

Modularity, Nestedness, and Resilience in an Urban Ecological Interaction Network

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Abstract

A biotic interaction network of Bogotá was analyzed using centrality and architectural metrics to compare the roles of indigenous and non-indigenous species and to evaluate the network's resilience to node removal. Nestedness (NODF) and modularity (greedy Newman algorithm) were computed across mutualistic and parasitic inter-kingdom subnetworks. Native and non-native species showed no significant differences in standard centrality distributions, although the highest-ranked nodes were mostly non-native. Simulated species removal revealed a marked sensitivity to the elimination of highly connected nodes. These results suggest that non-native species tend to occupy structurally influential positions, often associated with non-mutualistic interactions, and that the network's stability is strongly dependent on a small set of highly connected species.

Keywords

Modularity, Nestedness, Urban Biotic Network, Indigenous Species

1 Introduction

The importance of ecosystems for human life is undeniable [1]. However, not all cases are equivalent. Throughout its history, Bogotá has undergone not only cultural but also biological colonization, as exemplified by the introduction of *Eucalyptus globulus* [2], which has potentially altered the local ecosystem in a lasting manner. While several studies have focused on marine bioinvasions [3], or have provided initial insights into the structure of biological invasions within ecological networks [4], terrestrial urban systems have received comparatively less attention. The present study analyzes the current state of a terrestrial biotic network after decades of non-native species introductions, assessing the present condition of the network as a whole constitutes the main objective of this work.

To this end, we analyzed the biotic interaction network developed by the Bogotá Botanical Gar-

den, presented in *Data synthesis and dynamic visualization converge into a comprehensive biotic interaction network: a case study of the urban and rural areas of Bogotá D.C.* [5]. This network is structured as a hypergraph, in which interaction information is disaggregated by interaction type and by the organ through which each organism interacts with another. Additionally, nodes are classified by species and by their origin, distinguishing between native and non-native taxa. An example of how this information is represented is shown in Figure 1.

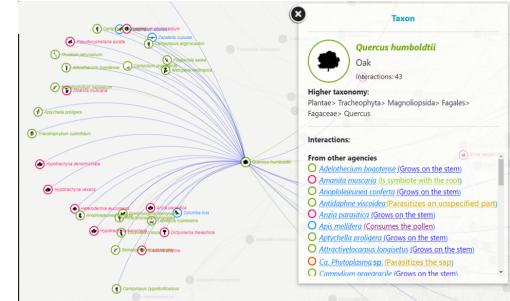


Figure 1: Example of a node within the biotic interaction network [5].

Furthermore, Figure 2, presents a set of pie charts describing the relative frequencies of interaction types, species origin, biological kingdoms, and data source categories. Together, these visualizations provide an overview of the structure and heterogeneity of the underlying data from which the biotic interaction network was built [5].

Given this comprehensive dataset, the network was processed using complex network analysis techniques, which are detailed in the following section. These include both architectural and centrality measures. The former were employed to characterize the topological properties of the network and to determine its structural organization, as well as to examine its response to species removals, whether random or targeted toward species with high out-degree. In addition, centrality measures were used to contrast the relative importance of native and non-native

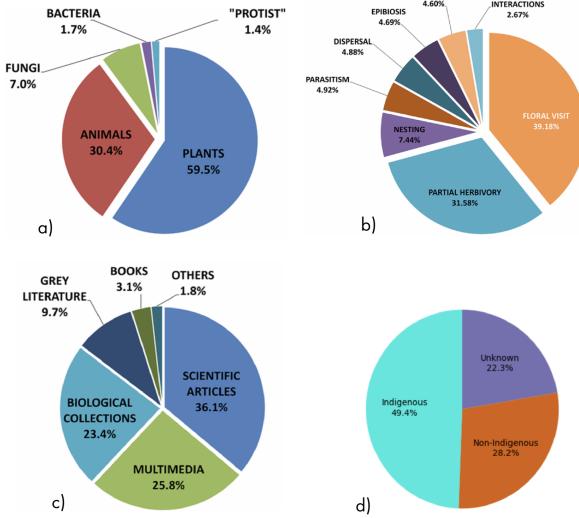


Figure 2: Summary of the biotic interaction network data. Pie charts show the distributions of a) biological kingdoms, b) interaction types, c) data source categories and d) species origin used in the construction of the network. (Graphs a, b and c were taken from [5])

species within the network. These analyses were primarily conducted using the *NetworkX* library, as described in the methodology section. Finally, the results were compared with the literature reviewed in the state-of-the-art section, leading to the findings summarized in the abstract and to several recommendations for future studies.

