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Determining key mammalian species and food web robustness across different land cover vegetation using network analysis

IDUNG RISDIYANTO[1,2,♥], YANTO SANTOSA[2], NYOTO SANTOSO[2], ARZYANA SUNKAR[2]
[1]Faculty of Mathematics and Natural Sciences, Institut Pertanian Bogor. Jl. Meranti, IPB Dramaga Campus, Bogor 16680, West Java, Indonesia. Tel.: +62-251-622642, ♥email: idungris@apps.ipb.ac.id
[2]Faculty of Forestry and Environmental, Graduate Program of Tropical Biodiversity Conservation, Institut Pertanian Bogor. Jl. Pinus, IPB Dramaga Campus, Bogor 16680, West Java, Indonesia

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Abstract. *Risdiyanto I, Santosa Y, Santoso N, Sunkar A. 2024. Determining key mammalian species and food web robustness across different land cover vegetation using network analysis. Biodiversitas 25: 3162-3177.* The ecosystem's food web depicts the intricate energy flow and complex interactions among its diverse organisms. Organisms are not confined to single trophic levels or food chains; they establish multiple food connections with other organisms within the ecosystem. This study aims to identify critical mammalian species and assess the robustness of various ecosystem types, considering the diversity of species presence, through food web analysis. Computational graphic-based network analysis is employed to achieve this goal. Ecosystem types, categorized by their land cover, include plantation/agricultural forests, Bushes and shrubss, forests, and mixed landscapes. Network centrality metrics such as degree, closeness, betweenness, and eigenvector centrality are utilized to evaluate the presence of key species and ecosystem robustness. The relative contribution of mammalian species as connectors and regulators of energy flow in the food web ranges from 8-23% of all nodes involved. Key mammalian species are classified into ecosystem stability and sustainability keys. In Bushes and shrubss ecosystems, key species predominantly consist of mammalian predator species that are crucial for maintaining ecosystem stability through population control. Conversely, in other ecosystems, key species are primarily connectors, ensuring the sustained energy flow. The most resilient food webs are observed in Bushes and shrubss and mixed ecosystems due to their higher biomass growth rates and abundant presence of mammalian species. Utilizing food web analysis can significantly contribute to species and ecosystem conservation efforts by offering a comprehensive understanding of interspecies interactions, food web structures, and ecosystem dynamics.

Keywords: Energy flow, food web, key species, network centrality, robustness

INTRODUCTION

The interaction between mammalian species and other organisms, which shape and influence the structure and dynamics of ecosystems, can be elucidated through food webs. This concept facilitates the understanding of the crucial roles played by mammals in maintaining ecosystem equilibrium and conserving their populations, as well as the roles of other organisms in the overall sustainability of ecosystems (Matsuda and Namba 1991; Landi et al. 2018). Ecological studies employ the concept and modeling of food webs to comprehend population, community, and ecosystem dynamics (Baiser et al. 2013; Ochoa-Hueso et al. 2021). This endeavor involves field data analysis, experiments, and the development of mathematical models and computer simulations (Thompson et al. 2012; Sunaryo et al. 2013).

The food web evolved from the concepts of food chains and pyramids, originally introduced by Charles Elton in 1927 through his book "Animal Ecology." A food chain represents a linear picture of the flow of energy and nutrients between organisms in an ecosystem. It provides a general idea of the sequence of consumers and organisms consumed within it. On the other hand, the food pyramid highlights the trophic structure and the amount of energy or biomass available at each trophic level in an ecosystem. Each level of the food pyramid indicates the amount of biomass or energy present, with lower trophic levels having greater biomass than higher trophic levels. The main difference between a food pyramid and a food chain lies in the presentation of information (Fretwell 1987; Trebilco et al. 2013). Although food pyramids provide a general overview of the biomass or energy available at each trophic level in an ecosystem, food chains summarize the linear sequence of energy and nutrient flows between organisms (Van Dover 2001; Agrawal and Gopal 2013; Galiana et al. 2021).

In contrast to food chains and food pyramids, the concept of food webs represents a more realistic portrayal of the flow of energy and nutrients within an ecosystem (Capocefalo et al. 2018), as it captures the intricate interrelationships in feeding dynamics among diverse organisms within an ecosystem (Landi et al. 2018; Lever et al. 2023). Organisms are not confined to singular trophic positions or linear food chains; they can establish multiple feeding connections with other organisms across the ecosystem. Food webs offer a more comprehensive depiction of ecosystem complexity than food chains (Borrelli and Ginzburg 2014; Dunne 2023). Certain mammalian species frequently exhibit dietary versatility and interact with various organisms in their surroundings.

