

1 **The presence of generalist plants in urban greenspaces predicts pollinator diversity**

2

3 Jacob S Francis<sup>1,2\*</sup>, Nadja Pernat<sup>3,4</sup>, Adam Bloom<sup>1,2</sup>, Antonia J. Millet<sup>1</sup>, James J. Lange<sup>6</sup>, Marina  
4 Marquis<sup>5</sup>, Brittany M. Mason<sup>5</sup>, Corey T Callaghan<sup>5</sup>

5 1: Department of Biological Sciences, Florida Atlantic University. Davie, Florida, USA

6 2: School of the Environment, Coastal, and Ocean Sustainability, Florida Atlantic University,  
7 Davie Florida USA.

8 3: Institute of Landscape Ecology, University of Münster, Münster, Germany

9 4: Centre for Integrative Biodiversity Research and Applied Ecology (CIBRA), University of  
10 Münster, Münster, Germany

11 5: Department of Wildlife Ecology and Conservation, University of Florida, Fort Lauderdale  
12 Research and Education Center. Davie, Florida, USA

13 6: Fairchild Tropical Botanic Garden, 10901 Old Cutler Road, Coral Gables, FL 33156

14 \*: Correspondence should be directed to [francisj@fau.edu](mailto:francisj@fau.edu)

15 ORCID: JSF: 0000-0002-3534-3113, NP: [0000-0003-2244-1002](https://orcid.org/0000-0003-2244-1002), AJM: 0009-0001-6154-2087,

16 JLL: 0009-0007-5230-0573, BMM: 0000-0002-5325-5686, CTC: 0000-0003-0415-2709

17 Target Journal: Biology Letters

18 Word Count: 3427 including figure captions, excluding supplement and bibliography.

19 Figure Count: 3

20 **Keywords:** Mutualistic Networks, Connectedness, Biodiversity, Citizen Science, iNaturalist,  
21 Network Hubs

22 **Contributions:** JSF and CTC conceptualized the project. JSF developed the hypotheses and  
23 drafted the initial analyses. All authors collected data. JSF, BMM, MM, and CTC drafted the  
24 manuscript with revisions contributed by all authors.

25 **Acknowledgements:** CTC acknowledges that this research was supported in part by the  
26 intramural research program of the U.S. Department of Agriculture, Hatch, FLA-FTL-006297.  
27 Additionally, this work is supported in part by the U.S. Department of Agriculture, McIntire-  
28 Stennis Program, project award no. FLA-FTL-006659. AB and AJM were supported by the  
29 Weiner ECOS Student Success Fund at Florida Atlantic University.

30 **Abstract:**

31 Urban greenspaces are increasingly important for pollinator conservation, yet it remains unclear  
32 whether pollinator diversity is better predicted by overall plant richness or by the presence of  
33 particular plant species with central roles in the pollination network, referred to as hub species.  
34 Using community science observations from 39 urban greenspaces in Broward County, Florida,  
35 we constructed a regional plant-pollinator metanetwork and identified the five most highly  
36 connected plant species as interaction hubs. We then tested whether greenspaces containing more  
37 of these hub plants supported greater pollinator richness. Pollinator richness increased with hub  
38 plant richness, and this relationship was nonlinear, with evidence of diminishing returns as  
39 additional hub species accumulated. The observed hub set explained pollinator richness better  
40 than randomly assembled plant sets of equal size, indicating that the effect reflects the network  
41 roles of particular plant species rather than the presence of any common taxa. Our results suggest  
42 that plant identity and interaction role can outperform plant richness alone in predicting  
43 pollinator diversity in urban greenspaces. Regional metanetworks may therefore provide a  
44 practical framework for identifying plant species that disproportionately support biodiversity in  
45 fragmented urban landscapes.

## 46 **Introduction**

47 Ecological communities are not simply collections of species, but networks of interactions whose  
48 structure shapes persistence, stability, and ecosystem functioning. In mutualistic systems such as  
49 plant-pollinator communities, changes in which species are present (i.e., overall species richness)  
50 can matter less than changes in who interacts with whom [1]. Interaction structure determines  
51 how resources move throughout the environment [2]; fitness for plants [3] and animals; and  
52 network stability to disturbance [4]. Yet predicting how mutualistic networks assemble, rewire,  
53 and respond to disturbance remains difficult, in part because network structure reflects processes  
54 operating across multiple spatial and temporal scales [5,6].

55 Understanding how plant-pollinator networks assemble is particularly important given their  
56 centrality in ecosystem function [7,8]. The structure of plant-pollinator networks predicts  
57 whether pollinator species persist in the landscape [9,10], and thus continue to provide critical  
58 ecosystem services. Further, many plant-pollinator networks are dominated by generalist  
59 pollinators with flexible foraging patterns. These generalist foragers can fluctuate between high  
60 individual specialization or generalization based on context [11] and this behavior can change  
61 network structure [12,13].

62 Plants also contribute strong constraints and opportunities for assembly. Plant species differ in  
63 the breadth of their visitor assemblages, ranging from interaction generalists to functional  
64 specialists, because phenology, floral display, reward quantity and quality, and morphological  
65 accessibility determine which pollinator taxa can detect, access, and exploit their flowers [14–  
66 16]. As a result, plant identity can structure local pollinator communities by concentrating or  
67 partitioning resources across space and time. However, the relative importance of interaction  
68 driven assembly processes vs other assembly processes (such as dispersal and patch suitability)  
69 is an open question [17]. In theory, a small subset of highly connected “hub” plant species may  
70 disproportionately mediate network assembly by attracting diverse pollinator assemblages and  
71 creating interaction opportunities among otherwise weakly connected species. Historically, the  
72 idea of “magnet species”, i.e., plants that are highly attractive to pollinators and facilitate  
73 pollination of co-flowering species has received significant attention [18], but how this  
74 phenomenon shapes network assembly is unclear. This role-based perspective predicts that local

75 network structure, and its assembly in metanetworks, may depend more on the presence and  
76 abundance of particular plant species than on plant richness alone.

77 Plant “roles” in regional interaction networks can be operationalized through connectedness—the  
78 number of distinct pollinator taxa a plant interacts with across all sites. Because mutualistic  
79 networks are typically heterogeneous [19] and nested [20], a small subset of highly connected  
80 plant species may function as regional hubs of interaction. When present locally, these hub plants  
81 could disproportionately structure pollinator assemblages by providing broadly accessible  
82 resources, attracting different assemblages of pollinators. However, they could also drive  
83 potentially nonlinear, saturating increases in pollinator richness if they attract strong competitors  
84 that limit the presence of other pollinators. Urban greenspaces offer a powerful natural  
85 experiment for understanding how communities of plants and pollinators [21], and their  
86 associated mutualistic networks assemble in metacommunities. This is because urban  
87 greenspaces serve as habitat “islands” that differ in size, composition, ecological quality,  
88 management, and connectivity [22,23] .

89 Here, we use a regional plant-pollinator metanetwork to identify highly connected hub plant  
90 species and test whether greenspaces that contain more hub species support greater pollinator  
91 richness. To assess whether hubs are unusually informative (rather than any set of common  
92 plants), we compare the observed hub set’s explanatory power to a null distribution generated by  
93 set randomization.

## 94 **Methods**

### 95 *Study site selection*

96 Our regional network was derived from pollinator and plant observation data from Broward  
97 County, Florida, United States. Broward County is Florida’s second most populated county and  
98 ranks among the 20 largest counties in the United States, with approximately 1.9 million  
99 residents. The county spans 342,655 hectares, of which approximately 8.5% consists of water.  
100 Much of the western portion of the county is encompassed by the Everglades Wildlife  
101 Management Area, while the eastern portion contains a sharply delineated urban matrix  
102 characterized by dense residential, commercial, and transportation infrastructure [Figure 1, 24].

103 We focused on public urban greenspaces within the developed portion of the county [sensu 25],  
104 where pollinator communities are embedded within a highly fragmented landscape and where  
105 management interventions are most likely to be implemented.

