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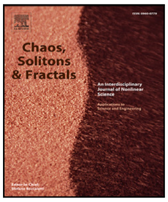

Species vulnerability and ecosystem fragility: A dual perspective in food webs

Emanuele Calò [a,*], Giordano De Marzo [b,c,d], Vito D.P. Servedio [d]

[a] IMT School for Advanced Studies Lucca, P.zza San Francesco 19, Lucca, 55100, Italy
[b] University of Konstanz, Universitaetstrasse 10, Konstanz, 78457, Germany
[c] Centro Ricerche Enrico Fermi, P.zza del Viminale 1, Rome, 00184, Italy
[d] Complexity Science Hub, Metternichgasse 8, Vienna, 1030, Austria

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ABSTRACT

Ecosystems face intensifying threats from climate change, overexploitation, and other human pressures, emphasizing the urgent need to identify keystone species and vulnerable ones. While established network-based measures often rely on a single metric to quantify a species' relevance, they overlook how organisms can be both carbon providers and consumers, thus playing a dual role in food webs. Here, we introduce a novel approach that assigns each species two complementary scores—an importance index quantifying their centrality as carbon source and a predatory index capturing their vulnerability. We show that species with high importance index are more likely to trigger co-extinctions upon removal, while high-robustness index species typically endure until later stages of collapse, in line with their broader prey ranges. On the other hand, low robustness index species are the most vulnerable and susceptible to extinctions. Tested on multiple food webs, our method outperforms traditional degree-based analyses and competes effectively with eigenvector-based approaches, while also providing additional insights. This scalable and data-driven approach, relying solely on interaction data, provides a cost-effective tool that complements expert classifications for prioritizing conservation efforts.

1. Introduction

The preservation of ecosystems is one of the most pressing challenges in contemporary ecology. A key aspect of this challenge lies in understanding the consequences of species loss and identifying the most vulnerable species. These tasks are increasingly urgent due to escalating anthropogenic pressures, such as climate change and over-exploitation, which severely disrupt ecosystems [1–8]. Species extinctions often lead to cascading effects throughout the ecosystem, triggering secondary extinctions that amplify the initial damage [9,10]. To mitigate these impacts, it is essential to quantify species' "relevance" and "robustness", guiding conservation policies to prioritize the preservation of fundamental and fragile species.

Ecosystems, like many complex systems, are characterized by non-linear interactions and intricate structures [11,12], where each component contributes to overall functionality. Similar dynamics are observed in other domains, such as interbank loan markets or supply chains, where the removal of a single bank or firm can significantly disrupt economic output [13–15]. In this context, network science has emerged as a powerful tool for studying such systems. By representing species as nodes and their interactions — such as mutualistic, host-parasite, or trophic relationships — as links, networks provide a mathematical framework for analyzing ecological systems [16,17]. Among these networks, food webs, which depict "who consumes whom" interactions, have been extensively studied to understand ecosystem dynamics [18–25]. Network-based measures, particularly those derived from PageRank or eigenvector centrality [26–28], have proven effective in quantifying species' relevance within food webs. These metrics identify species whose removal would have the most significant impact on biodiversity [29,30]. This approach is especially useful for large food webs, where exhaustive simulations of all extinction scenarios are computationally infeasible. However, while these methods excel at identifying critical species, they often overlook those that are highly vulnerable. For instance, some species may play a minor role in the food web economy but remain extremely susceptible to extinction due to specialized diets or habitat requirements—pandas being a notable example.

While network science has provided numerous metrics for quantifying species' roles in food webs, including measures of centrality and structural roles [31,32], and the concept of keystone species has been explored through various network approaches [33], our methodology

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* Corresponding author.
E-mail address: emanuele.calo@imtlucca.it (E. Calò).

