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### Comissão Julgadora:

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Dr(a).

Dr(a).

Dr(a).

Orientador

## DEDICATÓRIA

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*Para minha mãe Mirna,  
e minha vó Nadyr*

## EPÍGRAFE

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Um ecossistema se trata de um sistema. Um sistema! Um sistema mantém certa estabilidade fluída que pode ser destruída por um deslize em apenas um nicho. Um sistema tem ordem, uma correnteza que flui de um ponto a outro. Se algo represar a correnteza, a ordem desmoronará. Os inexperientes talvez só percebam esse desmoronamento quando já for tarde demais. É por isso que a função mais elevada da ecologia é a compreensão das consequências.

Pardot Kynes, o primeiro planetólogo de Arrakis  
(Frank Herbert. **Duna**. São Paulo: Aleph, 2017)

## AGRADECIMENTOS

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Agradeço a

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# Do we split or we merge? Exploitative interactions increase trait disparity and modularity through coevolution in mutualistic networks

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## Resumo

Coevolução, a mudança evolutiva recíproca entre espécies interagentes, é um processo fundamental que influencia a evolução fenotípica de múltiplas espécies. Em comunidades, interações entre indivíduos de espécies diferentes formam redes de interações. Devido a estrutura dessas redes, os efeitos evolutivos podem se propagar diferentemente entre espécies, podendo levar a novas dinâmicas evolutivas. Estas novas dinâmica evolutivas podem ser influenciadas por interações que apresentam consequências distintas para a aptidão dos indivíduos interagentes. Por exemplo, em mutualismos no qual a interação aumenta a aptidão dos indivíduos, emergem redes que podem favorecer a evolução de modos de vida exploradores de indivíduos mutualistas, reduzindo a aptidão dos indivíduos interagentes. Aqui, exploramos como diferentes frequências de exploração e seus diferentes padrões de interação influenciam a dinâmica coevolutiva em redes mutualísticas. Combinamos um modelo coevolutivo para redes ecológicas, dados sobre redes empíricas de mutualismos e simulações numéricas para sugerir que a presença de exploração aumenta a disparidade de traços entre espécies. Essa disparidade é caracterizada por grupos de espécies fenotipicamente similares entre si mas distintas de outros grupos de espécies. Porém, considerando espécies exploradoras aquelas que possuem o maior número de interações, a disparidade de traços é variável ou ausente entre diferentes redes de mutualismos. Finalmente, a evolução de traços impulsionada pelas interações de exploração altera a organização das interações em redes simuladas. Dado que mutualismos podem ser explorados por determinadas formas de vida, nossos resultados mostram como interações de exploração podem mudar a estrutura e a diversidade de traços em redes de mutualismos.

**Palavras-chave:** Coevolução, Interações ecológicas, Exploração de mutualismos, Teoria de redes, Disparidade de traços, Pilhadores.

## Abstract

Coevolution, the reciprocal change mediated by ecological interactions, is a major process affecting the phenotypic evolution of multiple species. In ecological communities, ecological interactions often form networks of interacting species. In these networks, evolutionary changes may cascade across the network, leading to novel evolutive dynamics. This novel dynamics could be driven by interactions with distinct fitness consequences for the individuals. For example, mutualisms, in which interactions increase the fitness of interacting individuals, assemble networks that allow the evolution of exploitative lifestyles, imposing a fitness decrease to the interacting individuals. Here, we explore how exploitation interactions affects the outcome of the coevolutionary dynamics in mutualistic networks. We combined a coevolutionary model to ecological networks, empirical mutualistic networks and numerical simulations to suggest that exploitation increases trait disparity between species. Trait disparity is characterized as species groups phenotypically similar between each other but distinct between other species groups. However, considering exploiter species those who maintain the majority of interactions, trait disparity becomes variable between different mutualistic networks. Finally, trait evolution fueled by exploitation interactions change how interactions are organized in the simulated networks. Because exploitation is one possible outcome for mutualisms in natural communities, we showed how exploitation interactions could feedback, reshaping the structure and trait diversity of mutualistic networks.

**Keywords:** Coevolution, Ecological interactions, Mutualism exploitation, Network Theory, Trait disparity, Larceny.

# Introduction

bla bla

## Material and Methods

### The model and the networks

(ABRAMS, 1987)

$$S_m = \sum_j^N m_{ij}^{(t)} (Z_j^{(t)} - Z_i^{(t)}) \quad (1)$$

$$S_a = \sum_j^N v_{ij}^{(t)} (Z_j^{(t)} \pm \epsilon_{ij} - Z_i^{(t)}) \quad (2)$$

$$S_e = (\theta_i - Z_i^{(t)}) \quad (3)$$

$$Z_i^{(t+1)} = Z_i^{(t)} + \varphi_i \{ (1 - \gamma_i) [S_m + S_a] + \gamma_i S_e \} \quad (4)$$

$$Z_i^{(t+1)} = Z_i^{(t)} + \varphi_i \{ (1 - \gamma_i) [\sum_j^N m_{ij}^{(t)} (Z_j^{(t)} - Z_i^{(t)}) + \sum_j^N v_{ij}^{(t)} (Z_j^{(t)} \pm \epsilon_{ij} - Z_i^{(t)})] + \gamma_i (\theta_i - Z_i^{(t)}) \} \quad (5)$$

$$q_{ij} = a_{ij} \frac{e^{-\alpha(Z_j^{(t)} - Z_i^{(t)})^2}}{\sum_{k,i \neq k} e^{-\alpha(Z_k^{(t)} - Z_i^{(t)})^2}} \quad (6)$$

$$MPD = \frac{\sum_i^N \sum_{j \neq i}^N \sqrt{(Z_j^{(t)} - Z_i^{(t)})^2}}{N(N-1)} \quad (7)$$