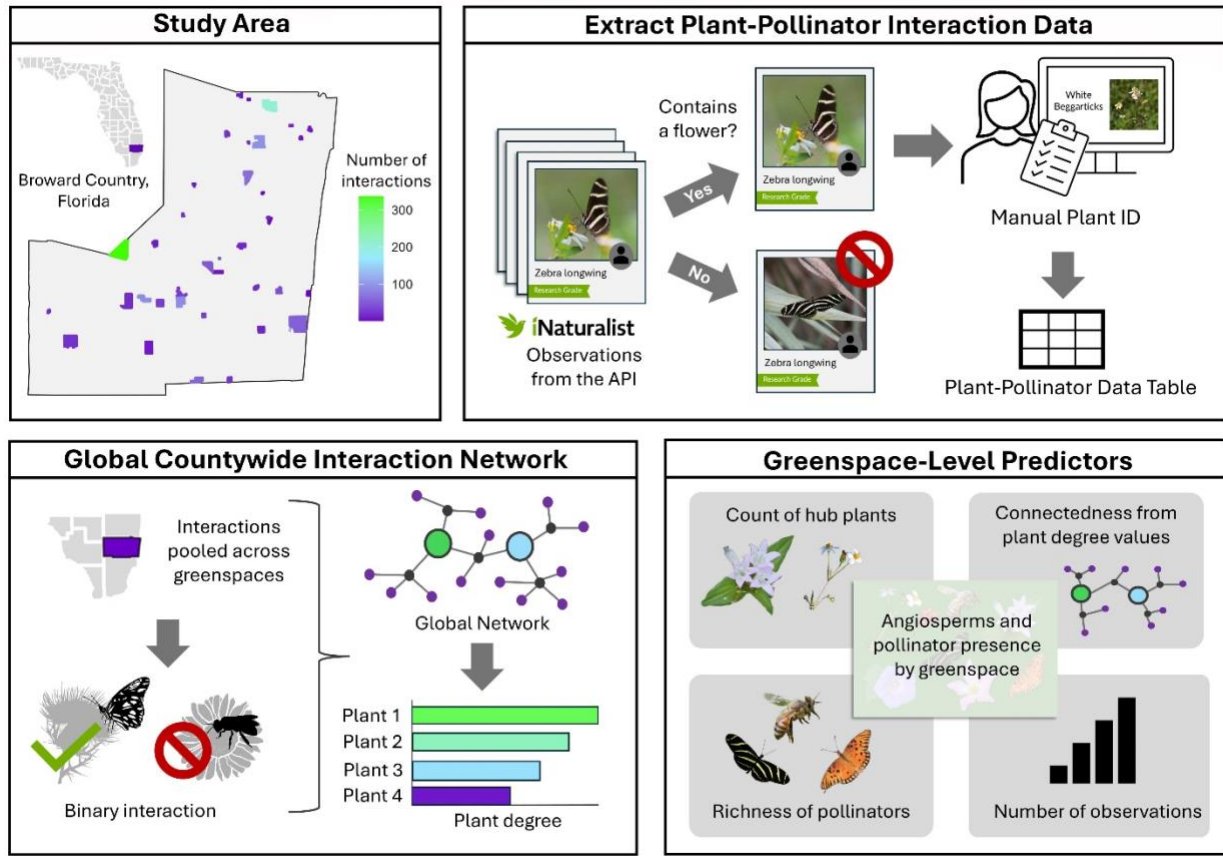
#### 106 *Data sources and processing*

##### 107 iNaturalist data acquisition and filtering

108 To obtain pollinator and plant occurrence data, we queried the iNaturalist Application  
109 Programming Interface (API) on 10 July 2024. We retrieved all “Research Grade” observations  
110 (i.e., observations with at least two-thirds agreement on taxonomic identification) from Broward  
111 County, Florida ([www.inaturalist.org](http://www.inaturalist.org)). Pollinator records included observations from the  
112 superfamily Apoidea, family Bombyliidae, subfamily Cetoniinae, order Lepidoptera, and  
113 subfamily Lepturinae. We also retrieved all Research Grade angiosperm observations from the  
114 same geographic area.

115 Using the iNaturalist API allowed us to precisely filter observations by taxonomic group and to  
116 obtain metadata for each observation, including image availability, image URLs, species  
117 identification, observation date, and geographic coordinates. We then filtered observations to  
118 include only those overlapping with mapped urban greenspace boundaries (N = 639). Urban  
119 greenspace shapefiles were obtained from [26]. To ensure sufficient sampling depth, we further  
120 restricted analyses to greenspaces with at least 100 combined angiosperm and pollinator  
121 observations, resulting in a final dataset of 39 urban greenspaces distributed across Broward  
122 County.

123



124

125 **Figure 1.** We combined iNaturalist observations, manual image review, and plant identification  
 126 to construct a curated plant-pollinator interaction dataset. Interactions were pooled across  
 127 Broward County urban greenspaces to build a regional bipartite network and identify highly  
 128 connected hub plants. All iNaturalist occurrence records in these greenspaces were then used to  
 129 calculate greenspace-level predictors, including hub plant richness, connectedness, pollinator  
 130 richness, angiosperm richness, and sampling effort.

131 Curated plant-pollinator interaction dataset

132 To characterize plant connectedness within a regional flower-visitor network, we used a curated  
 133 dataset of plant-pollinator interactions compiled from photo-vouchered observations  
 134 (Supplemental Materials 2). To identify observations that contained images of pollinators  
 135 visiting flowers, we manually reviewed images from all observations and denoted whether the  
 136 pollinator was on a flower. Interactions were then taxonomically harmonized to plant species and  
 137 pollinator taxon. Pollinator identifications came from iNaturalist, while plant species

138 identifications were made manually by the authors. We were able to identify 1,362 observed  
139 interactions across 406 plant-pollinator pairs.

#### 140 Construction of the regional interaction network

141 We constructed a bipartite plant-pollinator interaction network using the curated interaction  
142 dataset. Each unique plant-pollinator pair was treated as a binary interaction, regardless of how  
143 many times the interaction was observed, to avoid conflating observer effort with ecological  
144 interaction strength. All interactions were pooled across greenspaces to generate a single global  
145 network representing the regional structure of flower-visitor associations.

146 Plant connectedness was quantified as degree, defined as the number of distinct pollinator taxa  
147 interacting with a given plant species in the global network. Degree was chosen because it is  
148 intuitive, biologically interpretable, and directly reflects the breadth of pollinator associations.  
149 We identified the five most highly connected plant species (highest degree) in the global network  
150 and refer to these as “hub plants.” Hub plants were used to construct a greenspace-level predictor  
151 of hub presence (below) and to facilitate visualization and interpretation.

#### 152 Greenspace-level predictors derived from independent plant occurrence data

153 To quantify plant presence within each greenspace independently of the curated interaction  
154 dataset, we used angiosperm observations from the county-wide iNaturalist dataset. For each  
155 greenspace, we compiled a list of research-grade angiosperm species observed at least once,  
156 treating plant occurrence as presence-absence.

157 We then generated two complementary greenspace-level predictors. For each greenspace, we  
158 counted how many of the five hub plant species (defined from the global interaction network)  
159 were present based on iNaturalist angiosperm occurrences. This produced a discrete variable  
160 ranging from 0-5 (hub plant richness). Additionally, we calculated continuous connectedness  
161 within plant-pollinator interaction networks. As a sensitivity analysis, we calculated a continuous  
162 metric of greenspace-level connectedness based on the degree values of plants present in each  
163 greenspace. Specifically, for each greenspace we identified the five most connected plant species  
164 present (based on global degree) and computed the mean degree of those species (hereafter top 5  
165 mean degree). This metric allows the most strongly connected plants within a greenspace to  
166 dominate the predictor while avoiding reliance on a single fixed hub list.

167 Pollinator species richness was calculated for each greenspace using the independent iNaturalist  
168 dataset by counting the number of distinct pollinator taxa observed. To account for uneven  
169 sampling effort inherent in community science data, we quantified sampling effort as the total  
170 number of pollinator observations per greenspace and included the natural logarithm of this  
171 value ( $\log(\text{observations})$ ) as a covariate in all models. We also calculated angiosperm species  
172 richness per greenspace, defined as the total number of unique angiosperm Research Grade  
173 species, to control for broader plant diversity effects unrelated to hub identity.

