Title:

The Interaction Affinity Between Flowers and Their Pollinators

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Abstract

The probability of flower fertilization by its pollinator is widely recognized as being influenced by species abundances. However, this relationship has rarely been formalized for the analysis of pollination networks. In this study, I introduce a simple model, adapted from physical chemistry, to formalize this functional dependence. This approach draws upon the well-established biochemical concept of affinity, which quantifies the strength of the binding interaction between a protein and its ligand. Affinity, in this context, is explained as the "attraction" or "fit" between two molecules, stemming from their complementarity in shape, charge, and hydrophobic or hydrophilic properties. Analogously, pollinator-flower interactions can be conceptualized through the complementarity of their morphologies, as well as the pollinator's ability to locate and recognize the desired flower, often involving complex behaviors and memory utilization. Just as protein-ligand binding affinity is critical for metabolic efficiency, the affinity within pollination networks can determine the effectiveness of flower-pollinator interactions, offering novel insights into their functional mechanisms.

Keywords: Abundance, Affinity, Interaction, Pollination network

Introduction

Studies on pollination networks have advanced rapidly, particularly through the development of a wide range of quantitative analytical tools based on graph and network theory (Dale, 2017). These tools have uncovered several key characteristics, most notably the low levels of connectance and the nested distribution of interactions, patterns that are consistently observed across diverse habitats and communities (Bascompte & Scheffer, 2023; Lanuza et al., 2025). However, concerns have been raised about the disconnect between these advancements and foundational concepts in community ecology (Blüthgen & Staab, 2024; Peralta et al., 2024). For instance, the primary structural features of pollination networks — such as low connectance, nestedness, modularity, and asymmetry — are often derived from binary matrices that disregard variability in interaction strength and species abundances for both flowers and pollinators (Staniczenko et al., 2013). Overlooking this variability may significantly hinder our ability to fully understand the role of ecological interactions in community processes (Blüthgen & Staab, 2024; Peralta et al., 2024). In fact, abundance distribution has profound effects on species interaction networks. For example, studies have demonstrated that the resilience of a pollination network depends on the presence of abundant and highly connected species (Winfree et al., 2014). Since the probability of a pollinator visiting a flower is a function of their respective abundances (Vázquez et al., 2009), one might also assume the reverse to be true: logically, frequent encounters require numerous individuals, and *vice versa*. However, this is not always the case, and models attempting to extrapolate species abundances from interaction frequencies have often proven inaccurate and unreliable (Vizentin-Bugoni et al., 2014; Gardner et al., 2020). The importance of incorporating abundance distribution data has recently been acknowledged in the guidelines of the European Database of Plant-Pollinator Networks (EuPPollNet, Lanuza et al., 2025), which now requires contributors to report flower counts. Unfortunately, this approach remains overly "phytocentric," as it fails to mandate abundance distribution data for pollinators.

The frequency of pollinators visiting flowers is influenced not only by species abundances but also by additional factors such as weather, morphology (trait matching), and phenology (Peralta et al., 2024). While species abundance distribution patterns are remarkably consistent across ecosystems and communities (Ulrich et al., 2010), these additional factors are shaped by geographical, historical, and phylogenetic contexts. This highlights the importance of understanding abundance data. In this study, I propose that incorporating the abundances of both flowers and pollinators into the analysis of pollination networks could offer significant benefits. To demonstrate this, I introduce a simple model examining the dependence of interaction frequency on species abundance. The model is accompanied by an illustrative example and applied to a dataset that includes independently collected abundance data for both pollinators and flowers, along with interaction frequency data (Vizentin-Bugoni et al., 2016).

The data and their analysis

Before proceeding with the reanalysis, I introduce the model that links species abundances to interaction frequencies using an illustrative matrix. While smaller than the actual dataset, this matrix retains its essential properties (see the next section). After presenting the key concepts, I move on to the reanalysis of the real matrix.