2 State of the Art

Within the study of biotic networks, several relevant metrics have been identified, including nestedness [6], modularity [7], robustness [8], out-degree [9], among others. These metrics have been applied not only to biological ecosystems but also to financial systems [10], although their most common use remains in ecological contexts, as detailed below.

The use of centrality and architectural measures has proven valuable in conservation studies, particularly those examining the influence of abiotic factors on ecosystems [11] or the fragility of ecosystems under changes in network architecture [12]. Such approaches have also been employed for the optimization of biological networks in agricultural systems [13].

On the other hand, a less explored yet equally important research area concerns the assessment of invasive (non-native) species and their interactions and competition with native species [4]. Ecological networks can exhibit a wide variety

of interaction types, including parasitism, predation, oviposition, epibiosis, floral visitation, dispersal, mutualism, nesting, and hematophagy, among others. These interaction types are characterized by distinct structural properties. For instance, mutualistic networks [14, 15, 16] have been shown to correlate strongly with nestedness. In contrast, parasitic interactions [17] often display a modular structure. Nevertheless, modularity and nestedness are not mutually exclusive, as illustrated in Figure 3. Instead, connectivity has been identified as the primary predictor distinguishing between modular and nested architectures. Specifically, at low levels of connectivity, networks tend to exhibit both modular and nested structures, whereas at higher connectivity levels, networks tend to be predominantly nested [18].

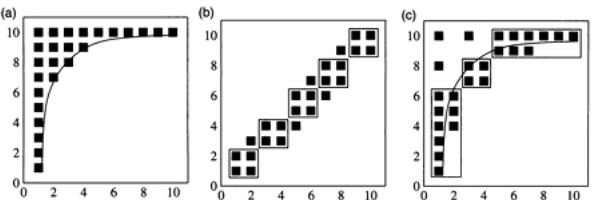


Figure 3: Three networks with the same number of species and interactions. **a** Purely nested network. **b** Purely modular network. **c** Network exhibiting both modularity and nestedness [18].

Robustness refers to the ability of a network to withstand node loss, including the emergence of isolated components [19]. This property has been extensively studied in pollination networks due to its relevance for agro-ecosystems [20, 8].

In addition to architectural measures, centrality metrics play a fundamental role in the analysis of biotic networks. Out-degree centrality, also referred to in the literature as species strength, is particularly important in ecology, as it describes how, within mutualistic networks, species with high out-degree often do so at the expense of species with lower degree [9]. In the context of pollination networks, animal pollinators typically exhibit higher degrees compared to the plants they pollinate. Another, less commonly used, measure for assessing species influence within biotic networks is PageRank, which assigns greater importance to species that contribute substantially to ecosystem support, such as those providing key resources or nutrients, highlighting several taxa within the *Plantae* kingdom [21].

Different centrality measures provide complementary insights into network structure. Eigenvector centrality has been identified as a predictor of network nestedness [22], while degree-based

measures have revealed that biotic interactions often follow power-law distributions with truncated exponential cutoffs [23], particularly in the case of floral visitation interactions [9]. These properties contribute to the characterization of biotic networks as complex systems [23]. Similarly, clustering centrality has been found to correlate with floral visitation interactions, where the small-world approximation becomes relevant [24].

Finally, centrality measures such as closeness and betweenness have been applied to the study of temporal interactions [25] and to the analysis of biological corridors, respectively [26].

3 Methodology

3.1 Biotic network processing

The biotic network [5] distinguishes the specific biological structures through which one species interacts with another, allowing for the existence of more than one edge between a given pair of nodes. Such redundancy arises from the presence of different types of biotic interactions; therefore, the network was not reduced to a simple directed or undirected graph unless explicitly stated in the following sections.

3.2 Architectural measures

First, the analysis of **nestedness** in this study was implemented using two distinct methodological approaches, depending on the specific objectives of each phase of the research. For the structural analysis of ecological subnetworks, the NODF index (*Nestedness based on Overlap and Decreasing Fill*) was employed. This metric, widely validated in ecological studies [27], quantifies the extent to which interactions of less-connected species form perfect subsets of those of more-connected species. The NODF index was computed using the following equation:

$$NODF = \frac{100}{k(k-1)/2} \sum_{i < j} \left[\frac{O_{ij}}{\min(k_i, k_j)} \cdot \delta(k_i > k_j) \right] \quad (1)$$

where O_{ij} represents the number of shared interactions between species i and j , k_i and k_j denote their respective degrees of connectivity, and δ is an indicator function that ensures comparisons are performed only between species with different degrees of connectivity.