#### 174 *Statistical analysis*

175 We evaluated the relationship between hub plants and pollinator richness using generalized  
176 linear models with a negative binomial error distribution to account for overdispersion in count  
177 data. Pollinator species richness was modeled as a function of hub plant richness (primary  
178 predictor), pollinator sampling effort (log-transformed), and angiosperm species richness. We  
179 included a quadratic term for hub plant richness to allow for saturating or nonlinear relationships,  
180 reflecting the hypothesis that additional hub species may yield diminishing returns for pollinator  
181 diversity. As a secondary analysis, we fit an analogous model replacing hub plant richness with  
182 the continuous connectedness metric (top 5 mean degree) and its quadratic term, to evaluate  
183 whether results were robust to a continuous summary of connectedness among plants present.

184 As a sensitivity analysis, we varied the definition of hub plants from the top 3 to the top 10  
185 species ranked by global degree in the regional network. For each hub-set size, we recalculated  
186 park-level hub richness and refit the primary negative binomial model including linear and  
187 quadratic hub-richness terms, pollinator sampling effort, and angiosperm richness. We  
188 summarized sensitivity by extracting the linear hub-richness coefficient from each model and  
189 converting it to an incidence rate ratio (IRR) with 95% confidence intervals.

190 To assess whether the observed association between hub plants and pollinator richness was  
191 stronger than expected by chance, we conducted a permutation test. We repeatedly generated  
192 random sets of plant species equal in number to the hub set (five species), recalculated  
193 greenspace-level pseudo-hub counts for each random set using the independent plant occurrence  
194 data, and refit the same negative binomial model. For each permutation, we calculated a  
195 likelihood ratio statistic comparing models with and without the hub predictor. The observed

196 likelihood ratio statistic was compared to the null distribution from randomly generated plant  
197 sets to obtain an empirical p-value. Model assumptions were evaluated using simulated residuals  
198 generated with the DHARMA package, including tests for dispersion, zero inflation, and residual  
199 structure [27]. All models were fitted in R using negative binomial regression [MASS; 28].

200 All analyses were conducted in R version 4.5.2 (R Core Team, 2025). Code and data are  
201 available in GitHub [https://github.com/jacobsfrancis/hub\\_plant\\_analysis](https://github.com/jacobsfrancis/hub_plant_analysis) and will be archived in  
202 a Zenodo repository following acceptance of this manuscript.

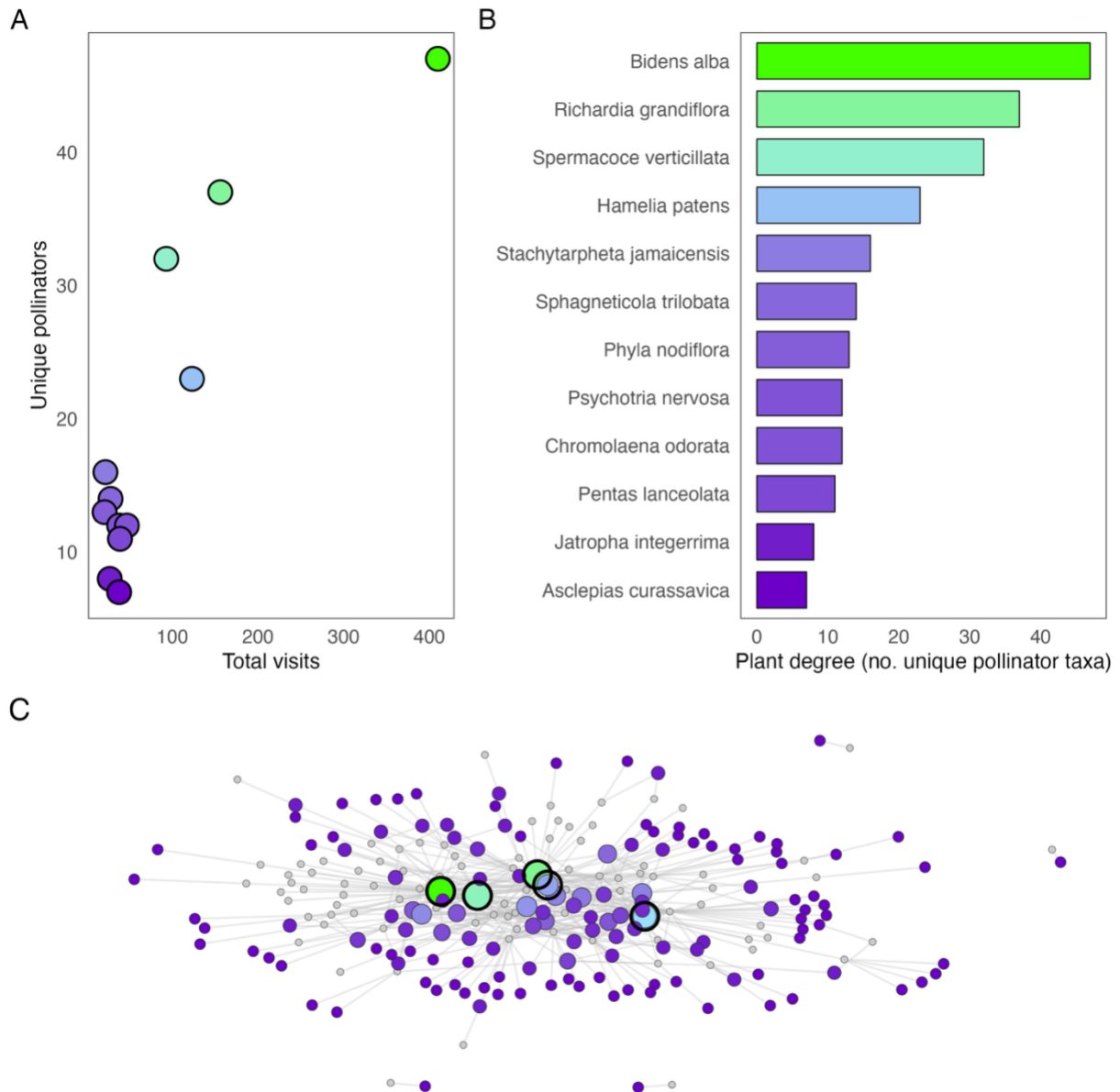
## 203 **Results**

### 204 *Greenspace-level dataset and predictors*

205 Our curated regional network included 142 plant species and 91 pollinator species. The county-  
206 wide iNaturalist greenspace diversity dataset comprised 4,404 pollinator observations (251 taxa)  
207 and 12,490 angiosperm observations (691 taxa) indicating that there were plants and pollinators  
208 observed in greenspaces that had no observed interactions. After filtering to greenspaces with  
209 complete data for all covariates, all 39 greenspaces were retained for analysis. Hub plant richness  
210 (number of hub species present) ranged from 1 to 5 across greenspaces, while observed  
211 pollinator richness ranged from 2 to 97 species. Angiosperm richness ranged from 5 to 218  
212 species.

### 213 *Global plant-pollinator network structure*

214 The curated plant-pollinator dataset yielded a global bipartite interaction network in which plant  
215 connectedness (degree) was highly right-skewed, with a small number of plant species  
216 interacting with a disproportionately large fraction of pollinator taxa (Figure 2 and S2). The five  
217 most connected plant species (“hub plants,” defined as the top-5 by global degree) were *Bidens*  
218 *alba* (degree = 47), *Richardia grandiflora* (37), *Spermacoce verticillata* (32), *Hamelia patens*  
219 (23), and *Stachytarpheta jamaicensis* (16).