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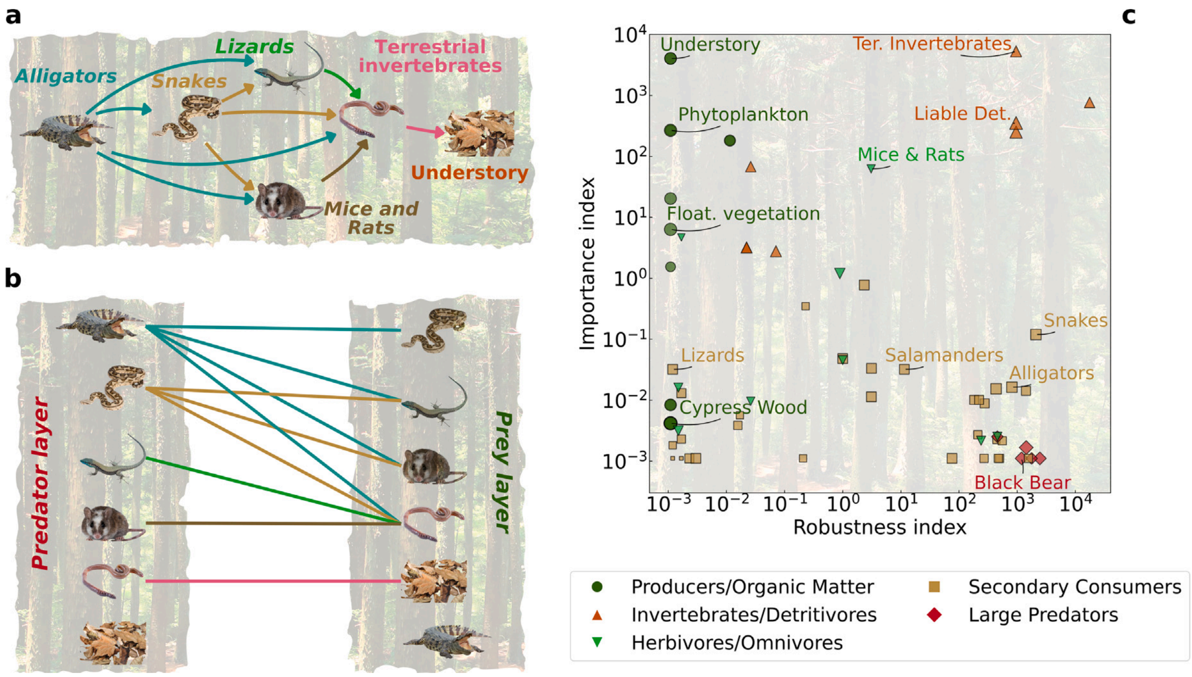

Fig. 1. Cypress food web: network representations and robustness index-importance index plane. a, Directed monopartite subnetwork illustrating predator–prey relationships. **b,** Equivalent undirected bipartite representation of the subnetwork. **c,** Robustness index-importance index plane depicting species' ecological roles. Points represent individual species, with colors indicating functional categories and sizes proportional to species biomass. Selected species are labeled for reference. This visualization reveals the dual roles of species as both predators and prey within the ecosystem. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

offers a distinct perspective by explicitly and simultaneously quantifying two complementary dimensions for each species: the importance index (measuring its centrality as a carbon source and its relevance within the food web) and the robustness index (capturing its predatory ability and resilience to extinction). Unlike single-index measures that characterize different aspects of species' network roles [34,35], this bi-dimensional framework provides a direct and separate assessment of these two fundamental ecological facets for each species, building upon the idea that considering both a species' dependence on resources and its impact on its prey is crucial for a comprehensive understanding of its ecological role, as also explored through combinations of centrality indices [36]. This bi-dimensional characterization then allows us to visualize the food web's structure, where each species is represented as a point on this plane. Our findings reveal that highly important species often drive significant extinction cascades when removed, whereas low-robustness index species exhibit limited resilience to such events. This methodology provides a more nuanced understanding of both critical and vulnerable species within ecosystems. By capturing the complex interplay between predation and survival in food webs, our approach offers a valuable, ecologically-informed perspective that could contribute to the broader framework of conservation strategies, potentially enhancing the prioritization of biodiversity protection efforts.