$$C_i = \frac{k_i}{N_0} \quad (8)$$

$$s_i = \frac{C_i - \bar{C}}{\sigma} \quad (9)$$

$$f(Ch) = \frac{n_{(-+)}}{n_{(-+)} + n_{(++)}} \quad (10)$$

$$\begin{cases} \left| Z_j^{(t)} - Z_i^{(t)} \right| > b \implies a_{ij} = 0 \\ \left| Z_j^{(t)} - Z_i^{(t)} \right| \leq b \implies a_{ij} = 1 \end{cases} \quad (11)$$

$$\Delta NODF = NODF_{final} - NODF_{initial} \quad (12)$$

$$\Delta Q = Q_{final} - Q_{initial} \quad (13)$$

## Results

bla

## Discussion

bla bla

## Figures and tables

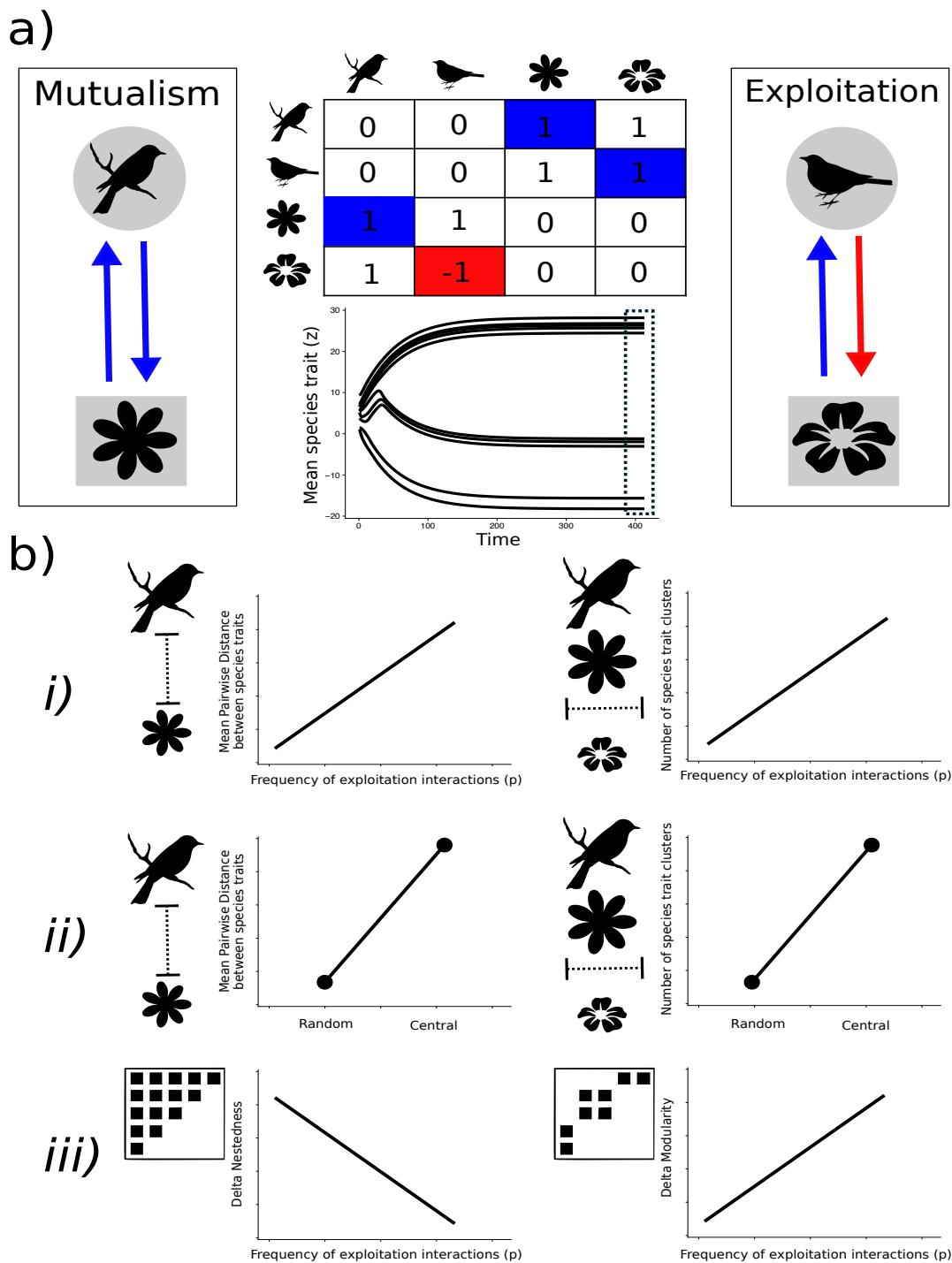


Figure 1: ...