The dataset reanalyzed in this study was contributed by Vizentin-Bugoni et al. (2016) and is available for download from the Interaction Web Database (IWB; see also Supplementary Material). The authors conducted intensive sampling in the Atlantic Rainforest of southeastern Brazil (23°S, 45°W) over a period of 4–10 days per month for two years. The network, or rather a subnetwork, comprises over 300 individuals of 9 hummingbird species and 83,931 counted flowers of 55 plant species. Crucially, the distributions of both flowers and hummingbirds were determined through independent sampling. A total of 2,793 interactions among 123 hummingbird-flower pairs were recorded. These data were organized into a network matrix (Table SI1 in the Supplementary Information), where abundances were standardized as densities (number of individuals per unit area). Metrics derived from the model (affinities) were standardized by dividing each by its maximum value and subsequently presented graphically.

An illustrative example

The illustrative example consists of five pollinator species and five flower species, demonstrating the same general characteristics as those observed in real network matrices (Table 1A).

Table 1. Illustrative matrices of pollination network including pollinator and floral abundances (highlighted in red font). A: raw data from the field; B: raw data in binary form

A

Species	Pollinators	Poll_1	Poll_2	Poll_3	Poll_4	Poll_5
Flowers	Abundances	160	80	40	20	10
Flor_1	1600		64	32		32
Flor_2	800	128			16	
Flor_3	400	300		64		
Flor_4	200		10			
Flor_5	100	128				

B

Species	Pollinators	Poll_1	Poll_2	Poll_3	Poll_4	Poll_5
Flowers	Abundances	160	80	40	20	10
Flor_1	1600	0	1	1	0	1
Flor_2	800	1	0	0	1	0
Flor_3	400	1	0	1	0	0
Flor_4	200	0	1	0	0	0
Flor_5	100	1	0	0	0	0

The matrix is considered “complete” as it includes abundance data for both pollinators and flowers (highlighted in red font). The columns and rows represent pollinator and flower species, respectively, while the cells indicate the frequency of interactions between pollinator-flower pairs. Empty cells signify the absence of interactions. In the binary version of this matrix (Table 1B), empty cells are represented by 0s, while cells with interactions are represented by 1s, regardless of the recorded interaction frequency.

A commonly calculated metric from binary matrices is connectance. Although modern software computes connectance in a more sophisticated manner, the original, simpler equation conveys the concept effectively:

$C = L / (M * N)$,

where C represents connectance, L is the number of links (the sum of cells with a value of 1 in the binary matrix), M and N are the numbers of flower and pollinator species, respectively. Connectance is simply the proportion of potential links between species that are realized. In the illustrative example, $L = 9$, $M = 5$ and $N = 5$, resulting in $C = 9 / (5 * 5) = 0.36$.

The binary matrix (Table 1B), however, fails to capture the strong differences in interaction frequencies. For instance, in the original matrix (Table 1A), the interaction frequency between Poll_1 and Flor_3 was recorded 300 times, whereas the minimum frequency, observed between Poll_2 and Flor_4, was only 10 — a 30-fold difference! In binary form, this critical information is lost, as all non-zero frequencies are reduced to a value of 1.

The majority of real network matrices available in open-access databases, unlike the illustrative example, lack species abundance data for both pollinators and plants. These matrices often only indicate which species are present within the network. However, the illustrative example highlights that the abundance of the most common species exceeds that of the least common species by a factor of 16 — a substantial difference. Matrices lacking abundance data, therefore, limit our ability to account for such variation in analyses.

In the real network matrix, differences in interaction frequencies and species abundances are equally, if not more, striking (Table SI1). The most frequent interaction was recorded 198 times, while the least frequent interaction occurred only once — a 198-fold difference. Similarly, the most abundant flower species was 5,191 times more abundant than the least abundant one. Though less extreme, the disparity among hummingbird species remains significant: the most abundant species was 113 times more numerous than the least abundant. These figures show the substantial loss of information when networks are presented without abundance data. However, when abundances are incorporated into the matrix, this information can be utilized in various ways — one such approach is described in the next section.

