**Title:**

# The affinity between flowers and their pollinators

**Author:**

Zaal Kikvidze

ORCID 0000-0002-5007-4484

**Affiliation**:

Institute of Botany, Ilia State University, Tbilisi, Georgia

**Corresponding author:**

Zaal Kikvidze, email: zaal.kikvidze@iliauni.edu.ge

## Abstract

It is a common knowledge that the probability of the fertilisation of a flower by its pollinator is a function of species abundances. However, this relation was rarely formalised for analysing pollination networks. In this opinion paper, a simple model borrowed from physical chemistry is introduced to formalise this functional dependence. This led to a well-known biochemical concept of affinity, which refers to the strength of the binding interaction of a protein to its ligand. This affinity is explained as the “attraction” or “fit” between the two molecules, and is attributed to complementarity or the precise matching of the protein's active site and the ligand's shape, charge, and hydrophobic or hydrophilic properties. Analogously, we can think of a complementarity between the pollinator and flower morphologies, the ability of a pollinator to locate the desirable flower, which might involve sophisticated behaviours and the use of memory. The protein-ligand affinity is considered to be crucial since it determines how effectively the metabolism functions. We can think in similar terms when analysing pollinator-flower interactions: affinity can define the effectiveness of a pollinating networks and give us new insights about its functional mechanisms.

**Keywords**: Abundance, Affinity, Interaction, Pollination network

## Introduction

Studies on pollination networks have seen rapid progress, particularly evident in the development of an array of quantitative tools of analysis based on graph and network theory (Dale 2017). These tools enabled to reveal several characteristics, the most salient of which are the low levels of connectance and the nested distribution of interactions, consistently repeating across various habitats and communities (Bascompte and Scheffer 2023; Lanuza et al. 2025). However, there are concerns that the achieved advances are not well connected with the key concepts of community ecology (Blüthgen and Staab 2024; Peralta et al. 2024). For example, the major structural characteristics of pollination networks, such as low connectance, nestedness, modularity and asymmetry, are being derived from the binary matrices which ignore the variability in the strength of interactions and abundances of both flower and pollinator species (Staniczenko et al. 2013). This is surprising since ignoring these variability can seriously deprive us from seeing clearly the place of ecological interactions in community processes (Blüthgen and Staab, 2024; Peralta et al. 2024). In fact, abundance distribution can have profound effects on species interaction networks, for example, it was shown that the resilience of a pollination network depends on the presence of abundant and highly linked species (Winfree et al. 2014). Since the probability that a pollinator visits a flower is a function of their abundances (Vázquez et al. 2009), one can assume that the reciprocal is true too: logically, frequent encounters require numerous individuals, and *vice versa*. Yet this is not be always the case and the models that attempt to extrapolate species abundances from the frequency of their interactions appeared to be inaccurate and little reliable (Vizentin-Bugoni et al. 2014, Gardner et al. 2020). The importance of having abundance distribution data has been recently recognised in the guidelines of the European Database of Plant-Pollinator Networks (EuPPollNet, Lanuza et al. 2025), which requires the contributors to provide flower counts. Regretfully, this approach is too "phytocentric" as it does not request abundance distribution data for pollinators.

The frequency of flower visits by pollinators depends not only on species abundances but also on other factors such as morphology (trait matching) and phenology (Peralta et al. 2024). Yet, while species abundance distribution types are remarkably consistent across ecosystems and communities (Ulrich et al. 2010), the other factors clearly depend on geographical, historical and phylogenetic contexts. Here I argue that we might expect important benefits from the inclusion of species abundance of both flowers and pollinators in the analyses of pollination networks. For this purpose, below I introduce a simple model of the dependence of interaction frequency on species abundance. The model is explained with the help of an illustrative example. Then the model is used to analyse a data set which does include species abundances of both pollinators and flowers collected independently from the data on the frequencies of their interactions (Vizentin-Bugoni et al. 2016).

## The data and their reanalyses

Before the reanalysis proper, I introduce the model that links species abundances with interaction frequencies using an illustrative matrix. It is smaller than the real one yet retains its essential properties (next section). After introducing the key ideas, I proceed with the reanalysis of the above real matrix.