In parallel, to analyze the resilience of the full network under progressive node removal, an

optimized version of the Atmar and Patterson method [28] was implemented. This approach evaluates the triangularity of the adjacency matrix using a computationally efficient algorithm ($O(n^2)$), which computes the proportion of interactions concentrated in the upper triangle of the matrix when it is ordered by node degree. Although this second approach is less ecologically detailed than NODF, it enabled repeated iterations of node removal based on out-degree (k_{out}) while preserving the computational feasibility of the study.

Regarding **modularity**, its analysis was incorporated exclusively during the phase assessing network resilience under progressive removal of key nodes, using Newman's *greedy* algorithm [29] to maximize the modularity metric Q . This approach, implemented through the `greedy_modularity_communities` function in NetworkX, operates by first converting the original directed graph into its undirected counterpart via `graph.to_undirected()`, allowing the application of the standard community detection algorithm. The modularity Q is computed using the fundamental equation:

$$Q = \frac{1}{2m} \sum_{ij} \left[A_{ij} - \frac{k_i k_j}{2m} \right] \delta(c_i, c_j) \quad (2)$$

where A_{ij} denotes the adjacency matrix, k_i and k_j are the degrees of nodes i and j , respectively, m is the total number of edges in the network, and $\delta(c_i, c_j)$ is the Kronecker delta function, which equals 1 when both nodes belong to the same community and 0 otherwise. The algorithm begins by treating each node as an independent community and then iteratively merges communities whose union yields the largest positive increase in Q , thereby constructing a complete hierarchy of partitions until the global maximum modularity is reached.

The **robustness** measure was implemented using a weighted combination of three key metrics: clustering coefficient, normalized average degree, and relative giant component size, with weights of 40–30–30%, respectively. This approach, empirically validated by [8], reproduces the behavior of standard robustness metrics ($R^2 > 0.85$) while significantly reducing computational complexity ($O(n^2)$ versus $O(n^4)$), enabling its iterative application during node removal procedures. The weighting scheme reflects that: (1) clustering captures critical local redundancy in ecological networks, (2) average degree represents global connectivity, and (3) the giant component quantifies overall structural integrity.

Finally, it is important to note that during node removal procedures, all nodes that became isolated were also removed from the network.

3.3 Centrality measures

Centrality analysis was implemented using a set of metrics to characterize the connectivity patterns of native and non-native species. For the **degree** of connectivity, the analysis was performed at the level of the full network using `nx.degree_centrality`, and the resulting distributions were compared between native and non-native species.

The same uniform methodology was applied to all other centrality metrics. **Closeness centrality** was computed using `nx.closeness_centrality`, quantifying the accessibility of each node within the network. **Betweenness centrality** was obtained with `nx.betweenness_centrality` to identify species that play a key role along shortest paths. **PageRank** was implemented using `nx.pagerank` to assess the relative importance of nodes based on the structure of directed interactions. **Eigenvector centrality** was computed via a lambda function calling `nx.eigenvector_centrality`, with adjusted parameters (`max_iter = 1000`, `tol = 10-4`) to ensure convergence. Finally, the **clustering coefficient** was calculated using `nx.clustering` to evaluate local connectivity and neighborhood cohesion.

In all cases, the original directionality of interactions was preserved when appropriate. Centrality values were computed individually for each node and subsequently grouped according to species origin, allowing for direct comparisons between native and non-native species. These comparative distributions facilitated the identification of structural differences in connectivity patterns across the biotic network.

4 Results

4.1 Interaction type distributions by species origin

To explore how interaction types are distributed across species of different origins, the network was partitioned into subnetworks based on the origin of the interacting species: Indigenous (I), Non-Indigenous (N), and Any origin (X). Figure 4 shows the relative frequency of interaction types for each possible origin combination, expressed as percentages of the total number of interactions within each subnetwork.