The evolution of food webs in ecology cannot be directly attributed to any individual or specific discovery. Instead, this theory has progressed alongside research and a deeper understanding of organism interactions in the natural world (Webb and Boltt 1990; Dunne 2023). Advances in bioinformatics technology and computer simulation modeling have also played a significant role in its development. Computational graphics-based system network analysis examines food webs within ecosystems (Kones et al. 2009; Steele and He 2019; Funes et al. 2022).

This study utilizes the food web concept to identify the roles of each mammalian species within an ecosystem. Key species within an ecosystem can be determined by assessing species' roles in the food web (Libralato et al. 2006; Cagua et al. 2019). By combining and analyzing the roles of these species comprehensively, we can gain deeper insights into how ecosystems withstand various disturbances (Evans et al. 2013). These disturbances might include environmental changes, climate fluctuations, or human interventions that could threaten ecosystem stability. A holistic understanding of each species' role within the food web allows us to predict and manage the impacts of such disturbances, ensuring the ecosystem remains stable and functions effectively. This integration helps us understand the individual contributions of species and how their interactions collectively support the ecosystem's resilience. This research aims to ascertain the main mammal species and the resilience of various ecosystem types through food web analysis. The findings can provide biodiversity conservation stakeholders with a novel approach to managing species conservation and serve as a reference for policy-making concerning the future of Indonesia's rich biodiversity, particularly on the island of Kalimantan.

MATERIALS AND METHODS

Data and tools

This study utilized survey data on species presence across 78 locations in Kalimantan Island, Indonesia, from 2015 to 2020 (Figure 1). The k-means algorithm was applied for cluster analysis, grouping species presence data based on land cover types, species richness, and tropical diversity. The analysis was conducted using Minitab version 20.0 software. The results of the cluster analysis revealed four distinct land cover type patterns: plantation and industrial forest plantation (K1), Bushes and shrubss (K2), forests (K3), and mixed (proportion of forest, plantation, and Bushes and shrubss areas tends to be similar) (K4). Each land cover type pattern was subdivided into sub-groups based on species richness and tropical diversity. These land cover patterns are herein referred to as ecosystem types.

The analysis and identification of key species in food webs were conducted using Gephi 0.10.1 software, a network analysis tool employing graphical algorithms that measure the relationships and vector distances between nodes (Bastian et al. 2009). In this study, the nodes represent mammalian species within an ecosystem. Each ecosystem type is represented by one example location with deviation values in land cover diversity and species presence closest to the average of the ecosystem subtype (Table 1).