The data set I reanalyse here is contributed by Vizentin-Bugoni et al. (2016), downloadable from the website of IWB (Interaction Web Data Base, see also Supplementary Material). The authors conducted an intensive sampling in the Atlantic Rainforest from in SE Brazil (23°S, 45°W) over 4–10 days per month for two years. Network or rather a subnetwork is represented by over 300 individuals of 9 hummingbird species and 83931 counted flowers of

55 plant species. Importantly, the distributions of both flowers and hummingbirds are known from independent sampling. 2793 interactions among 123 hummingbird-flower pairs were recorded. The data were organised in a network matrix (Table SI1 of Supplementary Information). The abundances in this matrix are standardised as densities (number of individuals per unit area). The new metrics (affinities) derived from the model were standardised by dividing by its maximum values and then presented graphically.

## An illustrative example

The illustrative example includes only five pollinator and five flower species, and shows the same general characteristics and real network matrices (Table 1A).

**Table 1**. Illustrative matrices of pollination network including pollinator and floral abundances (red font). A: raw data from the field; B: raw data in binary form; C: matrix of the same network with affinity values ($k_{ij}$).

**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 |

C

| 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 |

The matrix is “complete” in the sense that it is furnished with the abundance data both of pollinators and flowers (red font). The columns and rows represent the pollinators and the flower species, respectively. The frequency of interactions between pollinator-flower pairs are given in the cells. The empty cells show the absence of interactions. In the binary version of this matrix (Table 1B) empty cells are represented with 0-s and the links with 1, regardless of the frequency of interactions recorded). The metric usually calculated from the binary matrices is connectance. The modern software calculate connectance in a rather sophisticated way, but perhaps the simple original equation shows the idea of connectance equally well:

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

where $C$ is connectance, $L$ is the number of links (sum of cells with 1 in the matrix), $M$ and $N$ are the number of flower and pollinator species, respectively: $C$ is simply the proportion of possible links between species that are realised. For our illustrative example, $L = 9$, $M = 5$ and $N = 5$, consequently $C = 9 / (5 * 5) = 0.36$.

The binary matrix (Table 1B), however, does not show the differences in the frequencies of interactions, whilst from the previous matrix (Table 1A) we can see that the interaction was recorded 300 times for the pair of Poll_1 – Flor_3, the minimum detected interactions frequency being equal to 10 for the pair of Poll_2 – Flor_4: the difference is 30-fold! In binary form we loss this information, as all non-zero frequencies are equated to 1.

The great majority of real network matrices in open access data bases, unlike our illustrative example, lack species abundance data for pollinators and often for plants as well. We can only see what species are present in the network. But from the illustrative example we see that the difference between the most and least abundant species is 16, which is considerable. Thus, the matrices lacking abundance data deprive us opportunities to incorporate this variation in the analysis.

In the real network matrix, the differences in interaction frequencies and species abundances are comparable or even more impressive (Table SI1): the most frequent interaction was recorded 198 times, the least equalled to 1, which means 198-fold difference. Likewise, the most abundant flower exceeded the least abundant one 5191 times! The difference is less but still dramatic in hummingbirds: the most abundant species exceeded the least abundant one

113 times. This is the extent of information lost when presenting the network without abundance data. This information, if the abundances are given in a matrix can be used 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 below with the help of the same illustrative example matrix used in the previous section (Table 1C). The model is based on the common knowledge that the interaction frequency is a function of the abundances of participant species (Blüthgen and Staab, 2024; Vázquez et al. 2009). In the simplest form, this function can be presented as

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

where $x$ and $y$ are flower and pollinator species abundances, respectively; $z$ is the interaction frequency ("link strength"), and $k$ is the constant of proportionality. This constant can be understood as the "affinity" between the species of a given interacting flower-pollinator pair. The term "affinity" is borrowed from biochemistry where it refers to the strength of the binding interaction of an enzyme to its substrate. In our model, the high values of $k_{ij}$ mean high likelihood of interactions between a flower and its pollinator, and *vice versa*. The frequency of interactions thus will be high at high abundances of the interacting species and high values of their $k_{ij}$. The model allows for calculating the affinity for each pair of interacting species since all other variables are presented the matrix (Table 1A). Therefore:

$$k_{ij} = z_{ij} / (x_i * y_j),$$

which allows us to create a new matrix of affinities (Table 1C). We see that the $k_{ij}$ values are generally small but vary considerably.