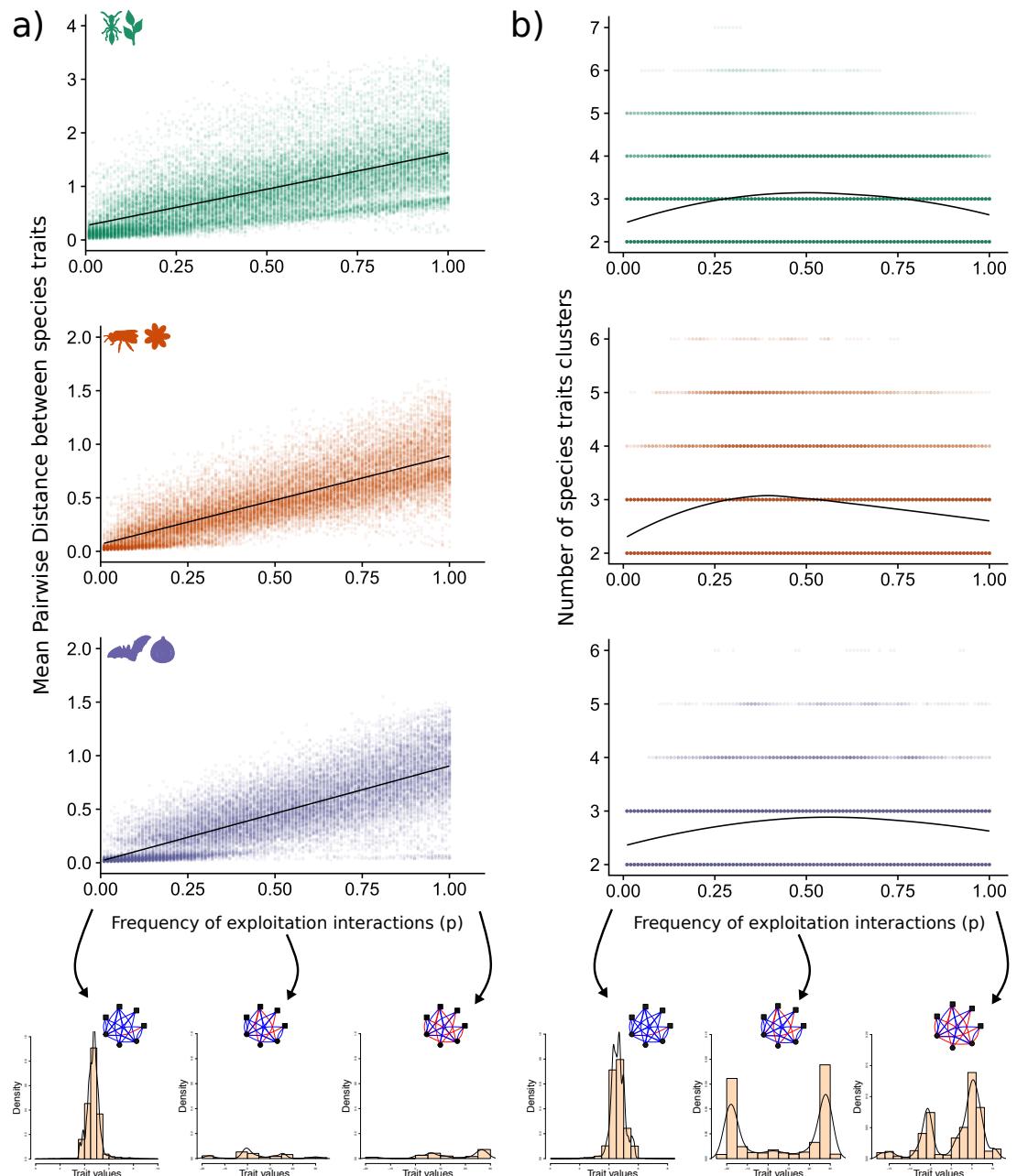


Figure 2: ...

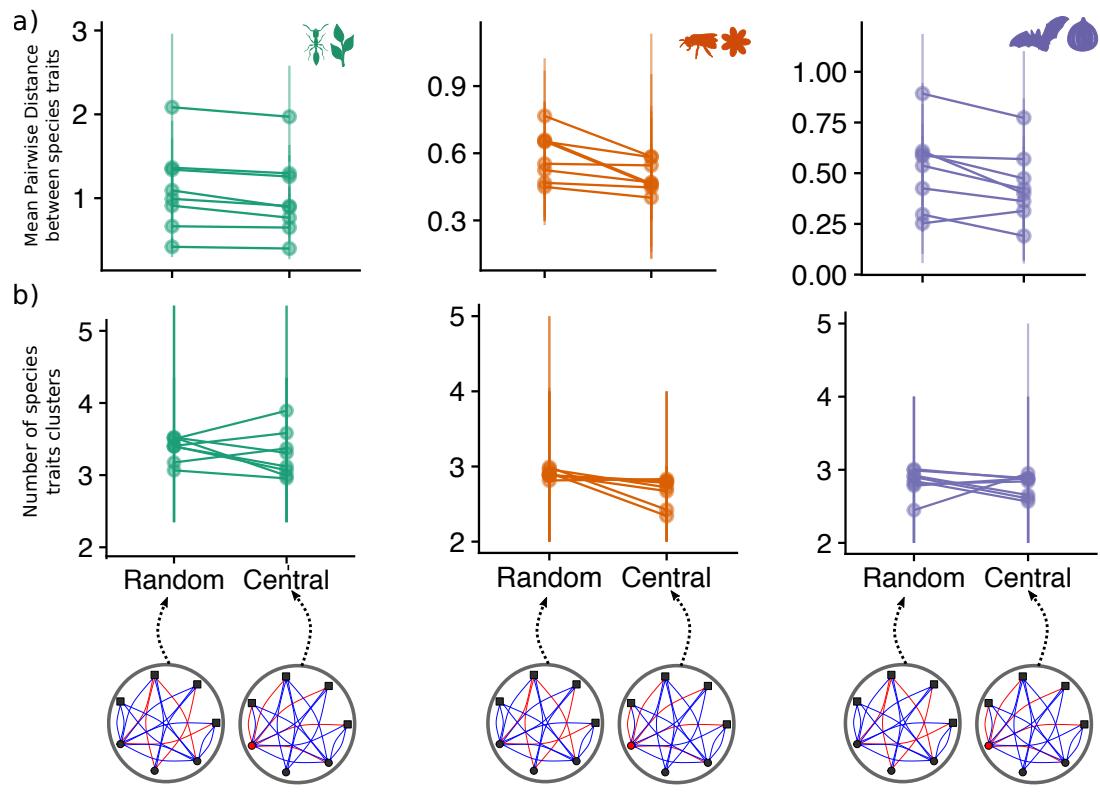


Figure 3: ...