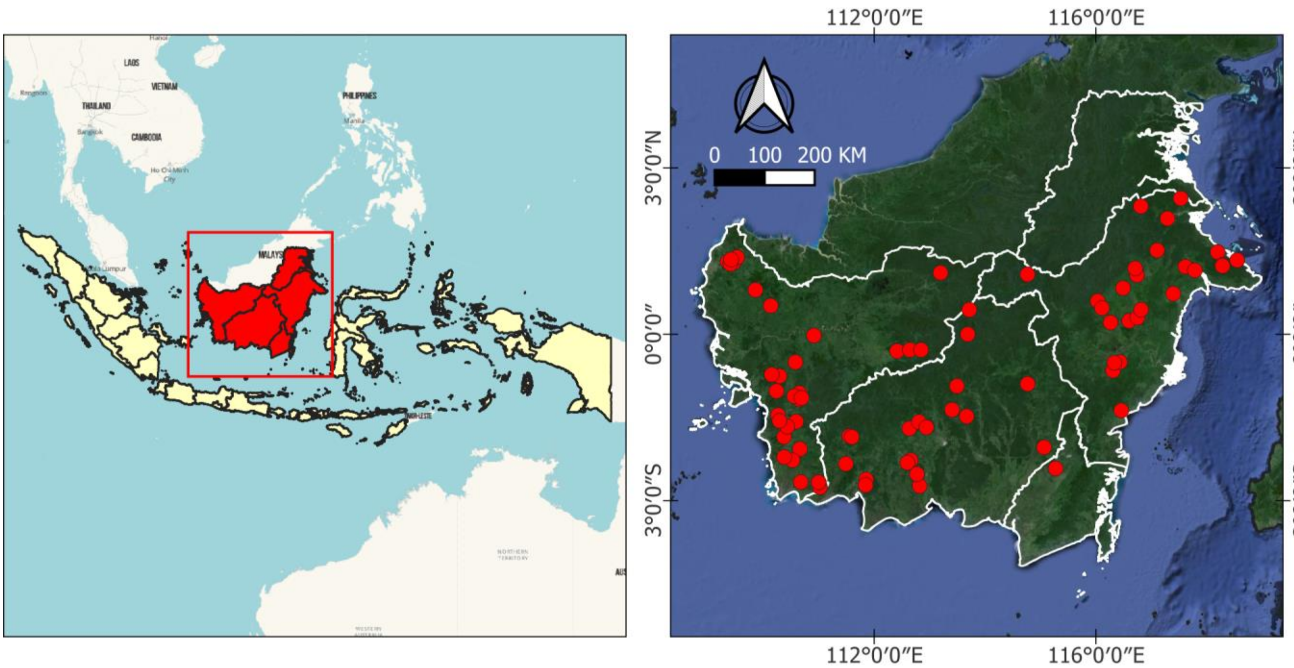


Figure 1. A survey of 78 locations identified the presence of mammal species on Kalimantan Island, Indonesia (marked with red dots)

Table 1. Ecosystem types, locations, and number of species presence for food web analysis

Ecosystem types	No.	Code	Location sub-dist/dist/prov	Lat/long centroid (dd)	Number of mammal species			
					Herbivore	Omnivore	Carnivore	Total
K1: Plantation and industrial plantation forest	1	K11	Simpang hilir/Kayong Utara,Ketapang/ Kalbar	-1.03 S/ 110.24 T	12	14	6	32
	2	K12	Bongan/Kutai Barat/Kaltim	-0.65 S/116.31 T	8	9	4	21
	3	K13	Mentaya Hilir/Kotim/Kalteng	-2.52 S/112.77 T	4	6	2	12
K2: Bushes and shrubss	4	K21	Serawai/Sintang/Kalbar	-0.30 S/112.41 T	10	14	9	33
	5	K22	Air besar, Kuala Behe/Sambas/Kalbar	0.80 U/109.86 T	8	10	4	22
	6	K23	Busang, Muara Ancalong/Kutai Timur/Kaltim	0.83 U/ 116.49 T	4	7	2	13
K3: Forest	7	K3	Kapuas Hulu/Kalbar	1.11 U/113.20 T	13	13	5	31
K4: Mixed	8	K41	Matan Hilir, Nanga Tayap/Ketapang/Kalbar	-1.56 S/110.29 T	10	14	5	29
	9	K42	Rungan/Gunung Mas/Kalteng	-1.48 S/113.67 T	9	10	4	23
	10	K43	Gunung Tabur/Berau/Kaltim	2.45 U/117.53 T	4	8	2	14

Food web network analysis

The food web network analysis aims to identify key mammalian species within an ecosystem. Additionally, it is utilized to determine the level of ecosystem stability (Dunne et al. 2002; Kones et al. 2009; Staniczenko et al. 2010). This process commences by constructing a graphical algorithm of the food web at each survey location using the Gephi 0.10.1 software tool. The assumption employed for developing the graphical algorithm is to assign non-mammalian organisms as constants based on the findings during the survey, such as plants, insects, birds, and herpetofauna, with their attributes as prey and predators. Decomposers are excluded from the formed food webs in each ecosystem. Although social factors, such as hunting and land cover change, are assumed not to occur in this analysis, it is important to recognize that, in reality, pressures on land cover can influence food availability for species. However, this study focuses on how mammalian species are endowed with attributes according to selected variables to determine key species without considering these external factors.

The position of mammal species in food webs is as actors that are either preyed upon or predators. These actors are called nodes in network analysis, and each species can play both roles. Interactions between species depict predation relationships. Species being preyed upon are called sources, predators are called targets, and directed edges represent these interactions. The weight of interactions between species (β_i) is obtained from the predation probability values (ω_i).Variables used in calculating predation probability include diet diversity and species body weight, which range from 0 to 1 (Woodward and Hildrew 2002). The values of these interaction weights are arranged in a matrix representing the relationships between nodes.