2. Results

2.1. The robustness index and importance index of species

Quantifying species' roles and impacts within ecosystems presents a significant methodological challenge in ecological research. Traditional network-based methodologies approach this task by looking at the food web formed by the species. This consists of a directed network, where nodes are the species, while edges signify carbon flow between these species. As predation represents a major pathway for carbon flow between species, these networks are frequently termed prey-predator networks. We show in Fig. 1a a schematized food web, where we adopt the convention of arrows going from predators to prey. Once a food web has been reconstructed, the standard approach consists in applying a centrality measure to rank the species. For instance, eigenvector centrality has proven very effective in determining which species have a stronger potential to cause chain extinctions if removed from an ecosystem [29]. These measures, however, are unable to assess which species are most in danger during these extinction cascades and may not fully capture species' vulnerability or the nuances of direct and indirect interactions (see also mixed trophic impact analysis [37] and loop analysis [38]).

To address this limitation, we introduce a novel algorithmic approach that quantifies species' dual roles through two distinct measures: the importance index and the robustness index. The importance index measures how important in the food web a species is, while the robustness index assesses a species' predatory capabilities and adaptability within the food web. The importance index of a species is high if it serves as prey for multiple species with a low robustness index. On the other hand, the robustness index evaluates a species' predatory efficiency by assessing both the quantity and the importance index of its prey species. Species that prey upon diverse taxa, particularly those of low importance index, demonstrate high predatory capacity and consequently receive high robustness index values. Mathematically, we formulate this framework as a bi-dimensional non-linear map. Let $\mathbf{M}$ represent the adjacency matrix of the food web. The element M_{ij} equals one if there is carbon transfer (predation) from species i to j, and zero otherwise. The robustness index (R_i) and importance index (I_i) of species i are computed through the following iterative map:

$$\begin{cases} R_i^{(n+1)} & = \quad \delta + \sum_j M_{ji} \,/\, I_j^{(n)} \\ I_i^{(n+1)} & = \quad \delta + \sum_j M_{ij} \,/\, R_j^{(n)} \end{cases} R_i^{(0)} = I_i^{(0)} = 1 \;\forall i. \qquad (1)$$

Here, $R_i^{(n)}$ and $I_i^{(n)}$ denote the robustness index and the importance index of the species i at iteration n, respectively. The quantity δ is a regularization term that guarantees convergence. It does not affect the final ranking, as soon as it is way smaller than $\mathbf{M}$'s elements. In this paper, we set it at 10^{-3}. The algorithm iterates until the convergence of both quantities. The first equation tells us that a species has a

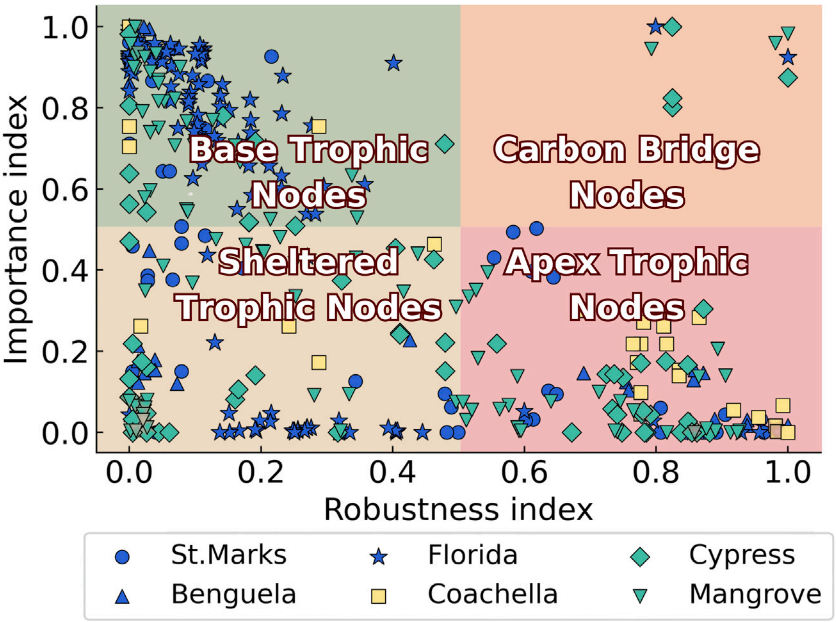

Fig. 2. Robustness index-importance index plane. In royal blue, the marine ecosystems; in khaki, the terrestrial one; in medium aquamarine the mixed ones. Values are log-transformed and normalized to [0,1] for cross-food web comparison. The plane is divided into four quadrants. Base Trophic Nodes (top left quadrant), Carbon Bridge Nodes (top right quadrant), Sheltered Trophic Nodes (bottom left quadrant), Apex Trophic Nodes (bottom right quadrant). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