Linking species abundances to the connectance in pollination networks

The model is introduced using the same illustrative example matrix as in the previous section (Table 1A). It is built on the widely accepted premise that interaction frequency is a function of the abundances of the participating species (Blüthgen & Staab, 2024; Vázquez et al., 2009). In its simplest form, this relationship can be expressed as:

$$z = k * x * y,$$

where x and y represent the abundances of flower and pollinator species, respectively; z denotes the interaction frequency ("link strength"); and k is the constant of proportionality. This constant, termed "affinity," is adapted from biochemistry, where it describes the strength of the binding interaction between an enzyme and its substrate. Within this model, high k values indicate a high likelihood of interaction between a flower-pollinator pair, while low values suggest weaker interactions. Consequently, interaction frequencies will be high when the abundances of the interacting species and their k values are also high. The model enables the calculation of interaction affinities for each species pair, as all other variables are provided in the matrix (Table 1A). This is achieved using the equation:

$$k = z / (x * y),$$

which allows for the creation of a new matrix of affinities (Table 2). The k values are generally small but exhibit considerable variation.

Table 2. An affinity matrix resulted from the illustrative example (Table 1A) showing the interaction affinity values (k). Pollinator and floral abundances are highlighted in red font)

Species	Pollinators	Poll_1	Poll_2	Poll_3	Poll_4	Poll_5
Flowers	Abundances	160	80	40	20	10
Flor_1	1600	0	0.0005	0.0005	0	**0.002**
Flor_2	800	0.0010	0	0	0.001	0
Flor_3	400	**0.0047**	0	**0.004**	0	0
Flor_4	200	0	0.0006	0	0	0
Flor_5	100	**0.0080**	0	0	0	0

How can “high” and “low” affinities be distinguished? A reference value of k can be introduced:

$$k_{\mathrm{ref}} = \underline{Z}_{\mathrm{tot}} / (X_{\mathrm{tot}} * Y_{\mathrm{tot}}),$$

where $\underline{Z}_{\mathrm{tot}}$, X_{tot} and Y_{tot} are the totals of interaction occurrences, floral abundances, and pollinator abundances, respectively. This reference value corresponds to a hypothetical network where all flowers and pollinators are represented by a single species each. For the illustrative example, $k_{\mathrm{ref}} = 0.0011$. Naturally, some k values will exceed k_{ref}, while others will fall below it (values greater than k_{ref} are highlighted in bold in Table 2).

The reference constant k_{ref} can also serve as a network metric that is closely tied to connectance. Consider a network where connectance is varied, while k_{ref} remains constant. This would correspond to a redistribution of interactions, such that their total frequency of occurrence remains unchanged. A decrease in connectance would imply fewer species are interacting, but with increased interaction frequency, and *vice versa*. In essence, there exists a certain reciprocity between C (connectance) and k_{ref}. By using both indices, we gain insight not only into which species interact, but also into the strength (or frequency) of these interactions, as expressed by the interaction affinity values.

The reanalyzed matrix of the real network includes species abundance data (Table SI1), enabling the application of all previously described procedures to construct an affinity matrix with k_{ref} values for each flower-pollinator species pair. Naturally, if no interaction is observed for a species pair, the affinity is equal to 0. In total, non-zero interaction affinities were calculated for 123 species pairs. The reference value k_{ref} for this matrix was determined to be 0.0001. Of the 123 pairs, 19 showed interaction affinity values below this reference level, while the maximum affinity reached 0.1050 — more than 1,000 times higher than k_{ref}. The affinity matrix can be visualized as a corresponding 3D chart (Figure 1, next page), which reveals a trend: the highest affinities tend to occur at low species abundances. Conversely, at high abundances of both flower and pollinator species, interaction affinities are generally smaller.