How to distinguish "high" and "low" affinities? A reference value of $k_{ij}$ could be introduced:

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

where $\underline{Z}_{tot}$, $X_{tot}$ and $Y_{tot}$ are the totals of interaction occurrence, floral and pollinator abundances respectively. This value corresponds to a network where all flowers and all pollinators are represented by a single species each. For our illustrative example $k_{\mathrm{ref}} = 0.0011$. Naturally, some values of $k_{ij}$ are more and others are less than the obtained $k_{\mathrm{ref}}$ (those more than $k_{\mathrm{ref}}$ are in bold font, Table 1C).

The reference constant $k_{\mathrm{ref}}$ can be used as a metric of a network related to the connectance. Imagine a network and let us vary its connectance but keep $k_{\mathrm{ref}}$ on the same level. This is translated into the redistribution of interactions while their total frequency of occurrence remains the same; if the connectance level lowers, this would mean less species interacting but with increased frequency and *vice versa*. In a word, there is a sort of reciprocal complementarity between $C$ and $k_{\mathrm{ref}}$, and if we use both of these indices, we will know not only the species which interact, but also how strong (frequent) these interactions are as expressed by the affinity values.

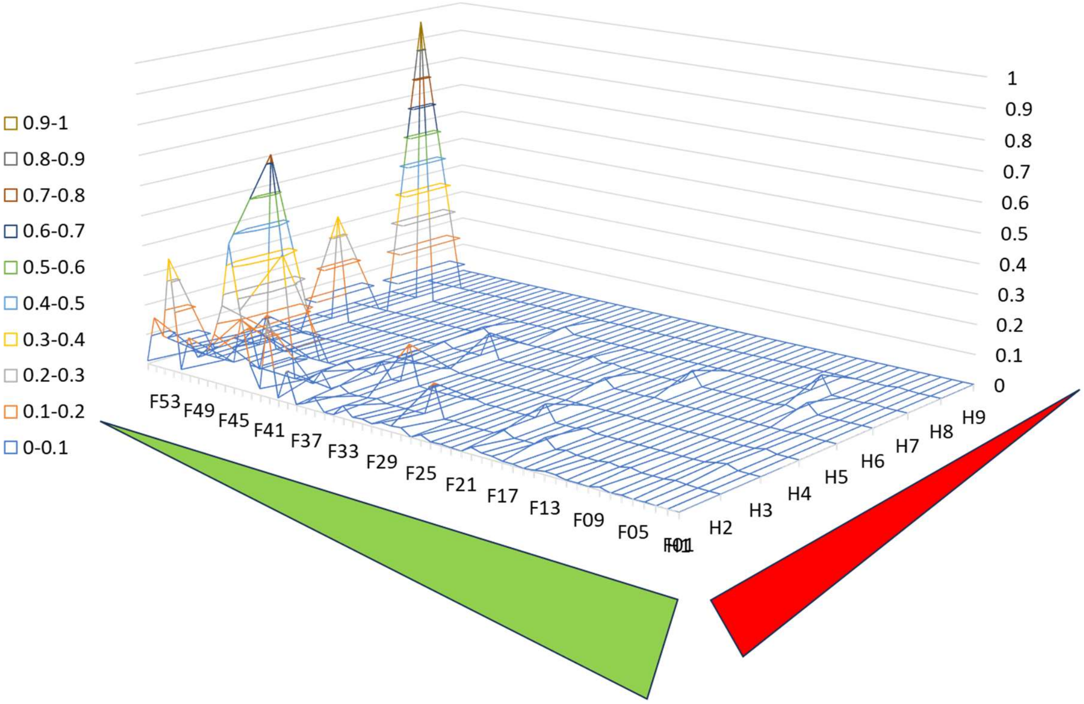

**Figure 1**. Affinities of pollinator-flower species pairs; The vertical axis shows standardised values of $k_{ij}$. The abundances are ranked in descending order, as indicated by the narrowing end of red (hummingbirds) and green (flowers) triangle arrows. The affinities are higher in the pairs made of less abundant “subordinate” species.

## The real network

The reanalysed matrix of the real network is furnished with species abundance data (Table SI1) and thus allows for performing all the above procedures to construct an affinity matrix with $k_{ij}$ values for each flower-pollinator pair of species. Naturally, if no interaction is detected for a species pair, the affinity becomes equal to 0. Altogether, non-zero affinities were calculated for 123 species pairs. Then we calculated the value of $k_{ref}$ for this matrix, which appeared to be equal to 0.0001. Nineteen out of 123 pairs showed affinity values below this reference level, while the maximum affinity was as high as 0.1050, which is over 1000 times higher than the values of $k_{ref}$. The affinity matrix can be shown as a corresponding 3D chart (Figure 1, the previous page), which reveals a trend that the highest affinities occur mostly at low species abundances. In other words, at high abundance of flower and pollinator species the affinity tends to be small, while at low affinities it tends to be large.