high robustness index if it can absorb carbon from several sources, in particular from those with a low importance index. Referring to the second equation, species with a low importance index are consumed by few species, which suggests they are harder to prey upon. Conversely, the second equation implies that the importance index of a species is high if it is consumed by several other species, particularly those with a low robustness index. Low-robustness index species can indeed only absorb carbon from a limited set of sources, so the extinction of any of those would put them in serious danger. For this reason, we identify vulnerability as the inverse of the robustness index. The lower the robustness index of a species, the more vulnerable to food web shocks it is expected to be.

This approach shares notable similarities with the algorithms developed for bipartite networks in the field of Economic Complexity [39–42], specifically with the algorithms of Economic Fitness and Complexity (EFC) [40,41]. While the EFC algorithm has successfully analyzed various bipartite nested networks, including ecological systems [17], its application to mono-partite directed networks represents a novel extension [43]. In ecological contexts, nestedness contributes significantly to ecosystem stability, biodiversity, and resilience, particularly in mutualistic networks where specialist species typically interact with generalist ones [44]. This similarity between the two approaches is not surprising, since Fig. 1b illustrates how the directed trophic interactions of a food web can be visually represented using a bipartite layout, which can be useful for specific analytical approaches. Differently from standard bipartite networks, layers contain the same set of species. The first looks at their role as predator, and the second one looks at their role as prey. Links between the two layers connect predators to their prey.

2.2. Robustness index-importance index plane

Our algorithm allows us to place all the species within an ecosystem on the 2-dimensional space defined by the robustness index and the importance index. Each axis captures a different aspect of species, namely their importance as prey and carbon suppliers and their prowess as predators and carbon absorbers. As an example, we show in Fig. 1c the robustness index-importance index plane for the Cypress dry season food web [45]. In this figure, each point corresponds to a species, different colors/shapes correspond to five different categories of species (see Methods for details), while point size is proportional to the biomass. Remarkably, species are not randomly scattered on the plane but tend to cluster following the classification. Producers and Organic Matter (dark green circles) are mostly placed on the top left corner since they are crucial carbon suppliers (high importance index) and they do not absorb carbon from other species (low robustness index). Conversely, large predators are placed in the bottom right corner, since they are both very hard to prey on and very good at preying. Also, a large fraction of secondary consumers are located in this region. The top right corner contains species that can absorb carbon from several other species, but that, at the same time, also transfer carbon to many other species. Not surprisingly in this area we find invertebrates and detritivores or mammals like rats. Finally, the bottom left corner mostly contains herbivores/omnivores and secondary consumers. These are species such as lizards that are not central in the food chain functioning, being hard to prey on, but with little to none preying capabilities.

In Fig. 2, the robustness index-importance index plane for each species is shown across all food webs. The plane is then divided into four regions:

- **Base Trophic Nodes (top left quadrant)**
  These species are characterized by poor predatory ability but are heavily preyed upon by a multitude of species. They form the foundation for energy and nutrient flow, providing a primary source of food for consumers. They are both very important and very vulnerable (low robustness index).
- **Carbon Bridge Nodes (top right quadrant)**
  These species excel at absorbing or transforming carbon (often from detrital or non-living sources) and are widely consumed by other species. They “bridge” carbon from lower-level or non-living pools into higher trophic levels. They are also very important, but not as vulnerable, since their high robustness index allows them to absorb carbon from very diverse sources.
- **Sheltered Trophic Nodes (bottom left quadrant)**
  These species are neither strong predators nor frequent prey; they have defenses, behaviors, or ecological niches that protect them

Table 1

Comparison of mean extinction area across ecosystems using different species ranking methods. We compute the in-degree, eigenvector-in, and importance index rankings at the outset and keep them fixed throughout the simulated extinction process. Values represent means and standard deviation. For eigenvector-in and importance index, the standard deviation is smaller than the last significative digit displayed. Higher percentages indicate greater ecosystem sensitivity to species loss based on the respective ranking method. Bold values indicate the best-performing method for each ecosystem.