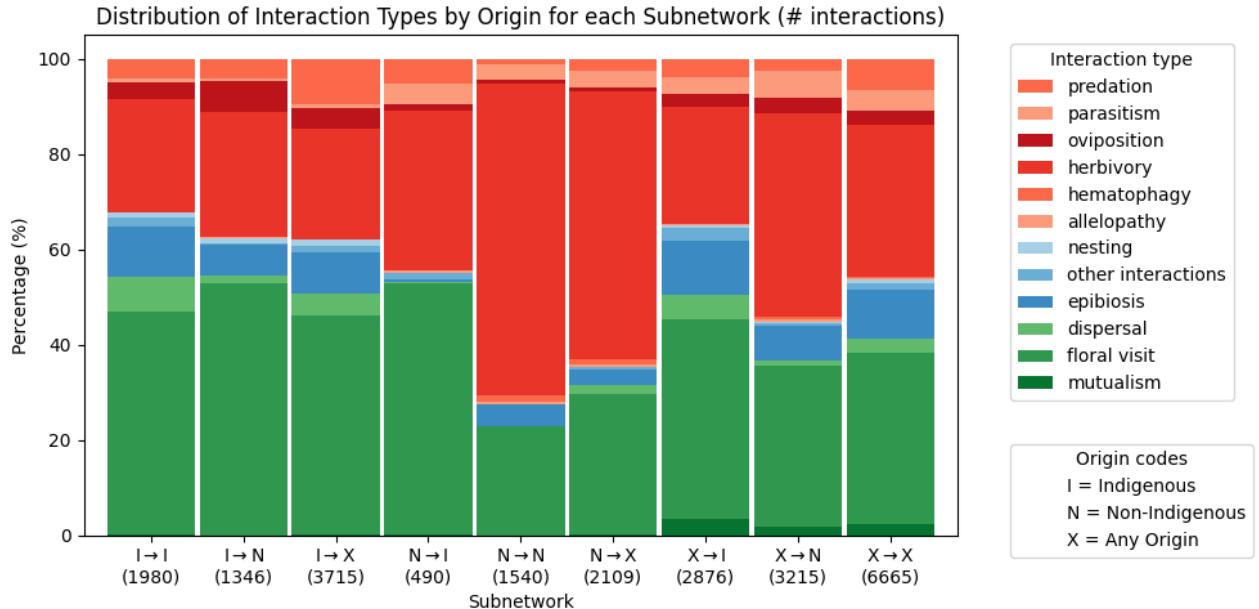


Figure 4: Distribution of interaction types across subnetworks defined by species origin. Bars represent the percentage contribution of each interaction type within subnetworks classified by source and target origin: Indigenous (I), Non-Indigenous (N), and Any origin (X). Non-mutualistic interactions are highlighted in red tones. The total number of interactions per subnetwork is indicated below each label.

Overall, subnetworks originating from Indigenous species ($I \rightarrow I$, $I \rightarrow N$, and $I \rightarrow X$) exhibit a lower proportion of non-mutualistic interactions (red tones) compared to the global network ($X \rightarrow X$). This pattern is most pronounced in the $I \rightarrow I$ subnetwork, which shows the smallest relative contribution of non-mutualistic interactions. In contrast, subnetworks involving Non-Indigenous species as interaction sources display higher proportions of non-mutualistic interactions, with the largest values observed for the $N \rightarrow N$ subnetwork, followed by $N \rightarrow X$.

These differences may suggest a tendency for non-indigenous species to engage more frequently in non-mutualistic interactions. However, alternative explanations cannot be excluded, including potential sampling biases, underrepresentation of mutualistic interactions involving non-indigenous species, or insufficient data coverage. Moreover, the observed differences may not necessarily correspond to statistically significant effects and should therefore be interpreted with caution.

4.2 Centrality Patterns of Indigenous and Non-Indigenous Species

To assess whether species origin is associated with differences in structural importance within the ecological network, centrality analyses were performed on the complete network, without subdividing it into interaction-specific subnetworks. Species were classified as Indigenous or Non-Indigenous, and their centrality distributions were compared across multiple standard metrics, including degree, betweenness, closeness, PageRank, clustering coefficient, and eigenvector centrality.

Figure 5 presents the probability distributions of these centrality measures for Indigenous and Non-Indigenous species. Across all metrics, both groups exhibit highly skewed distributions, characterized

by a large number of nodes with low centrality values and a small fraction of nodes with high centrality. This pattern is consistent with expectations for heterogeneous ecological networks and indicates the absence of systematic differences in the overall shapes of the distributions between Indigenous and Non-Indigenous species. In other words, at the global level, species origin does not appear to significantly alter the statistical behavior of centrality measures within the network.