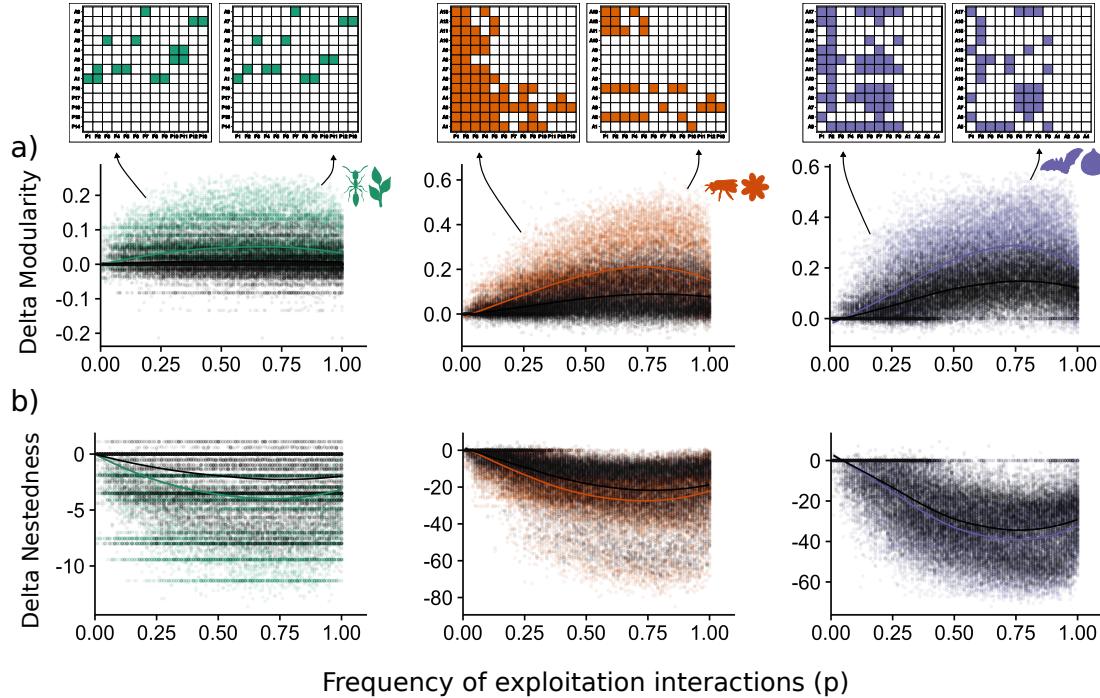


Figure 4: ....

Table 1: Variables and parameters of the model with descriptions and the sample or estimation method.

| Parameter          | Description  | How it was sampled       |
|--------------------|--|--------------------------|
| $Z_i$              | Initial mean trait value $Z$ of species $i$  | $Z_i \sim U(0, 10)$      |
| $\varphi_i$        | Parameter composed of the additive genetic variance and phenotypic variance of $Z$       | Usually fixed as 0.2     |
| $\varepsilon_{ij}$ | Trait barrier to happen the exploitation interaction between species $i$ and $j$         | Usually fixed as 5       |
| $\gamma_i$         | Strength of abiotic selection for trait change of species $i$                            | Usually fixed as 0.1     |
| $\theta_i$         | $Z_i$ optimum value for the environmental selection                                      | $\theta_i \sim U(0, 10)$ |
| $\alpha$           | Sensibility of evolutionary effect due to the trait matching between interacting species | Usually fixed as 0.2     |
| $p$                | Probability of an positive effect become negative in a mutualistic network               | $0.01 \leq p \leq 1$     |
| $b$                | Trait barrier for any interaction happen between species in the network                  | Usually fixed as 7       |

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ABRAMS, P. A. On Classifying Interactions between Populations. *Oecologia*, v. 73, n. 2, p. 272–281, 1987. ISSN 0029-8549.

## SUPPLEMENTAL INFORMATIONS

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### Coevolution model

(GUIMARÃES JR *et al.*, 2017)

$$\Delta z^{(t)} = h^2 \sigma^2 \frac{\partial \ln \bar{W}}{\partial z^{(t)}} \quad (\text{S.1})$$

$$z_{i,p+} = \sum_{j,j \neq i}^N (1 - \gamma_i) (x_{ij}^{(t)} m_{ij}^{(t)}) + \gamma_i \theta_i \quad (\text{S.2})$$

$$z_{i,p-} = \sum_{j,j \neq i}^N (1 - \gamma_i) [(x_{ij}^{(t)} \pm \epsilon_{ij}) (v_{ij}^{(t)} \delta_{ij})] + \gamma_i \theta_i \quad (\text{S.3})$$

$$\left| x_{ij}^{(t)} \pm \epsilon_{ij} - z_i \right| < \left| x_{ij}^t - z_i \right| \implies \delta_{ij} = 0 \quad (\text{S.4})$$

$$\begin{cases} \left| x_{ij}^{(t)} \right| > z_i \implies \delta_{ij} = 1 \implies x_{ij}^{(t)} + \epsilon_{ij} \\ \left| x_{ij}^{(t)} \right| < z_i \implies \delta_{ij} = 1 \implies x_{ij}^{(t)} - \epsilon_{ij} \end{cases} \quad (\text{S.5})$$

$$Z_i^{(t+1)} = Z_i^{(t)} + \varphi_i \{ (1 - \gamma_i) [\sum_j m_{ij}^{(t)} (Z_j^{(t)} - Z_i^{(t)}) + \sum_j v_{ij}^{(t)} (Z_j^{(t)} \pm \epsilon_{ij} - Z_i^{(t)})] + \gamma_i (\theta_i - Z_i^{(t)}) \} \quad (5)$$

$$q_{ij} = a_{ij} \frac{e^{-\alpha(Z_j^{(t)} - Z_i^{(t)})^2}}{\sum_{k,k \neq i} e^{-\alpha(Z_k^{(t)} - Z_i^{(t)})^2}} \quad (\text{S.6})$$

### Networks characterization

$$L = \frac{\sum_i^{N_A} \sum_{j \neq i}^{N_P} a_{ij}}{N_A N_P} \quad (\text{S.7})$$

$$Q = \frac{1}{2m} \sum_{ij} (A_{ij} - \frac{k_i k_j}{2m}) \delta(c_i, c_j) \quad (\text{S.8})$$

$$NODF = \frac{\sum N_{paired}}{\left(\frac{N_A(N_A-1)}{2}\right) + \left(\frac{N_P(N_P-1)}{2}\right)} \quad (\text{S.9})$$