Food web	In-degree (%)	Eigenvector-in (%)	Importance index (%)
St. Marks	84.8 ± 1.1	**91.6**	91.4
Benguela	77.3 ± 0.5	**94.6**	91.3
Coachella	70.9 ± 0.3	75.9	**78.8**
Florida	64.6 ± 0.4	**82.4**	82.2
Cypress	78.5 ± 0.4	81.9	**86.9**
Mangrove	72.5 ± 0.1	**95.0**	94.3

from heavy predation. They have a low robustness index, so high vulnerability, but their extinction would likely not cause cascades.

- **Apex Trophic Nodes (bottom right quadrant)**
  These species possess high predatory ability with low vulnerability. They regulate prey populations and structure ecosystem dynamics from the top of the food web. They have a low importance index, but also low vulnerability.

Fig. 2 is realized considering six different ecosystems from terrestrial, aquatic, and mixed domains. Note that we normalized the robustness index and the importance index to compare species from different ecosystems (details in Methods). Colors denote the ecosystem type, while symbols show the different food webs. We observe a predominance of species in the Base Trophic Nodes (42.09%) and Apex Trophic Nodes (32.65%) quadrants, only a few Carbon Bridge Nodes (2.30%) and a minority of Sheltered Tropic Nodes (22.96%). We report in SI, for each ecosystem, the detailed list of all species in each quadrant. It is important to stress that the robustness index and importance index only present a marginal anti-correlation (average Spearman $s = -0.60 \pm 0.18$ across the six food webs), confirming that the two quantities capture complementary species' properties. This moderate anti-correlation is notably lower than the correlation we observe between eigenvector in-centrality and importance index (e.g., $s = 0.93$ for the Cypress food web, as shown in Supplementary Information Section 3), indicating that the robustness index and importance index provide more distinct information.

2.3. Cascading extinctions and robustness of species

The picture suggested by the robustness index-importance index plane, while reasonable, needs stronger validation. In particular, we need to understand whether the two measures we introduced are correlated with the predatory capabilities of animals and their vulnerability and importance as prey. These are not easy quantities to measure, but we can indirectly assess them.

We start studying the importance index, which, as mentioned, is a measure of a species' relevance as a carbon source. High-importance index species play a major role in food webs since they represent the base of the food chain. This role can be quantified looking at the so called extinction curve of a food web. Such a curve is obtained by progressively removing species from the food web and looking at which other species get disconnected, thus remaining without any supplier. More details are reported in the Methods section. The premise is that a more accurate measure of species relevance within a food web should lead to a faster network collapse when species are removed in order of their ranking. Indeed, Eq. (1) implies that a species with a high importance index is preyed upon by several species of low robustness index. Therefore, its removal would likely cause many of these species with low predatory capabilities to be unable to survive. We quantify this effect using the mean extinction area (area under the extinction curve), where higher values indicate a better ability to identify critical species within the ecosystem. Table 1 presents the mean extinction areas following 3 different ranking strategies: in-degree, eigenvector-in centrality, and importance index. We establish the initial rankings and keep them fixed throughout the simulated extinction process, whereas in the Supplementary Information, we present the scenario where rankings are recalculated after each node removal, including extinction curves plots for both cases across all food webs. The results reveal that both the eigenvector-in and importance index consistently outperform the degree-centrality across all ecosystems studied. Notably, eigenvector-in centrality and importance index demonstrate comparable efficacy, with each measure excelling in different ecosystems. These results validate the importance index, confirming its ability to identify the most crucial species within food webs.

