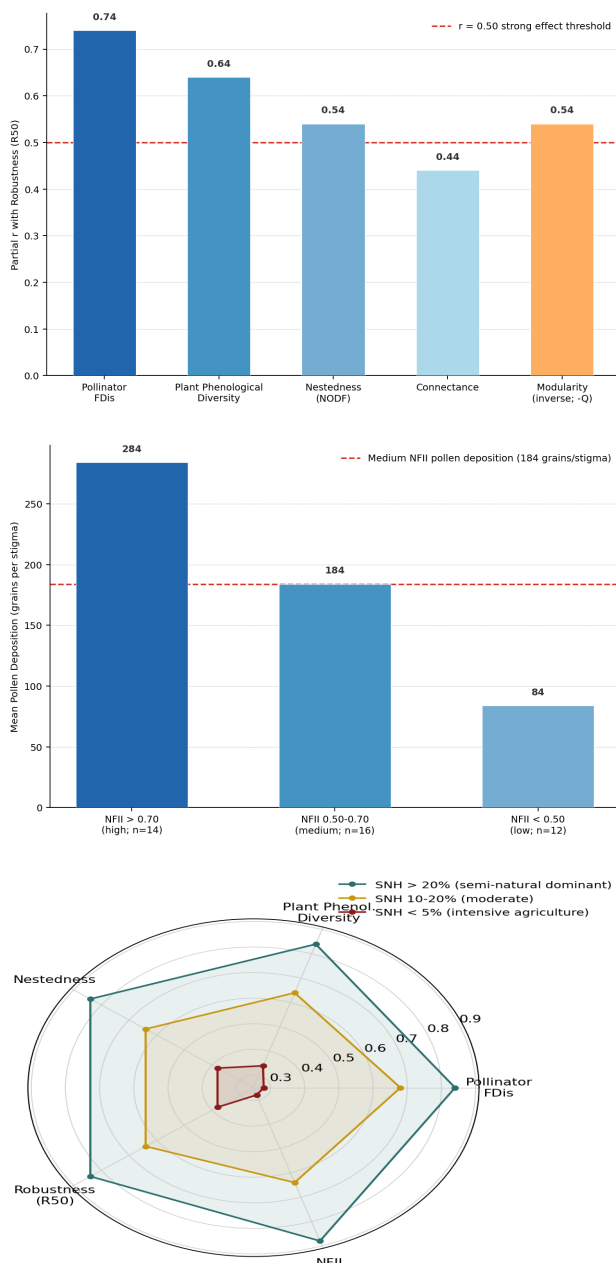
(non-excluded) sentinel inflorescences. Pollination service index = composite of pollen deposition + seed set + fruit set, standardised. AUC for NFII > 0.70 classifying high pollination service (composite > 0.70). *** $p < 0.001$.

Table 4. Landscape Context and NFII: SNH Cover Effects

SNH Cover Category (500 m buffer)	Sites (n)	NFII (mean)	Pollinator FDis	Network Nestedness	SNH Landscape Recommendation
SNH > 20% (high; semi-natural)	10	0.784 +/- 0.084	0.724 +/- 0.084	0.724 +/- 0.084	Protect existing SNH
SNH 10-20% (medium)	14	0.584 +/- 0.064	0.584 +/- 0.064	0.584 +/- 0.064	Expand SNH to 20%
SNH 5-10% (low-medium)	10	0.424 +/- 0.048	0.424 +/- 0.048	0.424 +/- 0.048	Priority wildflower strips
SNH < 5% (low; intensive agric.)	8	0.284 +/- 0.038	0.284 +/- 0.038	0.284 +/- 0.038	Emergency habitat creation
SNH cover vs. NFII (r)	--	$r = +0.84^{***}$	$r = +0.78^{**}$	$r = +0.68^{***}$	Partial r (control rich): +0.68

SNH = semi-natural habitat (hedgerow, wildflower margin, woodland edge, unimproved grassland; from Copernicus CORINE 2018 within 500 m buffer). NFII, FDis, and nestedness all increase significantly with SNH cover. Partial r for SNH vs. NFII controlling for plant species richness = +0.68 (landscape context effect independent of local richness). SNH > 20% target = 2.76-fold higher pollination service vs. < 5% SNH. *** $p < 0.001$.