220

221 **Figure 2.** Global plant-pollinator network structure and identification of hub plants. (A)  
 222 Relationship between total recorded flower visits and the number of unique pollinator taxa  
 223 observed per plant species in the curated interaction dataset. (B) Plant degree (number of unique  
 224 pollinator taxa) by plant species (ranked), highlighting a small subset of highly connected plants.  
 225 (C) Visualization of the pooled county-wide bipartite interaction network (plants and pollinator  
 226 taxa), with hub plants (top five plants by global degree) emphasized; edges represent unique  
 227 plant-pollinator interactions treated as binary links. Together, panels illustrate the strongly right-

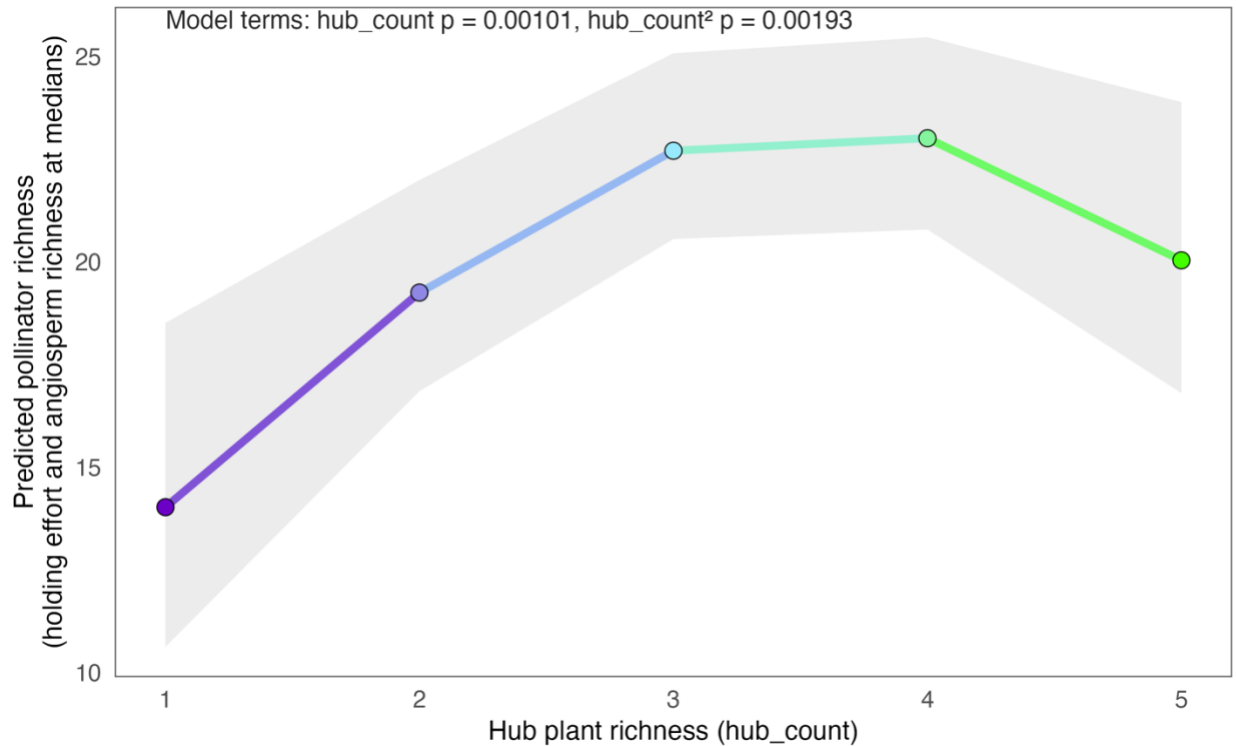
228 skewed distribution of plant connectedness and motivate hub-based predictors used in  
229 greenspace-level analyses.

230 *Primary model: hub plant richness predicts pollinator richness*

231 Observed pollinator richness increased with the number of hub plant species present, and this  
232 relationship was nonlinear (Figure 3). In the primary negative binomial model including  
233 sampling effort and angiosperm richness as covariates, the linear effect of hub plant richness was  
234 positive and significant ( $\beta = 0.544$ ,  $SE = 0.165$ ,  $z = 3.29$ ,  $p = 8.26e-04$ ;  $IRR = 1.72$ , 95% CI:  
235 1.25-2.39; Table S1), indicating that each additional hub species present was associated with a  
236 72% increase in expected pollinator richness (linear  $IRR = 1.72$ ). The quadratic term was  
237 negative and significant ( $\beta = -0.076$ ,  $p = 1.71e-03$ ), consistent with diminishing returns (a  
238 decelerating, hump-shaped relationship).

239 Sensitivity analyses showed that the positive association between hub richness and pollinator  
240 richness was qualitatively consistent across small hub sets, with the strongest effect sizes  
241 observed when hubs were defined using the top 3, 4 (only marginally so), 5, and 6 plant species  
242 by global degree (Fig. S1).

243 As expected, sampling effort was the strongest predictor of observed richness ( $\beta = 0.610$ ,  $IRR =$   
244  $1.84$ ,  $p < 0.001$ ). In contrast, angiosperm richness was not significantly associated with pollinator  
245 richness after accounting for hub plant richness and effort (Table S1).



246

247 **Figure 3.** Hub plant richness predicts pollinator richness after accounting for sampling effort.  
 248 Partial effect of hub plant richness (hub plant richness; number of the five globally most  
 249 connected “hub” plant species present in a greenspace) on predicted pollinator species richness  
 250 from the primary negative binomial model. Predictions are shown while holding pollinator  
 251 sampling effort (log(observations)) and angiosperm richness at their median values. Points/line  
 252 indicate model predictions and the shaded band shows the 95% confidence interval. P-values for  
 253 the linear and quadratic hub plant richness terms shown on the plot are Wald z-test p-values from  
 254 the negative binomial model. Results were consistent when using a continuous measure of  
 255 greenspace-level connectedness. (Figure S3)

256 *Are hub plants unusually informative?*

257 To test whether the observed hub set explains more variation in pollinator richness than expected  
 258 by chance, we conducted a set-randomization permutation test. The observed likelihood-ratio  
 259 statistic for the true top-5 hub set (LR = 8.75) exceeded the vast majority of the null distribution  
 260 generated from 5,000 random plant sets of the same size (empirical simulation-based  $p = 0.005$ );  
 261 Figure S2). This indicates that the plants identified as hubs based on the global interaction

262 network explain more variation in pollinator richness than would be expected for randomly  
263 selected plant species.

## 264 **Discussion**

265 Using a regional metanetwork, with 142 plant species, 91 pollinator species, and 406 unique  
266 plant-pollinator pairs, we found that greenspaces containing more of the most highly connected  
267 plant species (hub plants) supported greater pollinator richness. The effect was substantial:  
268 predicted pollinator richness increased from roughly 14 species in greenspaces with one hub  
269 plant to about 23 species in those with four hub plants, corresponding to an increase of  
270 approximately 60%. The explanatory power of the observed hub set exceeded that of randomly  
271 assembled plant sets of equal size, indicating that the result reflects role-based properties of  
272 particular plant species rather than simply the presence of any common or widespread taxa. This  
273 aligns with broader mutualistic network theory showing that species-rich plant-pollinator  
274 communities are typically organized around a highly connected generalist “core,” and that  
275 hubs/connectors can be structurally influential [19,20].

276 Highly connected plant species may increase pollinator richness because they act as broad-access  
277 floral resource hubs. By a mechanism conceptually similar to the “magnet species effect” which  
278 predicts that attractive plants can facilitate the pollination of neighbors by pulling in more  
279 pollinators to a patch [18], these hyper generalist plants may attract visitors into a  
280 metacommunity and may also create conditions under which additional, less common taxa can  
281 persist [29–31].

282 The saturating shape of this relationship is also biologically plausible. The first few hubs likely  
283 increase resource breadth and/or greenspace detectability for mobile pollinators, whereas  
284 additional hubs may yield diminishing gains because pollinators were already captured by a  
285 generalist “core”. These diminishing returns are consistent with prior theory and simulations  
286 showing that intact or restored mutualistic networks often contain redundancy [32] and that  
287 robustness depends strongly on a relatively small set of highly linked species [33]. Thus, hub  
288 plants may disproportionately elevate pollinator diversity, but with diminishing returns as local  
289 communities approach the limits imposed by overlap, competition, and patch context.

290 It's widely accepted that plant richness promotes pollinator diversity because more plant species  
291 provide a greater variety of floral resources [34,35]. However, our results suggest that plant  
292 identity and network role can matter more than richness alone [similar to findings in 36]. After  
293 accounting for overall angiosperm richness, greenspaces containing more highly connected hub  
294 plants still supported greater pollinator richness, indicating that the effect was not simply driven  
295 by larger local plant species pools. In this sense, plant richness and hub roles are not  
296 interchangeable: richness reflects the size of the local species pool, whereas hub roles reflect the  
297 functional position of particular species within the interaction network.

298 For managers hoping to maximize pollinator diversity on their lands, our results suggest that  
299 planting, or encouraging the growth of a small number of well-chosen highly connected plant  
300 species into urban greenspaces may disproportionately enhance pollinator diversity relative to  
301 simply increasing overall plant richness, for example *Hamelia patens* or *Stachytarpheta*  
302 *jamaicensis*. The saturating nature of the relationship supports the idea that a targeted effort  
303 could have outsized impacts [37–39]. This could sometimes mean adding new species to the  
304 greenspace's plant structure, but it could also look like adopting management practices (e.g.,  
305 prescribed fire, or mowing regimes) to maximize the opportunities for specific target species to  
306 flourish.