As a second step, we study the ability of the robustness index to measure species' vulnerability. A high-robustness index species can prey on many other organisms, including those with a low importance index, i.e., those that are very hard to prey on. As a consequence, we expect high-robustness index species to be less affected by extinctions within the ecosystem. They are indeed very diversified and less susceptible to such events. On the other hand, low-robustness index species are expected to be the most vulnerable and, thus, the first to get extinct during cascade events. We can measure this by looking at the average (log) robustness index of species that get extinct at a given step of the extinction curve construction. As shown in Fig. 3a for the cypress food web, this average increases with the step, meaning that high-robustness index species only get extinct when most other species are already gone. We report next to each point a sample species going extinct in that step, while the inset shows the same plot, but using the average eigenvector-out centrality to measure (inverse) vulnerability. A much weaker correlation is observed. We repeat the same analysis for all the six food webs we considered, reporting the results in Fig. 3b. Note that we normalized both the step and the robustness index for comparison reasons. In all cases, we observe the same behavior. More quantitatively, we can compute the Spearman correlation between the removal step and the (average log) robustness index of the removed species. The average of this quantity among all ecosystems is 0.98, while the average of the eigenvector-out centrality is 0.72, thus consistently lower. We repeat the analysis using eigenvector-in centrality for species removal, yielding similar results that support the robustness index as an effective measure of species' predatory skills and extinction resilience. In the Supplementary Information, we report details on Spearman correlation coefficients and eigenvector-in-based removals, along with additional comparisons between robustness index, importance index, and other centrality measures.

3. Discussion

Ecosystems face intensifying threats, making it urgent to identify vulnerable species, to prevent their extinction. Current network-based approaches often reduce the complex predator–prey interactions to a single metric. While this allows us to understand which species are crucial for the functioning of a food web, it tells little to nothing about the vulnerability of species. Our method, based on a bi-dimensional non-linear map, addresses this gap, associating to each species both an *importance index* and a *robustness index*. The former is linked to the susceptibility to predation and measures how crucial a species is in the food web. The latter measures predatory prowess and quantifies the robustness of species. High-importance index species, which often anchor lower trophic levels, appear critical to maintaining overall network stability, and their loss disproportionately impacts a wide range of other species. On the other hand, high-robustness index species thrive on diverse prey pools, making them more resistant to ecosystem perturbations. Our analysis confirms this intuition, showing that the importance index effectively identifies species whose removal triggers significant co-extinctions. At the same time, the robustness index highlights species capable of persisting until the late stages of collapse, with

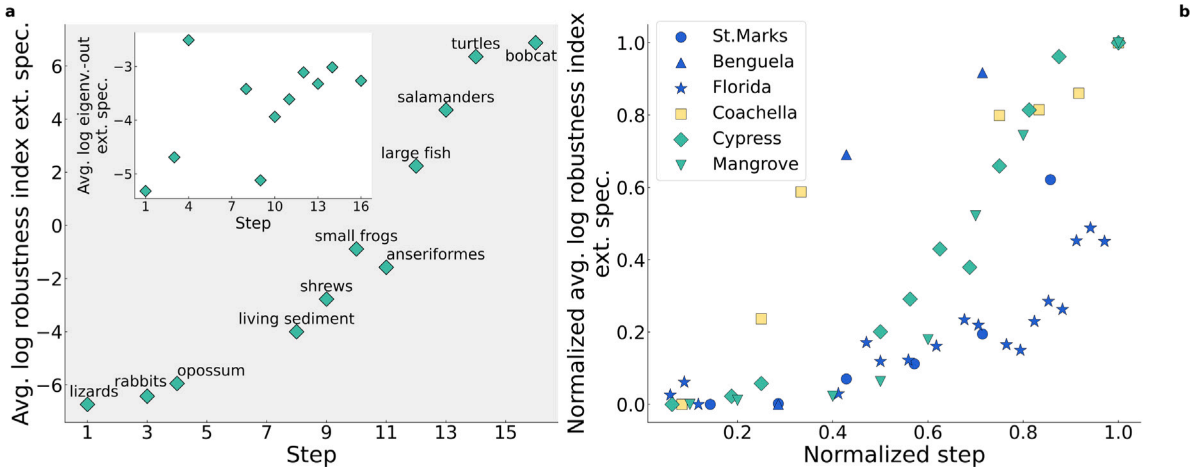

Fig. 3. **Ecological robustness: Species removal patterns in diverse food webs. Left:** Cypress food web: Average log robustness index of extinct species vs. extinction step, based on importance index ranking. Labels indicate representative species becoming extinct at each step. **Inset:** Average log eigenvector-out centrality of extinct species vs. extinction step. **Right:** Normalized average log robustness index vs. normalized extinction step for multiple food webs. Values are log-transformed and scaled to [0,1] for cross-ecosystem comparison. This plot illustrates ecosystem resilience patterns and differential impacts of species loss across varied food web structures.

the most vulnerable, low-robustness index species being the first to disappear. While eigenvector-in centrality can resemble our importance index ranking, neither eigenvector-in nor eigenvector-out centralities adequately capture the predatory strength and resilience that define a species' robustness index. This limitation arises from the linear nature of the eigenvector centrality, which is often incapable of capturing complex, non-linear interactions.