Key species within an ecosystem are identified based on the centrality values (C) attributed to each species. In network analysis, various methodologies exist for quantifying centrality (Lai et al. 2012). This investigation employs four distinct metrics to delineate key species: degree centrality (C_D), betweenness centrality (C_B), closeness centrality (C_C), and eigenvector centrality (C_E). The amalgamation of these centrality metrics is frequently practiced to ascertain key species (Jiang and Zhang 2015; Wu et al. 2020; Gouveia et al. 2021). The cumulative sum of these four metrics serves as a determinant for identifying key species in an ecosystem. Simultaneously, ecosystem stability is measured by computing a resilience network, synthesizing the centrality values associated with each species (Oehlers and Fabian 2021). Each centrality value is endowed with a weight (ρ) derived through the factor analysis (eq.1).

$$Rn \approx \sum_{i=1}^{n} C_i \approx \int (\rho_D \sum_{i=1}^{n} C_D \, , \rho_C \sum_{i=1}^{n} C_C \, , \rho_B \sum_{i=1}^{n} C_B \, , \rho_E \sum_{i=1}^{n} C_E) \quad (1)$$

If Rn represents the robustness value of a food web within an ecosystem, ρ denotes the weighted centrality values obtained from the factor analysis coefficients, F represents the factors with eigenvalues > 1, and φ signifies the relative contribution of factors to diversity. Eq. 1 can be derived as follows (eq. 2):

$$Rn = \varphi_1 \sum F_1 + \varphi_2 \sum F_2 + \ldots . \varphi_n \sum F_n \quad (2)$$

The value of F (i) for each species i is as follows:

$$F(n,i) = \rho_D^2 C_{D,i} + \rho_C^2 C_{C,i} + \rho_B^2 C_{B,i} + \rho_E^2 C_{E,i} \quad (3)$$

$$Kf_i = \sum_1^n F_i \quad (4)$$

The importance value of species within the food web (Kf) will be derived from Eq.3, which indicates key species. A ranking and quartile (Q) approach determines key mammalian species. Key species within a food web are determined if the value of $Kf_i \geq (Kf_{Q2}+Kf_{Q3})/2$. Establishing this threshold value for Kf considers taxa other than mammals involved in the ecosystem. In specific ecosystems, the likelihood of taxa other than mammals dominating the value of Kf ≥ Kf_{Q3} is substantial, as they have not yet been disaggregated into species within that taxon.

Degree centrality (C_D) in food web analysis measures species-i's interactions with other species. This metric indicates how extensively a species interacts with other species within an ecosystem (Lai et al. 2012). The C_D is a combination of in-degree and out-degree. In the context of food webs, in-degree describes how many interactions species-i receives as prey. At the same time, out-degree indicates how many interactions species-i serves as a food source for other species. If d_1 (i) represents interactions as a predator, d_2 (i) represents interactions as a food source, and n is the total number of species in the entire food web, then the C_D equation is as follows (eq.5):

$$C_D(i) = \frac{d_1(i)+d_2(i)}{n-1} \quad (5)$$

Closeness centrality (C_C) in food web analysis is a metric of i-species accessibility to other species. For predator species, this indicates efficiency in obtaining food sources from other species, while for prey species, this indicates vulnerability to becoming a food source for predators. Species exhibiting high closeness centrality tend to have close relationships with other species in the food (Chen and Zhang 2020),thus facilitating an efficient flow of energy and materials. Mathematically, the closeness centrality of species-i (C_C (i)) is computed as the inverse of the total distance from the species-i node to all other species nodes in a food web. Distance is measured by the number of edges required to traverse to reach other species nodes, denoted as d (i,j). A shorter distance implies that species-i is closer to other species in the network. The mathematical equation is expressed as follows (Brandes 2001) (eq.6).