The observed trend is in line with findings of Simmons et al. (2019) that hummingbird pollinators are generalised because they are abundant, but there was little evidence that hummingbirds are abundant because they are generalised. However, this study used a null model that assumed interaction neutrality (interaction probabilities defined by species relative abundances). Adding affinity to this model would be an interesting development.

The concept of affinity introduced above can also complement to the studies on the asymmetry of interactions in pollination networks. For example, Vázquez et al. (2007) constructed a null model with species interactions occurring at random among individuals; This model was used to test the hypothesis that the observed asymmetry is a result of the unequal abundances of species. They found that asymmetry correlated with abundance, and that rare species contributed more to the asymmetry than the abundant ones. They concluded that abundance provides a sufficient explanation of the asymmetry structure in some networks, but suggests the role of additional factors in others – this “additional factor” can be the affinities between flowers and pollinators developed through coevolution.

## Discussion

The presented model might be seen as a simplistic one, but I hope I have shown its potential analytical power. Certainly, the model is certainly open for adjustments, improvements and further sophistication. Importantly, the model can be used for individual species, small subnetworks or large networks depending on the design of data collection: as long as the densities or relative abundances of target species or taxonomic groups are reliably known, the affinities can be calculated. In biochemistry and physiology, affinity refers to the strength of the interaction between a protein (enzyme, receptor) and its binding ligand (substrate, ion, transmitter, hormone, biologically active compound). In textbooks it is often explained as the “attraction” or “fit” between the two molecules, and is attributed to complementarity or the precise matching of the protein's active site and the ligand's shape, charge, and hydrophobic or hydrophilic properties. Analogously, we can think of a complementarity between the pollinator and flower morphologies, the ability of a pollinator to locate the desirable flower, which might involve sophisticated behaviours and the use of memory (Kandori and Ohsaki 1996). The introduction of these details can enhance our understanding of pollinations networks. In metabolism, the protein-ligand affinity is considered to be crucial since it determines how effectively the metabolic reaction is catalysed or a regulatory act performed. We can think in similar terms when analysing pollinator-flower interactions: affinity can define the effectiveness of a pollinating interactions.

A high affinity both between molecules and organisms must be a result of long evolutionary processes, and therefore the model presented above can facilitate an introduction of phylogenetic history in pollination networks. By the same token, high affinity can be indicative of specialised interactions among a few species and by this define the breadth of ecological niche (Junker et al. 2013). The niche concept has been thought to be underutilised in the analyses of pollination networks (Phillips et al. 2020). A new metrics based on affinity might facilitate the integration of the concept in the theory of pollination networks. Altogether, linking species abundance with interaction frequency has a potential to change the angle we see the network properties. The suggested reference constant can be used jointly with the connectance, and see it not as a binary distribution of “permitted” and “forbidden” links in a network. Rather, we can talk about the continuum of the probabilities of concrete interactions to occur in a three-dimensional continuum of species abundance, their interaction frequencies and affinities of interacting species.

Knowing the affinity between concrete flower and pollinator species can be insightful in important instants. For example, a high affinity can be indicative of a long coevolution history of given species or groups, and thus help to introduce evolutionary history and contribute to “phylogenetically informed network ecology *sensu* Peralta (2016). The presented model can also help examine whether the affinity of a specialist species is high towards its target, or whether a generalist species shows a moderate to low affinity to a wide range of interacting species, or whether common pollinators become generalists because of their abundance (*sensu* Simmons et al. 2016).

## Conclusions

An introduction of species abundance data in pollination network analyses is possible with simple models, provided all necessary data are given. The model introduced here, despite its simplicity, can effectively connect species abundance distribution with the frequency of interactions. At the same time, it helps calculate an affinity of a given flower to its pollinator.

Sampling separately and independently for plants, pollinators and their interactions certainly necessitates a coordinated cooperation among botanists and zoologists. The increased efforts to achieve this will pay off with the opening of new avenues for data analyses and ultimately the better understanding of pollination network structure and functions.

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