By mapping species onto a *robustness index-importance index plane*, we can reveal patterns that align with known functional roles (e.g., apex predators, base trophic nodes). Although expert knowledge remains crucial for fully characterizing species' functional roles, our algorithmic and data-driven approach provides a valuable, complementary layer of insight. This framework holds clear promise for conservation and ecosystem management, where limited resources demand strategic prioritization. By jointly quantifying species' importance index and robustness index, practitioners can pinpoint "keystone" nodes — those whose loss risks triggering wider co-extinctions — thereby directing scarce funding and protective measures where they have the greatest impact. Particular attention can also be devoted to those species that despite a marginal role as carbon suppliers, are in severe danger due to their low robustness index. Because our algorithmic approach draws solely on quantitative interaction data, it readily scales to large, complex food webs. When combined with objective risk assessment, this scalability ensures broader applicability across diverse ecosystems, ultimately supporting more targeted and cost-effective biodiversity preservation efforts. However, we acknowledge that the implementation of actual conservation strategies requires the consideration of numerous additional ecological, social, and economic factors beyond the scope of this network-based analysis.

While our framework provides valuable insights into species' roles in food webs, certain aspects require further exploration. First, basal species are represented as individual nodes but are linked to a common root node that aggregates their shared reliance on environmental resources like light, water, and nutrients. This approach simplifies the analysis by not differentiating among their specific resource dependencies and instead focuses on their collective role as energy providers. Consequently, our analysis primarily examines the vulnerability and resilience of all other species in the food web. For basal species, however, additional factors such as Grime's classification [46] — based on competition, stress tolerance, and ruderality — may be necessary to better capture their ecological resilience and responses to cascading effects. Second, species such as lizards in the Cypress food web appear peripheral in our analysis due to their limited predatory skills and resistance to predation. This could reflect biological realities, such as population constraints driven by nesting site availability rather than trophic interactions. However, it may also result from aggregation biases in network construction, where diverse prey groups are aggregated into single nodes, masking their ecological importance. To preliminarily assess the influence of network resolution, we conducted node aggregation experiments. Our initial findings indicate that the impact of such aggregation on our metrics of ecosystem fragility is not uniform. Aggregating multiple basal trophic nodes yielded the most pronounced effects, suggesting that the resolution at lower trophic levels could be particularly critical for accurately assessing species' roles using our framework. Further details on these aggregation experiments and their results can be found in Section 6 of the Supplementary Information. Systematic investigation into the sensitivity of our results to food web resolution, across different aggregation strategies and trophic levels, represents a valuable direction for future research. Third, our analysis relies on a static and binary representation of food webs, which inherently simplifies the dynamic and often weighted nature of real ecological interactions. The species removal simulations, while useful for comparative purposes, also present a somewhat idealized view of extinction cascades, as they do not incorporate adaptive behaviors like prey switching or the continuous changes in interaction strengths that characterize natural ecosystems. Finally, while our initial study focused on demonstrating the methodology across a diverse set of six existing food webs, future research could readily expand this analysis to the larger collection of currently available food web datasets to assess the generality of our findings. Subsequently, experimental validation remains a critical avenue, where collecting data on real-world ecological networks under anthropogenic disturbances could provide empirical evidence for the predictive power of the proposed framework and help quantify species' actual endangerment levels across their ecosystems.

4. Methods

4.1. Data

We analyzed the following six food webs:

Florida Bay This network represents trophic flows through the ecosystem of Florida Bay. It includes various species such as seagrass and algae producers, microfauna, macroinvertebrates, fishes, mammals, and avifauna [45].

Cypress Dry Season This network depicts the cypress wetlands in South Florida during the dry season [45].

Mangrove Wet Season This network illustrates the mangrove ecosystem in South Florida during the wet season [45].