However, a more detailed inspection of the upper tail of the distributions reveals a subtler pattern. For each centrality metric, the origin of the top 10 highest-ranked nodes was analyzed and summarized using pie charts included within each panel of Figure 5. While the overall network composition shows an approximately balanced proportion of Indigenous and Non-Indigenous species (around 50% each), the top-ranked nodes display a noticeable bias toward Non-Indigenous species across most centrality measures.

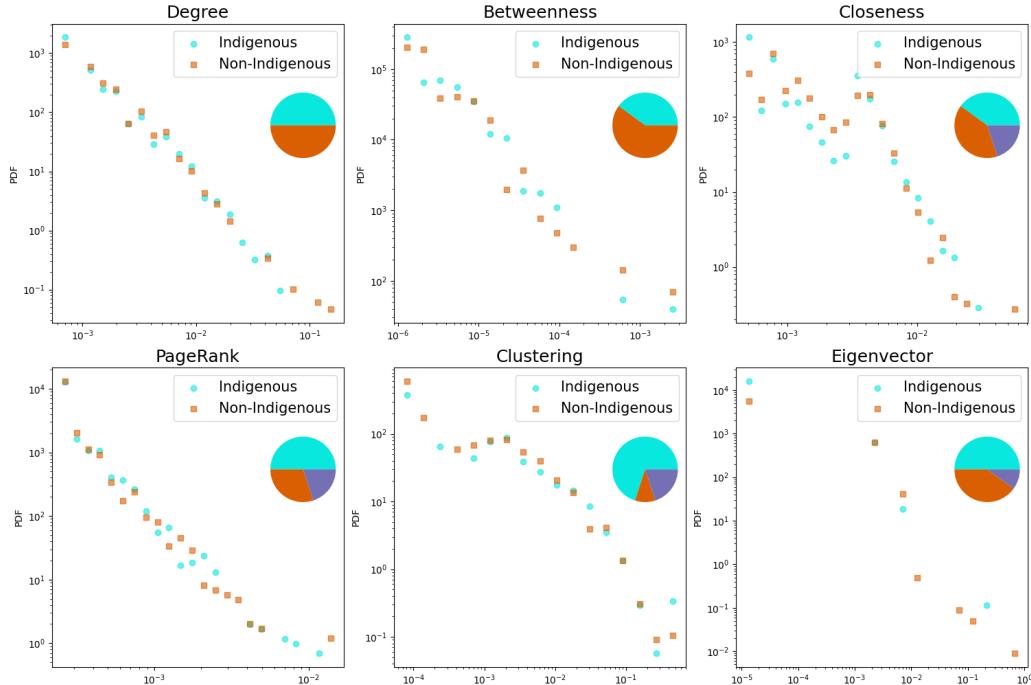


Figure 5: Centrality distributions for Indigenous and Non-Indigenous species in the complete ecological network. Probability distributions are shown for degree, betweenness, closeness, PageRank, clustering coefficient, and eigenvector centrality. Insets display pie charts indicating the origin of the top 10 highest-ranked species for each metric. While overall distributions are similar between groups, top-ranked nodes show a consistent bias toward Non-Indigenous species.

This tendency suggests that, although both Indigenous and Non-Indigenous species are similarly distributed throughout the network in general, Non-Indigenous species are disproportionately represented among the most structurally central nodes. Such nodes typically play a critical role in maintaining connectivity, facilitating information or interaction flow, and potentially influencing network robustness. Importantly, this bias is not evident from the full distributions alone and only emerges when focusing on the highest-centrality subset.

These results should be interpreted with caution. The observed bias may reflect genuine ecological differences, such as Non-Indigenous species occupying more generalist or structurally advantageous positions within the network. Alternatively, it may arise from sampling or reporting biases, including uneven documentation of interactions involving Non-Indigenous species or differences in research focus. Further statistical testing and sensitivity analyses would be required to determine whether the observed pattern is statistically significant or ecologically meaningful.

4.3 Inter-Kingdom Nestedness and Modularity

Nestedness and modularity were analyzed for mutualistic and parasitic subnetworks constructed between biological kingdoms. To ensure structural relevance, only subnetworks containing more than 20 nodes were considered. This analysis aimed to evaluate whether the expected structural differences

between interaction types were preserved across inter-kingdom networks as shown in Figure 6.