307 An important caveat is that highly connected species are not necessarily conservation-priority  
308 species. In our system, some hub taxa from our metanetwork are invasive species (e.g. *Richardia*  
309 *grandiflora*). In many regions, plant-pollinator network hubs can be non-native or invasive  
310 “super-generalists,” in part because disturbance tolerance and high local abundance increase  
311 encounter rates and broaden interaction opportunities [40–42]. Given the well-documented  
312 [43,44] and theorized [45] negative impact of alien plants, especially via reduced native  
313 pollination and reproduction [46] despite occasional facilitative “magnet” effects, our results  
314 should not be interpreted as recommending introduction of invasive hubs. Instead, the most  
315 defensible implication is to identify native functional analogs that occupy similar interaction  
316 roles within regional metanetworks, or to manage for native hub persistence.

317 Because our analyses relied on iNaturalist observations, the interaction network reflects known  
318 biases in community science data, including uneven sampling effort, detectability differences

319 among species, and preferential documentation of conspicuous taxa [47,48]. These processes  
320 could systematically underrepresent cryptic or less frequently photographed interactions,  
321 potentially affecting estimates of plant connectedness. However, if such biases are consistent  
322 within a region, relative differences among greenspaces in hub presence and pollinator richness  
323 can remain informative, particularly when analyses include sampling-effort controls and given  
324 our conclusions are based on role-based signals in the observation network rather than complete  
325 interaction censuses.

326 While our study focused on Broward County, similar patterns likely extend to other systems. The  
327 mechanism underlying the relationship between hub plant richness and pollinator diversity is still  
328 uncertain, but highly connected plants may promote richer pollinator assemblages by providing  
329 reliable resources, attracting diverse visitors, and helping sustain both generalist and specialist  
330 species. Accordingly, role-based predictors derived from regional metanetworks may prove  
331 useful across landscapes where plant-pollinator interactions are strongly uneven among species.  
332 Because our analysis was built from iNaturalist citizen science data, it also demonstrates that  
333 both this approach and its key insights are readily transferable to other regions.

### 334 **Data Accessibility**

335 Data and code supporting this article are available at  
336 [https://github.com/jacobsfrancis/hub\\_plant\\_analysis\\_pub](https://github.com/jacobsfrancis/hub_plant_analysis_pub). Upon acceptance, the repository will  
337 be archived in Zenodo and the DOI will be added.

### 338 **Competing Interests**

339 We declare no competing interest

### 340 **AI Declaration**

341 OpenAI's ChatGPT-5.5 thinking model was used between February 2026 and May 2026 to edit  
342 manuscript text for clarity, troubleshoot R code, and verify consistency between reported  
343 statistics and model outputs. The tool was not used to generate the research idea, conduct  
344 analyses, interpret results, or draft the initial manuscript. All AI-assisted edits and outputs were  
345 reviewed and verified by the authors.

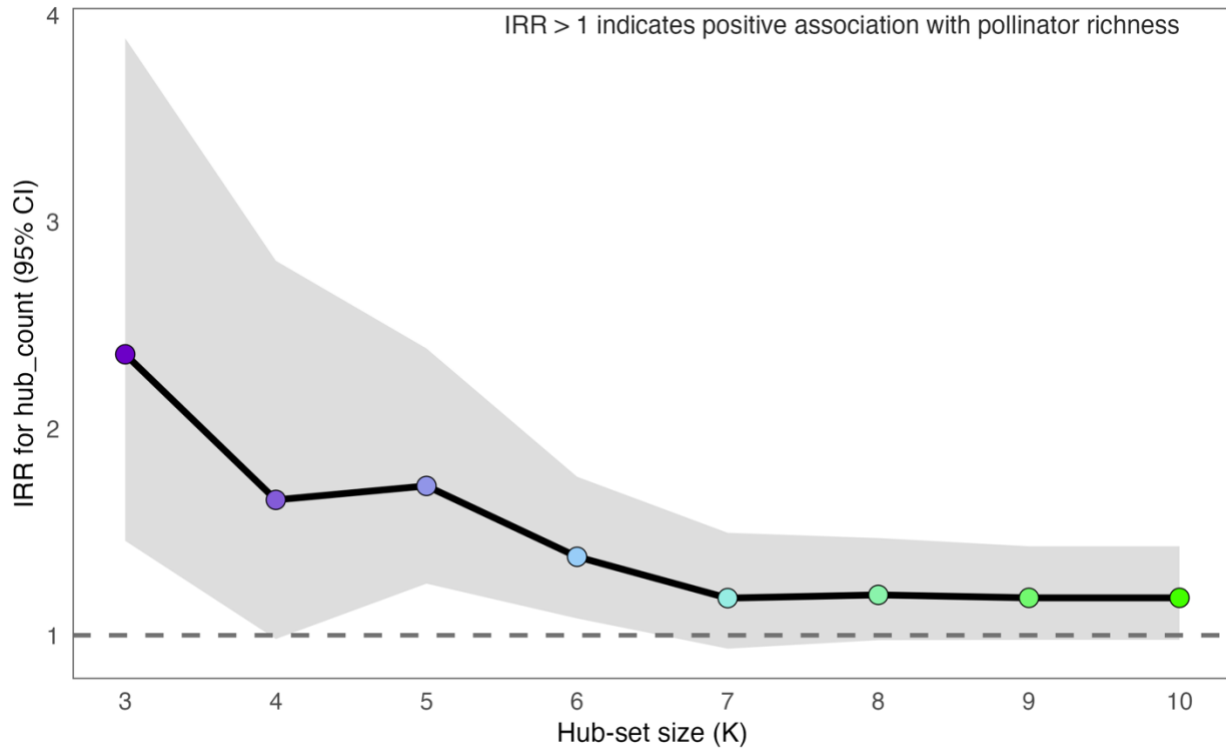
346 **Bibliography**

- 347 1. Petanidou T, Kallimanis AS, Tzanopoulos J, Sgardelis SP, Pantis JD. 2008 Long-term  
348 observation of a pollination network: fluctuation in species and interactions, relative  
349 invariance of network structure and implications for estimates of specialization. *Ecol. Lett.*  
350 **11**, 564–575. (doi:10.1111/j.1461-0248.2008.01170.x)
- 351 2. Vaudo AD, Dyer LA, Leonard AS. 2024 Pollen nutrition structures bee and plant community  
352 interactions. *Proc. Natl. Acad. Sci.* **121**, e2317228120. (doi:10.1073/pnas.2317228120)
- 353 3. Arceo-Gómez G, Carneiro LT. 2026 Empirical evidence for the ecological significance of  
354 interaction network indices within a mutualistic network. *New Phytol.* **249**, 1053–1062.  
355 (doi:10.1111/nph.70681)
- 356 4. Carpentier C, Barabás G, Spaak JW, De Laender F. 2021 Reinterpreting the relationship  
357 between number of species and number of links connects community structure and stability.  
358 *Nat. Ecol. Evol.* **5**, 1102–1109. (doi:10.1038/s41559-021-01468-2)
- 359 5. CaraDonna PJ, Petry WK, Brennan RM, Cunningham JL, Bronstein JL, Waser NM, Sanders  
360 NJ. 2017 Interaction rewiring and the rapid turnover of plant–pollinator networks. *Ecol. Lett.*  
361 **20**, 385–394. (doi:10.1111/ele.12740)
- 362 6. Ballarin CS, Amorim FW, Correa BA, Jordano P. 2026 Floral resource diversity drives  
363 spatiotemporal variation in plant–pollinator network structure. *Oikos* , e11730.  
364 (doi:10.1002/oik.11730)
- 365 7. Loy X, Brosi BJ. 2022 The effects of pollinator diversity on pollination function. *Ecology*  
366 **103**, e3631. (doi:10.1002/ecy.3631)
- 367 8. Ollerton J. 2017 Pollinator Diversity: Distribution, Ecological Function, and Conservation.  
368 *Annu. Rev. Ecol. Evol. Syst.* **48**, 353–376. (doi:10.1146/annurev-ecolsys-110316-022919)
- 369 9. Domínguez-García V, Molina FP, Godoy O, Bartomeus I. 2024 Interaction network structure  
370 explains species’ temporal persistence in empirical plant–pollinator communities. *Nat. Ecol.*  
371 *Evol.* **8**, 423–429. (doi:10.1038/s41559-023-02314-3)
- 372 10. Ponisio LC, Gaiarsa MP, Kremen C. 2017 Opportunistic attachment assembles plant–  
373 pollinator networks. *Ecol. Lett.* **20**, 1261–1272. (doi:10.1111/ele.12821)
- 374 11. Wang L, Yang Y, Duan Y. 2021 Pollinator individual-based networks reveal the specialized  
375 plant–pollinator mutualism in two biodiverse communities. *Ecol. Evol.* **11**, 17509–17518.  
376 (doi:10.1002/ece3.8384)
- 377 12. Brosi BJ. 2016 Pollinator specialization: from the individual to the community. *New Phytol.*  
378 **210**, 1190–1194. (doi:10.1111/nph.13951)
- 379 13. Valdovinos FS, Brosi BJ, Briggs HM, Moisset De Espanés P, Ramos-Jiliberto R, Martínez  
380 ND. 2016 Niche partitioning due to adaptive foraging reverses effects of nestedness and