St. Marks This network describes a winter's *Halodule wrightii* (shoal grass) community in Goose Creek Bay, St. Marks National Wildlife Refuge, Florida [47].

Coachella This network represents the sand community in the Coachella Valley desert. The biota includes species of vascular plants, vertebrates, arachnids, microorganisms, and insects [48].

Benguela This network characterizes the Benguela Marine Ecosystem, including marine mammals and fisheries [49].

4.2. Networks construction and preprocessing

Food webs are represented as directed monopartite networks, where edges denote energy flow between species. In our binary model, an edge from node i to node j indicates i preys upon species j, with no weights assigned to the links. Self-loops are included to account for cannibalism within species. We selected six food webs for analysis and modified them to ensure irreducibility and primitivity, following the method described by [29,50,51]. This modification process involved:

1. Adding a root node to represent the external environment.
2. Creating links from primary producers to the root, reflecting the origin of matter in the food web.
3. Establishing links from the root to every node, representing intrinsic matter loss and detritus accumulation, which is partially recycled back into the food web.

We remove three nodes (Input, Output, and Respiration) from the Florida Bay, Cypress Dry Season, and Mangrove Wet Season networks to maintain consistency across datasets. For the St. Marks food web, only step 3 (add the links between root and all other nodes) is performed, since the first two were already present in the data. Furthermore, we manually added one missing link, comparing the data with the adjacency matrix present in the original paper [47]. These preprocessing steps ensure that all networks represent comparable ecological entities. The macroscopic properties of these modified networks, including the number of nodes, links, and network density, are detailed in the Supplementary Information.

4.3. Robustness index-importance index plane

To categorize the species of the cypress food web into 5 categories, we use ChatGPT-4o (accessed on 24/10/2024). In particular, we use the following prompt, *Can you classify the nodes in this food web into 5 categories?*, followed by the list of species in the Cypress food web. The SI provides complete species categorizations.

To enable cross-network comparisons, we normalize the robustness index and importance index values for each food web using the following procedure:

1. Compute the robustness index and importance index for each species.
2. Take the logarithm of these values.
3. Scale the log-transformed values to the [0,1] interval using min–max normalization:

$$x_{\text{normalized}} = \frac{\log(x) - \min(\log(x))}{\max(\log(x)) - \min(\log(x))}.$$

This approach preserves relative differences while allowing for consistent comparison across different food webs.

4.4. Extinction areas

We implement the following species removal procedure to assess ecosystem robustness. Species are progressively removed based on rankings from specified algorithms, maintaining fixed rankings throughout the process. Cascading extinctions are monitored, with a species considered extinct when left without outgoing links or with only a self-loop. The procedure continues until all species go extinct. An extinction curve is generated by plotting the fraction of extinct species against the number of removed species. The extinction area, calculated as the integral of this curve, measures the ecosystem vulnerability. This area equals 1 when all species go extinct after the first removal and approaches 0.5 when no secondary extinctions occur. When ranking species for removal, multiple species can sometimes receive the same rank value (a situation known as rank degeneracy). To address this, we employ a randomized tie-breaker. When ties occur, we randomly select which of the equally ranked species to remove. To account for the variability introduced by these random choices, we average the results from 200 repetitions of the entire removal process. In each repetition, ties are broken randomly. We use this approach to compare rankings based on our importance index, eigenvector in-centrality, and in-degree centrality. For eigenvector-based rankings, we follow the method in [29]: at each step, we compute the dominant eigenvector of the column-normalized adjacency matrix and remove the highest-scoring node. The dominant eigenvalue is always 1, with its associated positive eigenvector summing to 1. For eigenvector-out rankings, we use the transpose of the adjacency matrix.

CRediT authorship contribution statement

Emanuele Calò: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Giordano De Marzo:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Vito D.P. Servedio:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

We acknowledge the use of LLMs for text refining. The authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.chaos.2025.116741.

Data availability

The edgelists and species' names for St.Marks, Coachella, and Beng uela food webs were constructed by examining the adjacency matrices in their original publications [47–49]. The edgelists and species' names for the Florida Bay, Cypress Dry Season, Mangrove Wet Season food webs [45] were originally available at [52], sourced from [53].

All the edgelists and species' names are available in the Zenodo repository [54].

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