This observed trend aligns with the findings of Simmons et al. (2019), who reported that hummingbird pollinators are generalized because they are abundant, but found little evidence that they are abundant because they are generalized. However, that study employed a null model assuming interaction neutrality, where interaction probabilities were defined solely by species relative abundances. Incorporating interaction affinity into this model would represent an intriguing future development.

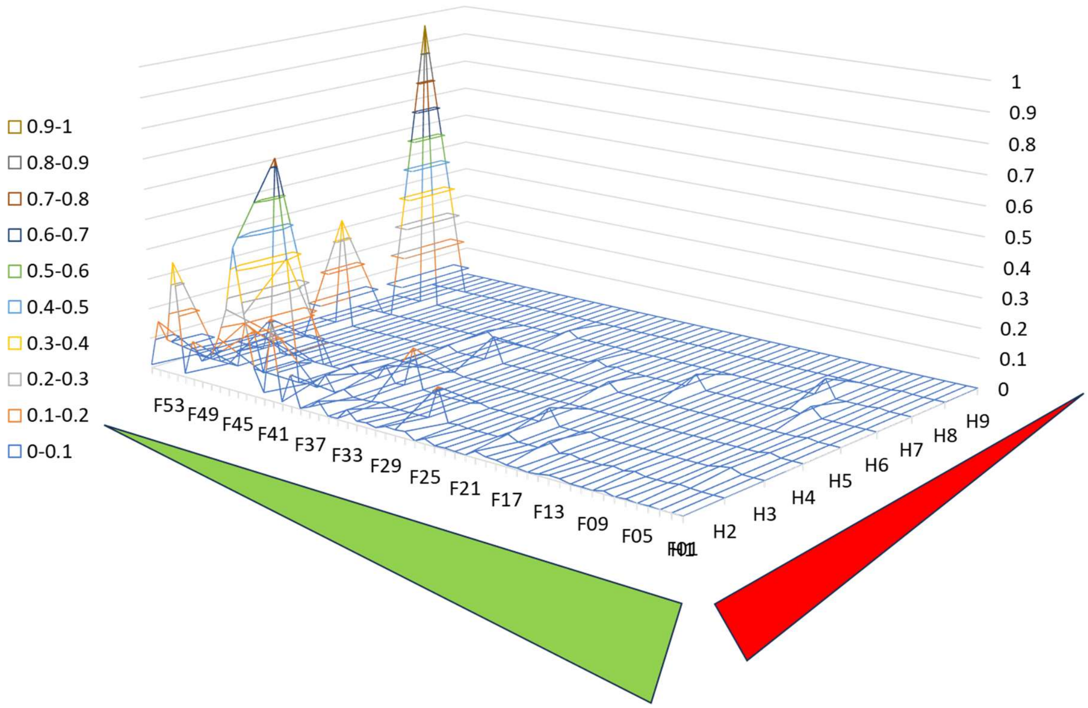

Figure 1. Affinities of pollinator-flower species pairs; The vertical axis shows standardized values of *k* (interaction affinities). The abundances are ranked in descending order, as indicated by the narrowing end of red (hummingbirds) and green (flowers) triangle arrows close to the horizontal axes. The affinities appear to be higher in the pairs made of less abundant "subordinate" species.

The concept of interaction affinity introduced here can also enhance studies on the asymmetry of interactions within pollination networks. For example, Vázquez et al. (2007) developed a null model in which species interactions occurred randomly among individuals. This model was used to test the hypothesis that the observed asymmetry arises from the unequal abundances of species. Their findings revealed that asymmetry correlated with abundance, with rare species contributing more to the asymmetry than abundant ones. They concluded that while abundance provides a sufficient explanation for the asymmetry structure in certain networks, additional factors likely play a role in others. One such "additional factor” could be the affinities between flowers and pollinators, which may have evolved through coevolution.