- 381 connectance on pollination network stability. *Ecol. Lett.* **19**, 1277–1286.  
382 (doi:10.1111/ele.12664)
- 383 14. Junker RR, Blüthgen N, Brehm T, Binkenstein J, Paulus J, Martin Schaefer H, Stang M.  
384 2013 Specialization on traits as basis for the niche-breadth of flower visitors and as  
385 structuring mechanism of ecological networks. *Funct. Ecol.* **27**, 329–341.  
386 (doi:10.1111/1365-2435.12005)
- 387 15. Erickson E, Junker RR, Ali JG, McCartney N, Patch HM, Grozinger CM. 2022 Complex  
388 floral traits shape pollinator attraction to ornamental plants. *Ann. Bot.* **130**, 561–577.  
389 (doi:10.1093/aob/mcac082)
- 390 16. Freytes-Rivera A, Rojas-Sandoval J, Fumero-Cabán JJ, Ackerman JD. 2025 Plant–pollinator  
391 interactions in a tropical dry forest: Spatiotemporal shifts in floral trait importance. *J. Ecol.*  
392 **113**, 3111–3123. (doi:10.1111/1365-2745.70156)
- 393 17. Marjakangas E, Muñoz G, Turney S, Albrecht J, Neuschulz EL, Schleuning M, Lessard J.  
394 2022 Trait-based inference of ecological network assembly: A conceptual framework and  
395 methodological toolbox. *Ecol. Monogr.* **92**, e1502. (doi:10.1002/ecm.1502)
- 396 18. Braun J, Lortie CJ. 2019 Finding the bees knees: A conceptual framework and systematic  
397 review of the mechanisms of pollinator-mediated facilitation. *Perspect. Plant Ecol. Evol.*  
398 *Syst.* **36**, 33–40. (doi:10.1016/j.ppees.2018.12.003)
- 399 19. Bascompte J, Jordano P. 2007 Plant-animal mutualistic networks: the architecture of  
400 biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **38**, 567–593.
- 401 20. Bascompte J, Jordano P, Melián CJ, Olesen JM. 2003 The nested assembly of plant-animal  
402 mutualistic networks. *Proc. Natl. Acad. Sci. U. S. A.* **100**, 9383–9387.  
403 (doi:10.1073/pnas.1633576100)
- 404 21. Liere H, Bichier P, Gonzales E, Lin BB, Jha S, Lucatero A, Philpott SM. 2025  
405 Metacommunities in community gardens: relative strength of environmental, spatial, and  
406 social filters for species assembly in highly managed urban patches. *Landsc. Ecol.* **40**, 209.  
407 (doi:10.1007/s10980-025-02237-3)
- 408 22. Chiron F *et al.* 2024 How do urban green space designs shape avian communities? Testing  
409 the area–heterogeneity trade-off. *Landsc. Urban Plan.* **242**, 104954.  
410 (doi:10.1016/j.landurbplan.2023.104954)
- 411 23. Lepczyk CA, Aronson MFJ, Evans KL, Goddard MA, Lerman SB, MacIvor JS. 2017  
412 Biodiversity in the City: Fundamental Questions for Understanding the Ecology of Urban  
413 Green Spaces for Biodiversity Conservation. *BioScience* **67**, 799–807.  
414 (doi:10.1093/biosci/bix079)
- 415 24. Volk M, Hocht T, Nettles B, Hilsenbeck R, Putz F. 2017 Florida Land Use and Land Cover  
416 Change in the Past 100 Years. In *Florida's Climate: Changes, Variations, & Impacts*,  
417 Florida Climate Institute. (doi:10.17125/fci2017.ch02)

- 418 25. Miguez NG, Mason BM, Qiu J, Cao H, Callaghan CT. 2025 Urban greenspaces benefit both  
419 human utility and biodiversity. *Urban For. Urban Green.* **107**, 128791.  
420 (doi:10.1016/j.ufug.2025.128791)
- 421 26. Miguez NG, Mason BM, Qiu J, Cao H, Callaghan CT. 2025 Urban greenspaces benefit both  
422 human utility and biodiversity. *Urban For. Urban Green.* **107**, 128791.  
423 (doi:10.1016/j.ufug.2025.128791)
- 424 27. Hartig F. 2026 *DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed)*  
425 *Regression Models*. See <https://github.com/florianhartig/dharma>.
- 426 28. Venables WN, Ripley BD. 2002 *Modern Applied Statistics with S*. Fourth. New York:  
427 Springer. See <https://www.stats.ox.ac.uk/pub/MASS4/>.
- 428 29. Biella P, Akter A, Ollerton J, Tarrant S, Janeček Š, Jersáková J, Klecka J. 2019 Experimental  
429 loss of generalist plants reveals alterations in plant-pollinator interactions and a constrained  
430 flexibility of foraging. *Sci. Rep.* **9**, 7376. (doi:10.1038/s41598-019-43553-4)
- 431 30. Jolls CL, Inkster JN, Scholtens BG, Vitt P, Havens K. 2019 An endemic plant and the plant-  
432 insect visitor network of a dune ecosystem. *Glob. Ecol. Conserv.* **18**, e00603.  
433 (doi:10.1016/j.gecco.2019.e00603)
- 434 31. Wei N, Kaczorowski RL, Arceo-Gómez G, O'Neill EM, Hayes RA, Ashman T-L. 2021  
435 Pollinators contribute to the maintenance of flowering plant diversity. *Nature* **597**, 688–692.  
436 (doi:10.1038/s41586-021-03890-9)
- 437 32. Kaiser-Bunbury CN, Mougat J, Whittington AE, Valentin T, Gabriel R, Olesen JM,  
438 Blüthgen N. 2017 Ecosystem restoration strengthens pollination network resilience and  
439 function. *Nature* **542**, 223–227. (doi:10.1038/nature21071)
- 440 33. Memmott J, Waser NM, Price MV. 2004 Tolerance of pollination networks to species  
441 extinctions. *Proc. Biol. Sci.* **271**, 2605–11. (doi:10.1098/rspb.2004.2909)
- 442 34. Lilkendey T, Mason BM, Pernat N, Marquis M, Francis JS, Callaghan CT. 2025 Proportion  
443 of native plants is a key predictor of pollinator richness in urban greenspaces. *Urban Ecosyst.*  
444 **28**, 233. (doi:10.1007/s11252-025-01854-9)
- 445 35. Philpott SM, Pardee G, Hsu J, Kulikowski AJ, Bichier P, Liere H, Lin BB, Jha S. 2025 Floral  
446 richness shapes plant-pollinator networks in urban agroecosystems. *Basic Appl. Ecol.* **88**,  
447 114–127. (doi:10.1016/j.baae.2025.10.004)
- 448 36. Martín González AM, Dalsgaard B, Olesen JM. 2010 Centrality measures and the  
449 importance of generalist species in pollination networks. *Ecol. Complex.* **7**, 36–43.  
450 (doi:10.1016/j.ecocom.2009.03.008)
- 451 37. Nichols RN, Goulson D, Holland JM. 2019 The best wildflowers for wild bees. *J. Insect*  
452 *Conserv.* **23**, 819–830. (doi:10.1007/s10841-019-00180-8)