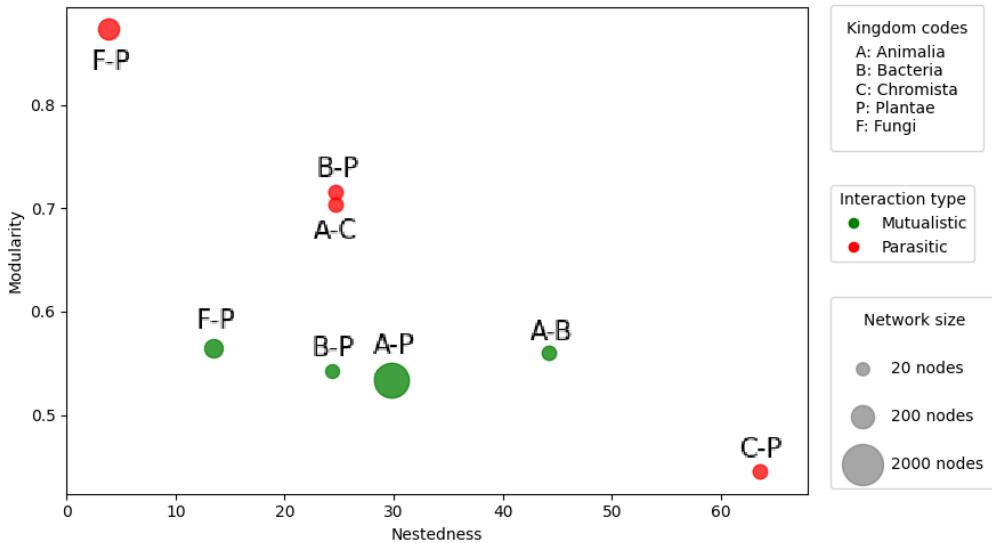


Figure 6: Nestedness (NODF) versus modularity for inter-kingdom subnetworks, separated by interaction type. Only subnetworks with more than 20 nodes were included. Point colors indicate interaction type (mutualistic or parasitic), while point size reflects network size. Parasitic subnetworks tend to exhibit higher modularity than mutualistic ones, whereas no clear or consistent pattern is observed for nestedness.

In general, parasitic subnetworks exhibited higher modularity than mutualistic ones, in agreement with theoretical expectations that antagonistic interactions promote compartmentalized structures. However, the expected contrast in nestedness was not clearly observed. Nestedness values varied across subnetworks and did not show a consistent tendency for mutualistic networks to be more nested than parasitic ones. Instead, the highest NODF values were found in the smallest subnetworks, suggesting a strong sensitivity of nestedness metrics to network size.

Direct comparisons between interaction types were only possible for a limited number of kingdom pairs, most notably Fungi–Plantae (F–P) and Bacteria–Plantae (B–P). In both cases, parasitic subnetworks showed higher modularity. For nestedness, the F–P pair exhibited a lower NODF value for the mutualistic subnetwork, contrary to expectations, while both interaction types in the B–P pair displayed similar nestedness values.

Overall, these results indicate that modularity provides a clearer structural distinction between parasitic and mutualistic subnetworks than nestedness. The lack of a consistent nestedness pattern may reflect data limitations or the sensitivity of NODF to network size, and therefore should be interpreted with caution.

4.4 Network Resilience under Node Removal

To evaluate the resilience of the network, we analyzed its response to both random and targeted node removal strategies, using out-degree as a proxy for species interaction strength. Figure 7 summarizes the main results of this analysis.

The top-left panel shows the ten species with the highest out-degree in the full network. Notably, the three most connected species are non-indigenous, and the top ten species are evenly split between indigenous and non-indigenous taxa. This contrasts with the overall composition of the network, which contains a higher proportion of indigenous species, indicating that non-indigenous species are overrepresented among the most influential nodes in terms of outgoing interactions.

Subsequently, progressive node removals were performed under four different strategies: random removal, targeted removal ordered by out-degree, targeted removal prioritizing indigenous species first, and targeted removal prioritizing non-indigenous species first. The evolution of nestedness, modularity, and robustness under these scenarios is shown in Figure 7.

Across all metrics, directed removals produce trajectories that differ markedly from those obtained

under random removal, confirming the critical role of out-degree in maintaining network structure. This result highlights that highly connected species disproportionately contribute to the stability and organization of the network.