Discussion

The presented model may appear simplistic, but I hope to have demonstrated its significant analytical potential. Undoubtedly, the model is open to adjustments, improvements, and further refinement. Crucially, it can be applied to individual species, small subnetworks, or large networks, depending on the design of data collection. As long as the densities or relative abundances of the target species or taxonomic groups are reliably known, interaction affinities can be calculated.

In biochemistry and physiology, binding affinity refers to the strength of the interaction between a protein (enzyme, receptor) and its binding ligand (substrate, ion, transmitter, hormone, or other biologically active compound). Textbooks often describe this affinity as the “attraction” or “fit” between the two molecules, attributed to complementarity — precise matching of the protein's active site and the ligand's shape, charge, and hydrophobic or hydrophilic properties. Similarly, pollination networks can be understood through the lens of complementarity between pollinator and flower morphologies, as well as the ability of pollinators to locate and recognize desirable flowers. This process may involve complex behaviors and the use of memory (Kandori & Ohsaki, 1996). Incorporating such details can deepen our understanding of pollination networks.

In metabolism, the binding affinity between a protein and its ligand is considered crucial, as it determines how effectively metabolic reactions are catalyzed or regulatory processes are performed. Similarly, in pollination networks, interaction affinity can define the effectiveness of flower-pollinator interactions, providing novel insights into their functional mechanisms.

A high interaction affinity among organisms is likely the result of long evolutionary processes. Consequently, the model presented here has the potential to facilitate the incorporation of phylogenetic history into the study of pollination networks. Similarly, high interaction affinity may signal specialized relationships among a limited number of species, thereby helping to define the breadth of ecological niches (Junker et al., 2013). The concept of ecological niches has been considered underutilized in the analysis of pollination networks

(Phillips et al., 2020). Metrics derived from interaction affinity could promote the integration of this concept into the theoretical framework of pollination networks.

Altogether, linking species abundance with interaction frequency has the potential to transform our understanding of network properties. The proposed reference constant, used alongside connectance, shifts the perspective from binary categorizations of “permitted” and “forbidden” links to a continuum of probabilities for specific interactions. This approach situates interactions in a three-dimensional framework encompassing species abundances, their interaction frequencies, and the affinities between interacting species.

Understanding interaction affinity between specific flower and pollinator species can yield valuable insights. For instance, high interaction affinity may reflect a long coevolutionary history between particular species or groups, helping to introduce evolutionary perspectives and advance “phylogenetically informed network ecology” (*sensu* Peralta, 2016). Additionally, the model can explore whether a specialist species exhibits high interaction affinity with its target, whether a generalist species has moderate to low affinity across a broad range of interactions, or whether common pollinators become generalists as a result of their abundance (sensu Simmons et al., 2016).

Conclusions

The integration of species abundance data into pollination network analyses is achievable through the use of simple models, provided that all necessary data are available. The model presented here, despite its simplicity, effectively links species abundance distributions to the frequency of interactions. Moreover, it facilitates the calculation of interaction affinity for specific flower-pollinator pairs.

The independent and separate sampling of plants, pollinators, and their interactions requires close collaboration between botanists and zoologists. The additional effort necessary to achieve this coordination will undoubtedly be rewarded, as it opens new pathways for data analysis and ultimately deepens our understanding of the structure and functioning of pollination networks.

Author contributions

Not applicable, ZK is a single author

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Conflict of interest statement

No competing interests to declare.

Data availability statement

Not applicable, opinion paper.

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Supplementary Material

Table S1. A pollination network matrix from Brazilian Atlantic Forest including pollinator and floral abundances (highlighted in red font). The matrix is derived from data of Vizentin-Bugoni et al. (2016), downloadable from the website of IWB (Interaction Web DatBase, http://www.ecologia.ib.usp.br/iwdb/html/vizentin-bugoni_et_al_2016.html).