- 453 38. Nichols RN, Holland JM, Goulson D. 2023 A novel farmland wildflower seed mix attracts a  
454 greater abundance and richness of pollinating insects than standard mixes. *Insect Conserv.*  
455 *Divers.* **16**, 190–204. (doi:10.1111/icad.12624)
- 456 39. Monteiro BL, Souza CS, Maruyama PK, Camargo MGG, Morellato LPC. 2025 Applying  
457 plant-pollinator network to identify priority species for conservation in a biodiversity  
458 hotspot. *Biol. Conserv.* **302**, 110979. (doi:10.1016/j.biocon.2025.110979)
- 459 40. Stout JC, Tiedeken EJ. 2017 Direct interactions between invasive plants and native  
460 pollinators: evidence, impacts and approaches. *Funct. Ecol.* **31**, 38–46. (doi:10.1111/1365-  
461 2435.12751)
- 462 41. Albrecht M, Padrón B, Bartomeus I, Traveset A. 2014 Consequences of plant invasions on  
463 compartmentalization and species' roles in plant–pollinator networks. *Proc. R. Soc. B Biol.*  
464 *Sci.* **281**, 20140773. (doi:10.1098/rspb.2014.0773)
- 465 42. Zaninotto V, Thebault E, Dajoz I. 2023 Native and exotic plants play different roles in urban  
466 pollination networks across seasons. *Oecologia* **201**, 525–536. (doi:10.1007/s00442-023-  
467 05324-x)
- 468 43. Pyšek P *et al.* 2020 Scientists' warning on invasive alien species. *Biol. Rev.* **95**, 1511–1534.  
469 (doi:10.1111/brv.12627)
- 470 44. Vilà M *et al.* 2011 Ecological impacts of invasive alien plants: a meta-analysis of their  
471 effects on species, communities and ecosystems: Ecological impacts of invasive alien plants.  
472 *Ecol. Lett.* **14**, 702–708. (doi:10.1111/j.1461-0248.2011.01628.x)
- 473 45. Tallamy DW, Narango DL, Mitchell AB. 2021 Do NON-NATIVE plants contribute to insect  
474 declines? *Ecol. Entomol.* **46**, 729–742. (doi:10.1111/een.12973)
- 475 46. Morales CL, Traveset A. 2009 A meta-analysis of impacts of alien vs. native plants on  
476 pollinator visitation and reproductive success of co-flowering native plants. *Ecol. Lett.* **12**,  
477 716–728. (doi:10.1111/j.1461-0248.2009.01319.x)
- 478 47. Lowe SK, Mason BM, Guralnick R, Morales NA, Callaghan CT. 2025 Participation Intensity  
479 Influences Motivations for Contributing to iNaturalist. *Citiz. Sci. Theory Pract.* **10**, 25.  
480 (doi:10.5334/cstp.823)
- 481 48. Grady EL, Campbell CJ, Callaghan CT, Guralnick RP. 2026 iNaturalist Users Exhibit  
482 Distinct Spatiotemporal Sampling Preferences, with Implications for Biodiversity Science  
483 and Project Planning. *Citiz. Sci. Theory Pract.* **11**, 3. (doi:10.5334/cstp.868)

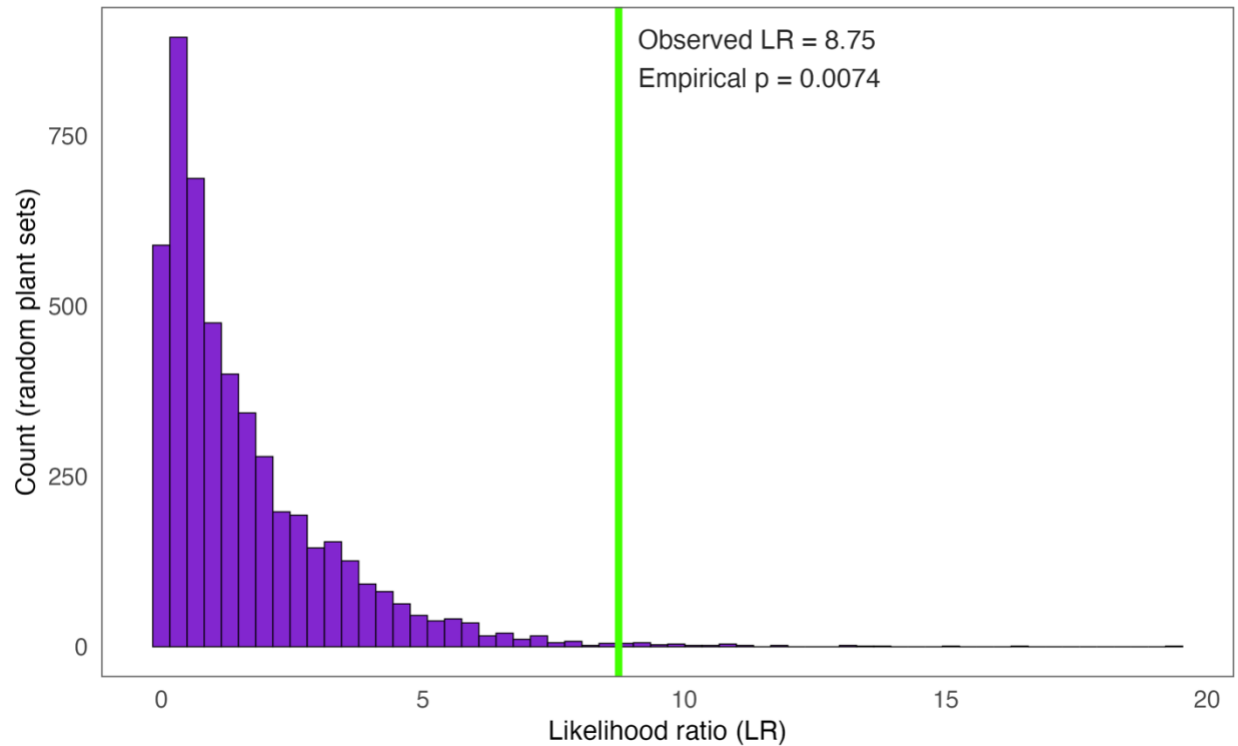


485

486 **Figure S1. Sensitivity of the hub effect to hub-set size.** Incidence rate ratios (IRRs) for the  
 487 linear effect of hub richness on pollinator richness across sensitivity analyses in which “hub  
 488 plants” were defined as the top  $K$  most connected plant species in the regional plant-pollinator  
 489 metanetwork ( $K = 3-10$ ). For each value of  $K$ , hub richness was recalculated for each greenspace  
 490 and a negative binomial model was fit including hub richness, its quadratic term, pollinator  
 491 sampling effort, and angiosperm richness. Points show the estimated IRR for the linear hub-  
 492 richness term and the shaded band indicates 95% confidence intervals. The dashed horizontal  
 493 line at  $IRR = 1$  indicates no association with pollinator richness. Positive effects were strongest  
 494 when hubs were defined using relatively small sets of the most highly connected plants  
 495 (approximately the top 3-6 species), and weakened toward 1 as additional, less-connected plant  
 496 species were included, indicating that the predictive signal is driven primarily by the most  
 497 strongly connected regional hub plants.