Table S1: 24 Empirical networks used to parametrize our numerical simulations. We have eight networks for each type of mutualism (Pollination, Seed Dispersal and Ant-Plant) varying in species richness ( $N$ ), connectance ( $L$ ), modularity ( $Q$ ) and nestedness ( $NODF$ )

| Net | Type           | N  | L    | Q    | NODF  | Location         | Reference                            |
|-----|----------------|----|------|------|-------|------------------|--------------------------------------|
| 1   | Pollination    | 26 | 0.42 | 0.17 | 84.93 | Brazil           | Bezerra, Machado, and Mello (2009)   |
| 2   | Pollination    | 30 | 0.23 | 0.36 | 42.72 | Canadá           | Mosquin and Martin (1967)            |
| 3   | Pollination    | 27 | 0.28 | 0.28 | 51.87 | Mauritius        | Olesen (2012)                        |
| 4   | Pollination    | 22 | 0.25 | 0.43 | 35.96 | Portugal         | Olesen (2012)                        |
| 5   | Pollination    | 39 | 0.14 | 0.53 | 29.53 | Argentina        | Valiente-Banuet <i>et al.</i> (2015) |
| 6   | Pollination    | 42 | 0.15 | 0.60 | 18.65 | Argentina        | Valiente-Banuet <i>et al.</i> (2015) |
| 7   | Pollination    | 39 | 0.14 | 0.56 | 26.31 | Argentina        | Valiente-Banuet <i>et al.</i> (2015) |
| 8   | Pollination    | 34 | 0.17 | 0.54 | 23.27 | Argentina        | Valiente-Banuet <i>et al.</i> (2015) |
| 9   | Seed dispersal | 28 | 0.34 | 0.28 | 50.98 | USA              | Baird (1980)                         |
| 10  | Seed dispersal | 40 | 0.42 | 0.20 | 67.66 | Papua New Guinea | (BEEHLER, 1983)                      |
| 11  | Seed dispersal | 36 | 0.16 | 0.42 | 34.16 | Puerto Rico      | Carlo, Collazo, and Groom (2003)     |
| 12  | Seed dispersal | 33 | 0.44 | 0.22 | 78.75 | Spain            | Jordano (1985)                       |
| 13  | Seed dispersal | 32 | 0.63 | 0.15 | 67.34 | México           | Kantak (1979)                        |
| 14  | Seed dispersal | 23 | 0.43 | 0.32 | 48.29 | Panamá           | Poulin <i>et al.</i> (1999)          |
| 15  | Seed dispersal | 24 | 0.37 | 0.22 | 73.89 | Panamá           | Poulin <i>et al.</i> (1999)          |
| 16  | Seed dispersal | 26 | 0.27 | 0.30 | 42.70 | United Kingdom   | (SORENSEN, 1981)                     |
| 17  | Ant-Plant      | 11 | 0.23 | 0.69 | 8     | Brazil           | Thiago Izzo, unpublished data        |
| 18  | Ant-Plant      | 16 | 0.17 | 0.77 | 7.01  | Brazil           | Thiago Izzo, unpublished data        |
| 19  | Ant-Plant      | 21 | 0.16 | 0.68 | 11.32 | Brazil           | Thiago Izzo, unpublished data        |
| 20  | Ant-Plant      | 15 | 0.16 | 0.79 | 0     | Brazil           | Thiago Izzo, unpublished data        |
| 21  | Ant-Plant      | 21 | 0.14 | 0.78 | 4.90  | Brazil           | Thiago Izzo, unpublished data        |
| 22  | Ant-Plant      | 18 | 0.15 | 0.77 | 4.10  | Peru             | Thiago Izzo, unpublished data        |
| 23  | Ant-Plant      | 26 | 0.13 | 0.77 | 3.49  | Brazil           | DAVIDSON (1991)                      |
| 24  | Ant-Plant      | 41 | 0.12 | 0.64 | 13.63 | Brazil           | Fonseca and Ganade (1996)            |

## Interaction shifts

sadasjkcs

## Trait clustering analysis

sadjndfdsj

## Figures and tables

|  | 0 | 1  | 1 | 1 |
|--|---|----|---|---|
|  | 1 | 0  | 1 | 1 |
|  | 1 | 1  | 0 | 1 |
|  | 1 | -1 | 1 | 0 |

### Positive effects

$$z_{i,p+} = \sum_{j,j \neq i}^N (1 - \gamma_i) \left( x_{ij}^{(t)} m_{ij}^{(t)} \right) + \gamma_i \theta_i$$

### Negative effects

$$z_{i,p-} = \sum_{j,j \neq i}^N (1 - \gamma_i) \left[ \left( x_{ij}^{(t)} \pm \varepsilon_{ij} \right) \left( v_{ij}^{(t)} \delta_{ij} \right) \right] + \gamma_i \theta_i$$

Figure S1: Each effect between interacting species (+ or -) in a community represented by an adjacency matrix of interactions are described by an adaptive peak. Each peak is influenced by the environmental factors of importance  $\gamma_i$  favouring a trait value called  $\theta_i$  and the ecological interactions which the positive effects favoured the species trait matching and the negative effect the trait decoupling due to the  $\varepsilon_{ij}$ . Finally, the sum of all the effects (positive and negatives) for a single species defines the final adaptive peak equations for that species