Species	Hummingbirds	Pe	Tg	Cr	Ff	La	Sl	Av	Lc	Em
Flowers	Abundances	86.923	78.462	66.923	21.538	20	13.077	8.462	5.385	0.769
Ery_spe	57102	107	137	95	0	0	0	1	5	1
Psy_lei	8704	0	2	0	0	0	0	1	0	0
Fuc_reg	5485	6	5	15	0	0	0	0	0	0
Ing_ses	2265	44	32	198	41	23	0	8	2	0
Spi_riv	1980	0	74	102	4	0	0	0	5	0
Nid_ino	1005	36	0	2	0	0	0	0	0	0
Lan_cam	600	1	0	0	0	0	26	0	0	0
Man_cor	591	50	0	0	0	0	0	0	0	0
Mac_rub	568	6	33	2	0	1	6	30	0	0
Nid_lon	446	11	0	0	0	0	0	0	0	0
Bes_lon	445	9	19	0	0	0	0	0	0	0
Nid_pro	378	31	0	0	0	0	0	0	0	0
Nem_flu	373	36	0	0	0	0	0	0	0	0
Vri_car	359	16	0	0	0	0	0	0	0	0
Nem_fri	339	4	18	0	0	0	0	0	0	0
Nem_gre	300	15	0	0	0	0	0	0	0	0
Can_pan	289	14	68	18	1	0	0	0	0	0
Als_ino	280	30	0	0	0	2	18	0	0	0
Sip_con	189	22	1	0	0	0	0	0	0	0
Sin_coo	179	35	0	0	0	0	0	0	0	0
Cal_ruf	162	1	22	60	0	0	0	0	0	0
Sip_lau	159	4	0	0	0	0	0	0	0	0
Sin_ela	158	7	0	0	0	9	0	0	0	0
Sin_gla	146	4	0	0	0	0	0	0	0	0
Aph_col	120	18	0	0	0	0	0	0	0	0
Til_str	114	1	3	1	0	0	1	0	0	0
Vri_inc	110	22	0	0	0	0	0	0	0	0
Aec_dis	106	18	95	6	0	0	2	0	0	0
Pyr_ven	91	17	1	0	0	1	0	0	0	0
Jus_sp2	67	5	0	0	0	0	0	0	0	0
Vri_inf	65	9	0	0	0	0	0	0	0	0
Jus_sp1	64	7	0	0	0	0	0	0	0	0
Cen_cor	62	23	0	0	0	0	0	0	0	0
Til_sp	60	2	4	1	0	0	0	0	0	0
Psi_dic	56	1	1	53	1	10	0	1	0	0
Nid_rut	52	20	0	1	0	0	0	0	0	0
Sip_lon	49	7	0	0	0	0	0	0	0	0

Table S1 continued

Species	Hummingbirds	Pe	Tg	Cr	Ff	La	Sl	Av	Lc	Em
Plants	Abundances	86.923	78.462	66.923	21.538	20	13.077	8.462	5.385	0.769
Aec_gam	41	1	6	15	0	0	0	0	0	0
Bil_amo	38	36	0	0	0	0	0	0	0	0
Til_gem	30	2	12	2	0	1	1	0	0	0
Can_per	29	65	0	0	0	0	0	0	0	0
Nem_ser	26	5	1	4	0	0	0	0	0	0
Vri_sp	24	20	0	0	0	0	0	0	0	0
Wit_sup	23	55	77	0	0	0	0	0	0	0
Aec_van	22	95	132	0	0	0	0	0	0	0
Edm_lin	22	53	26	0	0	0	0	0	0	0
Aph_lon	21	31	0	0	0	0	0	0	0	0
Aec_org	19	15	21	1	0	0	0	0	0	0
Aec_nud	19	12	24	0	0	0	0	0	0	0
Nem_mac	19	22	0	0	0	0	0	0	0	0
Men_sp	18	2	0	14	0	0	0	16	0	0
Mut_spe	18	62	0	0	0	14	0	0	0	0
Vri_ery	17	17	0	0	0	0	0	0	0	0
Vri_sim	16	24	0	0	0	0	0	0	0	0
Til_dur	11	1	0	0	0	0	0	0	0	0