Moreover, the different directed strategies are not equivalent. In particular, the removal strategy that targets non-indigenous species first leads to a faster and more pronounced evolution of all metrics, either through a rapid increase followed by collapse or an accelerated decline, compared to the strategy that removes indigenous species first. This suggests that non-indigenous species play a distinct structural role, potentially acting as connectors between different parts of the network and contributing to the maintenance of modularity, nestedness, and overall robustness.

While these results do not allow for definitive causal conclusions, they indicate that non-indigenous species may be disproportionately important for the structural stability of the network. This pattern may reflect differences in ecological roles, interaction breadth, or data coverage, and warrants further investigation using null models and statistical tests to assess its robustness.

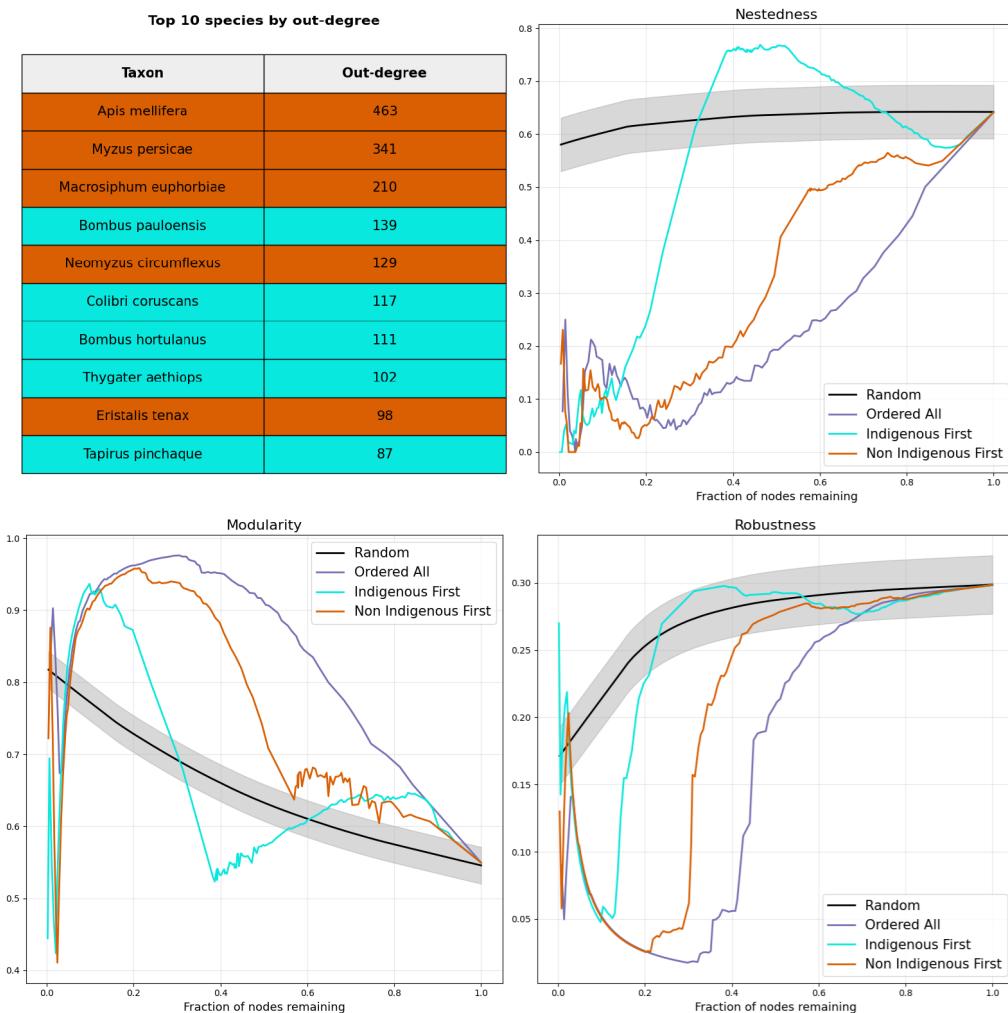


Figure 7: Network resilience under random and targeted node removal. The top-left panel shows the ten species with the highest out-degree. The remaining panels display the evolution of nestedness, modularity, and robustness as a function of the fraction of nodes remaining, under four removal strategies: random removal, removal ordered by out-degree, removal prioritizing indigenous species first, and removal prioritizing non-indigenous species first. Shaded areas represent variability under random removals. Directed removals lead to markedly different trajectories, with faster structural changes observed when non-indigenous species are removed first.