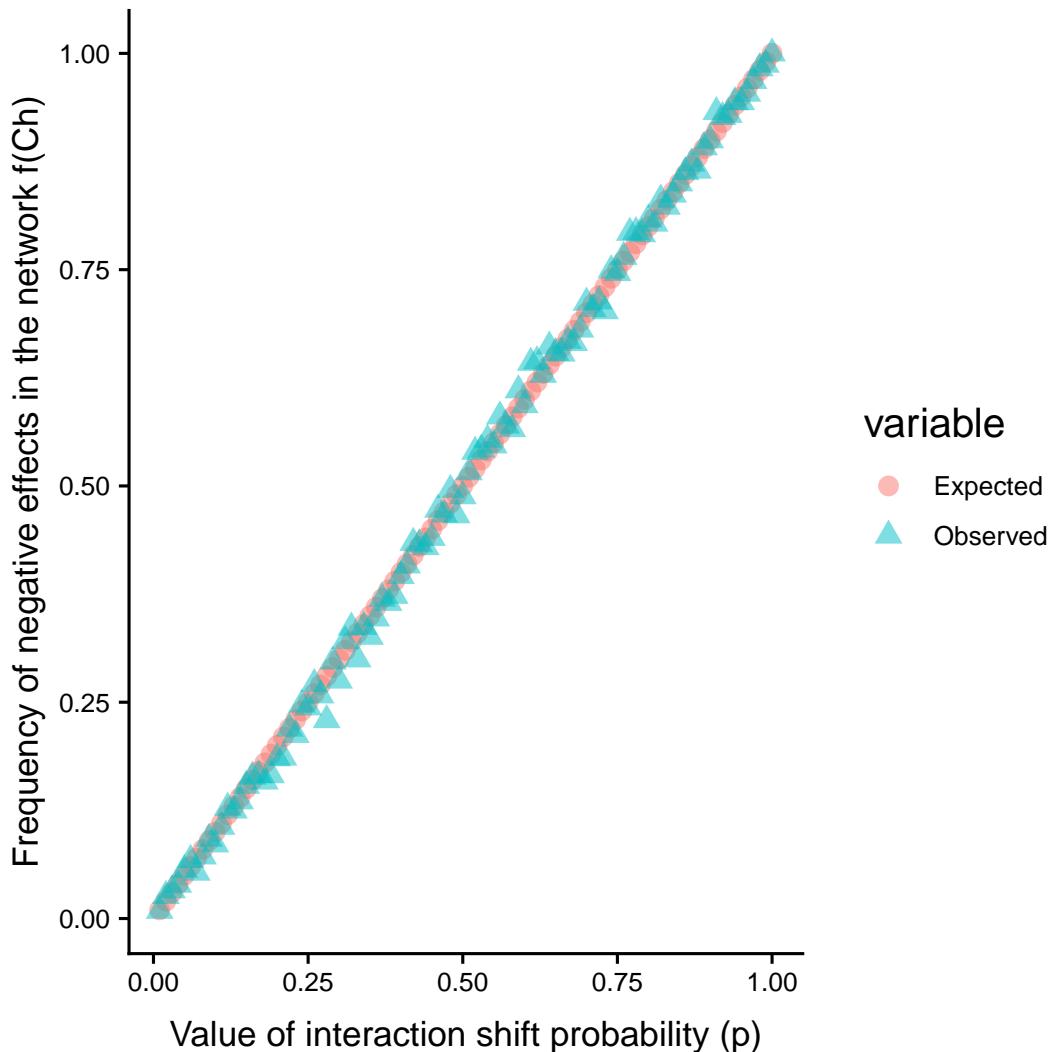


Figure S2: Consistency test of expected frequency of exploitation interactions in a fully connected bipartite network with 50 species. For  $p$  ranging from 0.01 to 1, we plot the expected and observed value of frequency of negative effects in the network. The expected frequency it's simply the value of  $p$  used and the observed values are the frequency of interactions in the  $V$  matrix. The value of  $p$  used is a good proxy for the frequency of exploitation interactions in networks

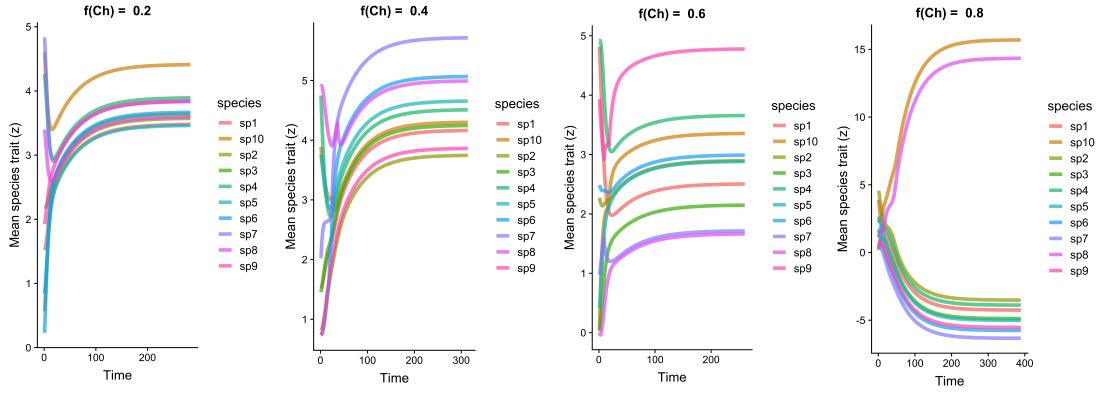


Figure S3: Four theoretical examples of coevolutionary dynamics showing  $Z$ , the mean trait values of 10 species described by our main model in a theoretical fully connected bipartite adjacency matrix with different values of frequency of exploitation interactions  $f(Ch)$  inserted in a mutualistic network. Each graph is a single simulation where we show the increase in trait disparity and the gradual formation of species traits aggregation as we insert a higher quantity of negative effects in a mutualistic network, drawing attention to the Y axis scale in the  $f(Ch) = 0.8$  graph.