498

499



500

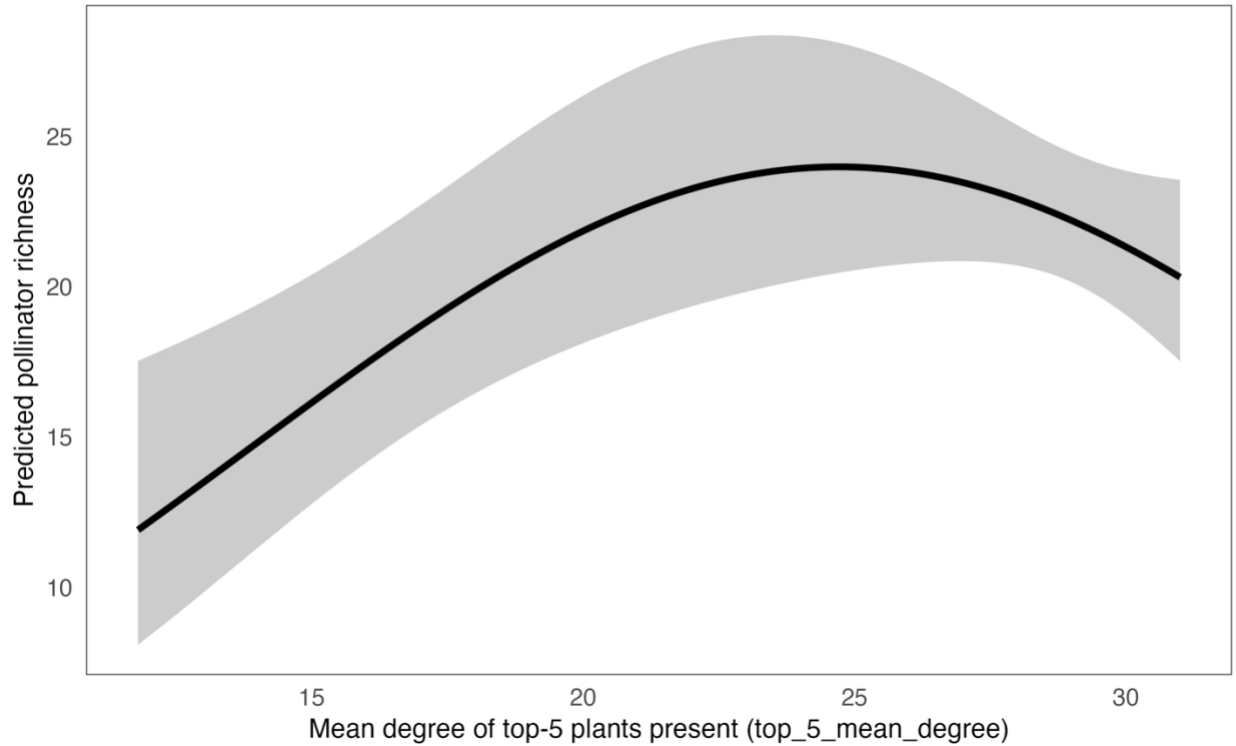
501 **Figure S2. Hub plants outperform random plant sets in predicting greenspace-level**  
 502 **pollinator richness.** Null distribution of likelihood-ratio (LR) statistics from a set-randomization  
 503 permutation test comparing negative binomial models with and without the hub predictor. For  
 504 each of 5,000 permutations, the five hub plants were replaced with a random set of five plant  
 505 species from the same species pool, greenspace-level “hub plant richness” was recomputed using  
 506 independent plant occurrence data, and the LR statistic was calculated from nested models. The  
 507 vertical line indicates the observed LR for the true hub set (LR = 8.75); the empirical one-sided  
 508 p-value ( $p = 0.005$ ) is the proportion of randomized plant sets with  $LR \geq$  observed.

509

510

511

512



513

514 **Figure S3. Robustness check using continuous plant connectedness.** In a secondary model  
 515 that replaced *hub plant richness* with top 5 mean degree (the mean global degree of the five  
 516 most-connected plant species present in each greenspace), top 5 mean degree was positively  
 517 associated with pollinator richness ( $\beta = 0.208$ , IRR = 1.23,  $p = 0.008$ ) and the quadratic term was  
 518 negative and significant, consistent with a nonlinear, saturating relationship between plant  
 519 connectedness and pollinator diversity. Plot: Partial effect of top 5 mean degree (mean global  
 520 degree of the five most-connected plant species present in each greenspace) on predicted  
 521 pollinator richness from the secondary negative binomial model; shaded band shows 95%  
 522 confidence intervals with other covariates held at their median values.

523

524 **Table S1 Primary model results:** Negative binomial model coefficients are shown on the log  
 525 scale with corresponding Wald  $\chi^2$ , *p-values*, incidence rate ratios (IRRs), and 95% confidence  
 526 intervals. All values are based on type II sums of squares (i.e. marginal on all other terms).  
 527 Significant terms are shown in bold.

Term	Estimate	Std. Error	LR $\chi^2$	p	IRR	IRR CI (min - max; 95%)	
<b>Hub Plant Richness</b>	<b>0.54</b>	<b>0.17</b>	<b>11.18</b>	<b>8.26E-04</b>	<b>1.72</b>	<b>1.25</b>	<b>2.39</b>
<b>Hub Plant Richness (quadratic)</b>	<b>-0.08</b>	<b>0.02</b>	<b>9.84</b>	<b>1.71E-03</b>	<b>0.93</b>	<b>0.88</b>	<b>0.97</b>
<b>Sampling Effort</b>	<b>0.61</b>	<b>0.04</b>	<b>241.22</b>	<b>5.59E-49</b>	<b>1.84</b>	<b>1.70</b>	<b>2.00</b>
Angiosperm Richness	0.00	0.00	0.33	5.66E-01	1.00	1.00	1.00

528

529

530

531

532

533 **Supplement 2: Protocol for Tagging Pollinator iNaturalist Images**

534

535 For this project, we aim to document pollinator interactions with flowers using iNaturalist  
536 images. We define pollinators as bees, apoid wasps, bee flies, fruit and flower chafers, and  
537 butterflies and moths. This protocol describes how we tagged images with details on whether a  
538 flower is visible, the insect's life stage (adult or immature), and the insect's behavior.

539 Data is collected via a Google Sheets database. Below is an overview of the column names and  
540 how to best fill out each blank column (image number, flower visible, life stage, insect behavior,  
541 and notes):

542 **id:** Unique number that identifies the observation.

543 **park\_name:** The name of the park where the pollinator images were obtained.

544 **observed\_on:** The date the iNaturalist observation was taken on. This column can be used to  
545 verify that the URL is directing you to the correct observation.

546 **taxon\_name:** The scientific name of the organism in the iNaturalist observation. This column  
547 can be used to verify that the URL is directing you to the correct observation.

548 **URL:** This is the URL link to the observation. Click on this link to view the observation and fill  
549 out the following columns.

550 **number\_of\_observation\_photos:** This column indicates the number of photos in each  
551 observation. Please refer to this field when completing the 'Image Number' column.

552 **Image Number:** Observations may have multiple images. For tagging purposes, select the most  
553 representative image in each observation.

554 If available, select the image that best depicts a pollinator interaction. Look for an image where a  
555 flower is visible and shows the best insect behavior, with the insect perched on a flower being  
556 the best choice, followed by perched near a flower or flying (depending on the distance to the  
557 flower, with images of insects closer to a flower ranking higher), and 'other (add note)' being the

558 least preferable. If multiple images meet these criteria, choose the first suitable image. If none of  
559 the images have a visible flower, then simply choose the first image.

560 After selecting your reference photo, please enter the corresponding image number in this field.  
561 The image number should match the order in which the images are displayed on iNaturalist  
562 (refer to the image on the right). If the observation has only one image, enter '1' in this field.  
563 Ensure that the image number you enter is equal to or less than the number listed in the  
564 'number\_of\_observation\_photos' column.

565 **Flower Visible:** A yes/no field to denote if a flower is visible in the iNaturalist image. If a  
566 flower is visible in the image, no matter where the insect is located, select “Yes.” If you do not  
567 see a flower, select “No.” If you are unsure, select “I don’t know.”

568 **Life Stage:** This field is used to denote if the individual is an adult or immature. If the image is  
569 of insect eggs, larva (i.e., a caterpillar), or pupa then select “Immature.” If the image is of a  
570 mature insect that has wings, then select “adult.” Note: Only fill in this field if there is a flower  
571 visible in the image.

572 **Insect Behavior:** Use this field to denote the behavior of the insect: perched on flower, perched  
573 near flower, flying, or other (add note) (see below for definitions). Note: Only fill in this field if  
574 there is a flower visible in the image and the insect is an adult.

- 575 • Select “Perched on Flower” when the insect is directly perched on the flower or on  
576 nearby surface where at least part of the insect is touching the flower.
- 577 • Select “Perched near Flower” when the insect is perched on a surface near the flower, but  
578 is not touching the flower.
- 579 • Select “Flying” when the insect is flying near the flower.
- 580 • Select “Other (add note)” if the insect does not fit into any of the other categories. Then,  
581 provide a brief description of the behavior in the “Notes” column.

582 **Notes:** Use this column to add any additional notes about the observation. This column is  
583 optional unless you select “Other (add note)” for insect behavior. In this case, briefly describe  
584 the insect behavior in the observation.

585 **Entered by:** Enter your name in this column to indicate that you entered the data for this  
586 observation.

587

588

589