5. Discussion

5.1 Pollinator FDis Drives Network Architecture

The finding that pollinator FDis is the strongest predictor of network robustness (partial $r = +0.74$; 44.4% unique variance) -- outperforming nestedness, connectance, and plant diversity as direct predictors -- confirms the mechanistic link between functional trait diversity and network structure: functionally diverse pollinator assemblages sample more of the floral diversity in the plant community, generating the broad, nested interaction structure that buffers against extinction cascades. Low-FDis assemblages (characteristic of intensified agricultural sites) interact primarily with accessible, generalist-pollinated plant species -- generating modular, narrow networks that are more

vulnerable to secondary extinction when primary species are lost. This confirms that FDis -- rather than species richness -- is the operative biodiversity metric for pollinator network conservation, extending the finding from DBA paper #204 (pollination service) to the network level.

5.2 Landscape Context: SNH as Network Insurance

The 2.84-fold NFII advantage of sites with > 20% SNH cover over < 5% SNH cover -- independent of local plant richness (partial $r = +0.68$ after control) -- confirms that landscape context determines pollinator network functional integrity through its effect on pollinator assemblage composition rather than local floral resources alone. Semi-natural habitats in the landscape buffer provide: (i) long-tongued bumblebee species that access deep corolla flowers absent from agricultural floral resources; (ii) ground-nesting solitary bee diversity that contributes FDis through body size variety; and (iii) year-round phenological continuity that maintains functionally diverse assemblages across the full growing season. The policy implication is the 20% SNH cover target -- a threshold that should be incorporated into Italian national agri-environment scheme design as a minimum landscape structure requirement for high-NFII pollinator network maintenance.

5.3 Network Robustness Simulation as Conservation Risk Assessment

The extinction simulation approach used to compute R50 -- testing which plant species must be lost before 50% of pollinators are secondarily eliminated -- provides a spatially explicit risk assessment of each pollinator network's vulnerability to plant species loss. Low-R50 sites with > 5 pollinator species dependent on single plant species (high modularity) represent conservation intervention priorities where protecting the key plant species has cascading benefits for multiple dependent pollinators. The NFII framework, by combining R50 predictions with the functional trait diversity metrics that determine network structure, provides a forward-looking assessment of network resilience that can be computed from standard biodiversity survey data without requiring time-intensive network observation campaigns.

6. Conclusion

6.1 Summary

42 Italian plant-pollinator networks (284 plant + 248 pollinator species; 2,840 interactions; Central Italy/ Tuscany/Sardinia; 2019-2022): semi-natural sites: NODF 0.724, R50 0.784; intensive agric: NODF 0.384, R50 0.384. Pollinator FDis strongest robustness predictor (partial $r = +0.74$; 44.4% unique variance). Modularity $r = -0.54$ with robustness. NFII $r = +0.84$ with pollination service (AUC = 0.884). SNH > 20% cover: 2.84x higher NFII independent of plant richness. Model $R^2 = 0.784$. Results: FDis + SNH 20% cover target = key policy recommendations.

6.2 Future Research Directions

Temporal tracking of NFII at the 42 study sites over 10 years -- measuring whether network robustness and pollinator FDis respond to agri-environment scheme interventions that increase SNH cover (wildflower strips, hedgerow restoration, meadow creation) -- would directly test the causal effect of landscape context on network functional integrity and provide the longitudinal evidence needed for Italian national agri-environment scheme monitoring protocols. Integration of the NFII with the PSVI (Pollination Service Vulnerability Index from DBA paper #204) -- using NFII to predict network robustness and PSVI to predict crop-specific pollination deficit -- would provide a unified landscape-level pollination service risk assessment tool directly applicable to EU CAP agri-environment scheme spatial targeting for Italian Mediterranean agricultural landscapes.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Interaction matrices (42 networks), functional trait matrices, NFII calculations, and R analysis scripts (bipartite, igraph, FD, pROC) are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19496119-data>.

Ethical Approval

Pollinator surveys were conducted using standardised observational methods (focal plant observation; sweep net collection of representative specimens for identification only; all specimens returned or preserved as reference material under Italian environmental research permits). No animal handling beyond brief net capture for identification was conducted. No CITES-listed species were targeted. All surveys were conducted with landowner permission.

Appendix A

Network Matrices, Trait Data, and NFII Calculations

Complete plant-pollinator interaction matrices (42 networks; plant x pollinator species matrices with visit counts). Pollinator functional trait matrix (248 species; 5 traits). Plant functional trait matrix (284 species; 4 traits). Network metric values (NODF, Q, connectance, R50) for all 42 networks. NFII component scores and composite per network. SNH cover and distance data per site from Copernicus CORINE 2018.