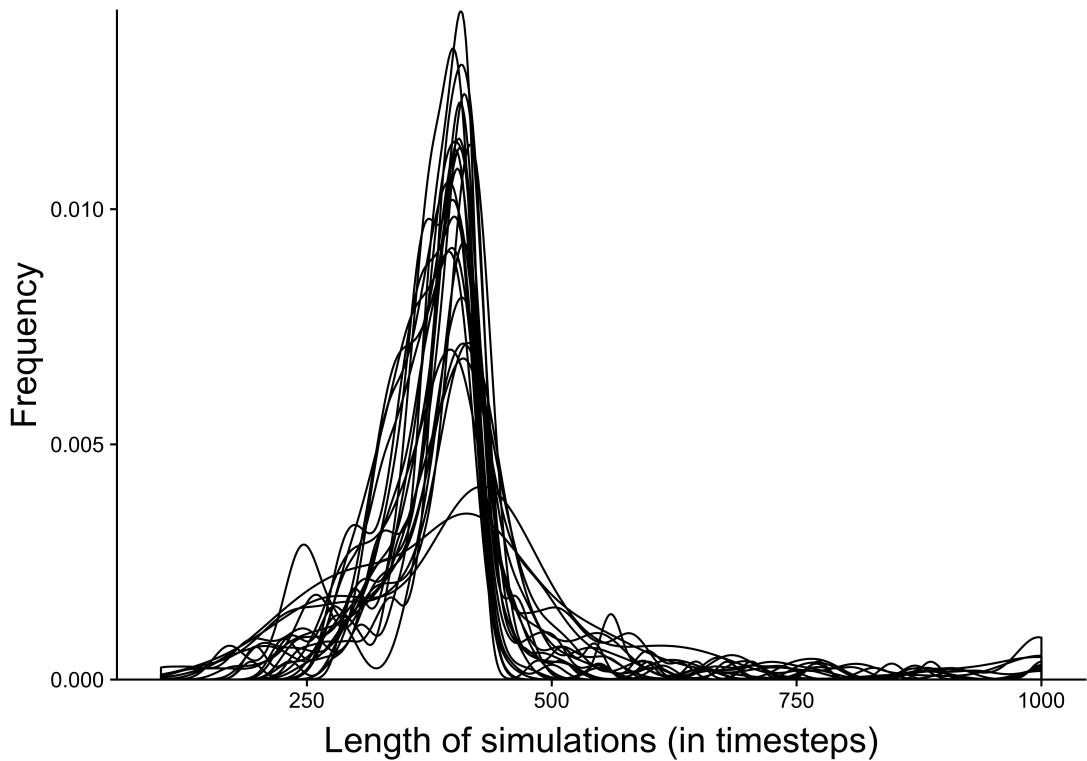


Figure S4: Four theoretical examples of coevolutionary dynamics showing  $Z$ , the mean trait values of 10 species described by our main model in a theoretical fully connected bipartite adjacency matrix with different values of frequency of exploitation interactions  $f(Ch)$  inserted in a mutualistic network. Each graph is a single simulation where we show the increase in trait disparity and the gradual formation of species traits aggregation as we insert a higher quantity of negative effects in a mutualistic network, drawing attention to the Y axis scale in the  $f(Ch) = 0.8$  graph.