5 Discussion and Conclusions

5.1 Inter-kingdom nestedness and modularity

The analysis of nestedness and modularity across inter-kingdom subnetworks revealed patterns that are strongly influenced by both interaction type and network size. Only subnetworks with more than 20 nodes were considered in order to ensure the relevance of the computed metrics. As expected from ecological theory, parasitic subnetworks tend to display higher modularity than mutualistic ones, while mutualistic interactions are generally expected to be more nested [18]. However, this expected contrast was only partially observed.

Direct comparisons between kingdoms were limited by data availability, with *Fungi–Plantae* (F–P) being the only pair allowing a consistent comparison between mutualistic and parasitic subnetworks. In this case, parasitic interactions showed higher modularity, in agreement with theoretical expectations, although the mutualistic subnetwork unexpectedly exhibited a lower nestedness value. A similar pattern was observed for *Bacteria–Plantae* (B–P), where parasitic interactions were more modular, but both interaction types displayed comparable nestedness values.

Overall, nestedness did not show a clear or systematic dependence on interaction type. In fact, the highest NODF values were consistently found in the smallest subnetworks, regardless of whether interactions were mutualistic or parasitic. This suggests that nestedness metrics are highly sensitive to network size and sparsity, as previously reported [6], and that the observed values may not be statistically robust. Consequently, differences in nestedness across interaction types and kingdoms should be interpreted with caution.

5.2 Roles of indigenous and non-indigenous species

The analysis of interaction type distributions across subnetworks revealed systematic differences associated with species origin. Subnetworks originating from indigenous species tend to exhibit a lower proportion of non-mutualistic interactions compared to the global network, with the indigenous–indigenous subnetwork showing the lowest fraction of antagonistic interactions. In contrast, the highest proportion of non-mutualistic interactions was observed in the non-indigenous–non-indigenous subnetwork, followed

by non-indigenous–any origin interactions. While this pattern may indicate a tendency of non-indigenous species toward antagonistic interactions, potential sampling biases and incomplete documentation of mutualistic interactions involving non-native species cannot be ruled out [5].

Regarding centrality measures, no significant differences were observed between indigenous and non-indigenous species in the overall distributions of degree, betweenness, closeness, PageRank, eigenvector centrality, or clustering. In all cases, the distributions followed the expected heterogeneous pattern, where most nodes exhibit low centrality values and a few nodes concentrate high centrality. However, when focusing on the top-ranked species for each metric, a consistent bias emerged: non-indigenous species were overrepresented among the top 10 nodes, despite indigenous species being more abundant in the network as a whole. This suggests that non-indigenous species tend to occupy disproportionately influential positions without altering the global statistical structure of centrality distributions.

5.3 Network resilience under node removal

The resilience analysis demonstrated that the network responds very differently to random versus targeted node removals. Directed removals based on out-degree produced markedly distinct trajectories for nestedness, modularity, and robustness compared to random removals, confirming the critical role of highly connected species in maintaining network structure [9]. This validates out-degree as an effective proxy for interaction strength and structural importance.

Moreover, targeted removal strategies were not equivalent. Removing non-indigenous species first led to a faster evolution of all metrics, including accelerated structural reorganization and collapse, compared to strategies prioritizing indigenous species. This suggests that non-indigenous species play a key role in connecting different parts of the network and stabilizing its architecture. Their removal appears to disrupt modular organization, nested structure, and robustness more rapidly, indicating a disproportionate contribution to network integrity.

5.4 Conclusions

The results indicate that the Bogotá biotic network exhibits a predominantly modular organization, particularly when considering indigenous

species. However, introduced species such as *Apis mellifera* act as strong generalists that significantly alter network structure, pushing it away from purely modular configurations. Despite the lack of clear differences in global centrality distributions between indigenous and non-indigenous species, non-indigenous species consistently occupy top-ranked structural positions and play a central role in network resilience.

These findings highlight that the key distinction between indigenous and non-indigenous species lies not in their average centrality values, but in their interaction strategies and structural roles. Future work should focus on improving data coverage for underrepresented taxa, incorporating null models to assess statistical significance, and explicitly accounting for isolated nodes and secondary extinctions to better capture network reorganization dynamics [12].

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