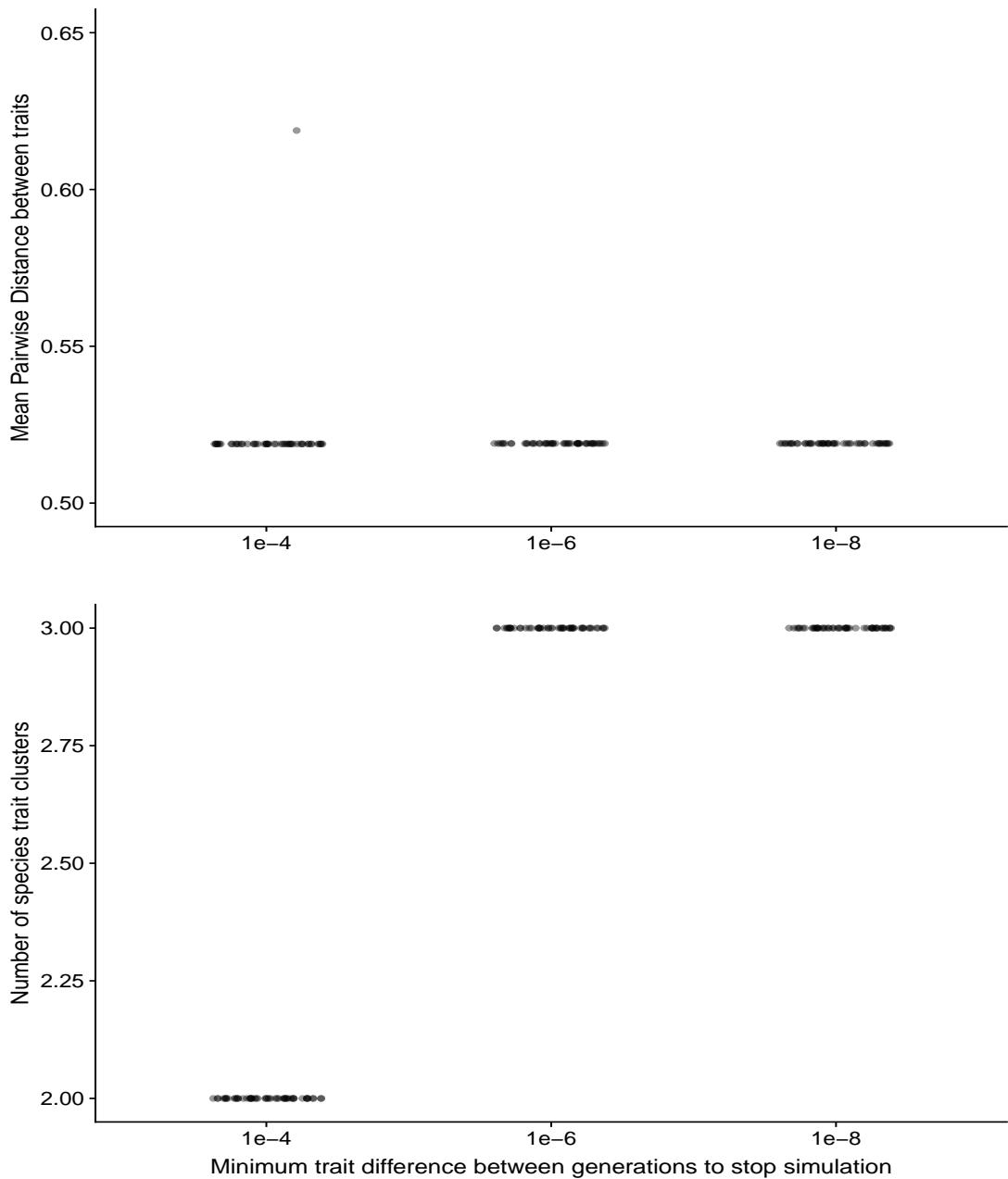


Figure S5: Sensibility analysis showing our metrics with different equilibrium conditions to our simulations. Each point in the graph shows the Mean pairwise distance and clustering of species traits in three different trait equilibrium values:  $10^{-4}$ ,  $10^{-6}$  e  $10^{-8}$ . We have 50 simulations for each scenario totaling 150 simulations.

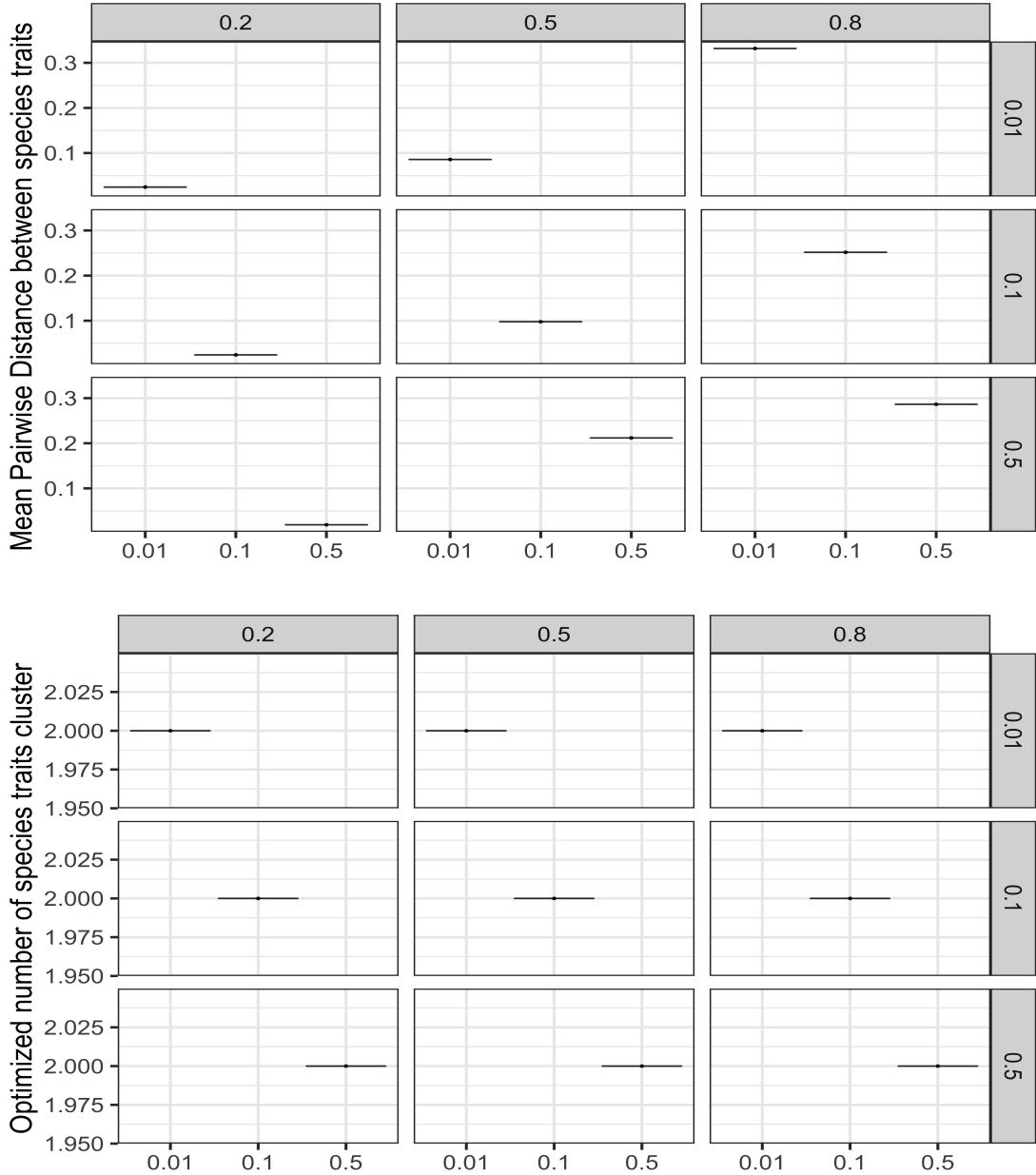


Figure S6: Four theoretical examples of coevolutionary dynamics showing  $Z$ , the mean trait values of 10 species described by our main model in a theoretical fully connected bipartite adjacency matrix with different values of frequency of exploitation interactions  $f(Ch)$  inserted in a mutualistic network. Each graph is a single simulation where we show the increase in trait disparity and the gradual formation of species traits aggregation as we insert a higher quantity of negative effects in a mutualistic network, drawing attention to the Y axis scale in the  $f(Ch) = 0.8$  graph.

## Code and data accessibility

All the functions, scripts, results and figures used in the paper are available online in the GitHub platform in the *coevo mut antag* repository. Additional to

the code, you will find small guides and tutorials where we shown the basic process of simulation and how the main figures was generated. Also, we provide a link to the database's where all the empirical networks could be find and downloaded.

- GitHub repository
- Web of Life website
- Interaction Web Data Base

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