$$C_C(i) = \frac{1}{\sum_{i \neq j} d(i,j)} \quad (6)$$

Betweenness centrality (C_B) within food webs is a metric for quantifying the degree to which species-i is positioned along energy or biomass transfer pathways between two species (Kolesnikov et al. 2019). This suggests that species-i serves as a conduit for interactions between species. Hence, a higher C_B (i) value indicates the heightened importance of species-i on the food web. The absence of species-i would disrupt energy flow pathways, impacting the ecosystem's overall structure and function. These species play a regulatory role in governing energy flux within the ecosystem. Species-i may act as a key predator regulating the populations of other species or serve as essential prey situated in the intermediate tiers of the food chain. Mathematically, C_B of species-i within a food web is expressed as the ratio of all shortest paths between every pair of species that pass through it. If σjk represents the total number of shortest paths between species j and k, and σjk (i) represents the number of shortest paths between j and k that traverse through species i, then the equation for C_B (i) is formulated as follows (Brandes 2001) (Eq.7).

$$C_B(i) = \sum_{j \neq i \neq k} \frac{\sigma_{jk}(i)}{\sigma_{ik}} \quad (7)$$

The eigenvalue centrality (C_E) value in a food web within an ecosystem is employed to ascertain the significance of species-i based on its connections and relationships with other species. This metric also accounts for the importance of other species connected to species-i (Allesina and Pascual 2009). Mathematically, eigenvalue centrality is defined as the eigenvector corresponding to the largest eigenvalue of the network's adjacency matrix. This matrix represents the relationships between species in the network, where the values within the matrix indicate the presence or strength of relationships between species. Thus, species-i, linked to crucial species in the food web, will obtain a higher weight resulting from iterative eigenvalue calculations. Consequently, eigenvalue centrality offers insights into the structure and hierarchy within the network and identifies the most pivotal or influential species within it.If $\alpha_{i,j}$ denotes the relationship value between species-i and j, the relative centrality value of species-i in a set of matrices M (v) comprising numerous species is defined by eq.5. Therefore C_E for species-i is the solution to eq.6. Here, Ax represents the adjacency matrix indicating connections between species, x signifies the eigenvector centrality for species, and λ stands for the eigenvalue for each species (eq.8 and eq.9).

$$x_i = \frac{1}{\lambda}\sum_{j \in M(v)} x_j = \frac{1}{\lambda}\sum_{j \in V} \alpha_{i,j} x_j \quad (8)$$

$$Ax = \lambda x \quad (9)$$

RESULTS AND DISCUSSION

Ecosystem centrality values

The accumulation and average C_D values increase with the greater diversity of species within an ecosystem. The cumulative C_D value reflects the extent of species involvement in food interactions with others in the ecosystem, while a higher average value indicates a more intricate food web (Lai et al. 2012; Kortsch et al. 2015; Delmas et al. 2019). Comparative analyses across ecosystem types and species presence suggest that food webs in Bushes and shrubss ecosystems exhibit the highest and most complex species interactions (Table 2). The cumulative C_C values correlate with the number of species in an ecosystem. Network analysis findings indicate that as the number of species and inter-species distances decrease, the accumulation of C_C values increases (Table 2). This metric illustrates how rapidly a species can access others within the food web. On average, C_C values across ecosystems are consistent, implying uniform resource access efficiency within food webs. However, higher species diversity within ecosystems offers more opportunities for energy transfer among species (Meilhac et al. 2019; Correia and Lopes 2023).

Table 2. The accumulation and average centrality of food webs in each ecosystem

Ecosystem types	Code	∑ Species	$\sum C_D$	$\overline{C_D}$	$\sum C_C$	$\overline{C_C}$	$\sum C_B$	$\overline{C_B}$*)	$\sum C_E$	$\overline{C_E}$
K1: Plantation	K11	32	234.7	5.5±4.21	32.0	0.7±0.29	5.3	0.12±0.27	8.5	0.2±0.16
and industrial	K12	21	154.7	4.8±3.19	24.6	0.8±0.30	3.9	0.12±0.23	9.4	0.3±0.17
forest plantation	K13	12	85.6	3.7±1.98	15.3	0.7±0.34	3.7	0.16±0.24	11.6	0.5±0.23
K2: Bushes and	K21	33	324.1	7.4±4.90	32.2	0.7±0.29	4.1	0.09±0.21	7.9	0.2±0.20
shrubs	K22	22	181.2	5.5±3.70	22.7	0.7±0.32	4.7	0.14±0.28	9.4	0.3±0.17
	K23	13	99.5	4.2±2.11	17.3	0.7±0.32	3.4	0.14±0.23	10.5	0.4±0.20
K3: Forest	K3	31	280.8	6.7±5.06	33.7	0.8±0.24	4.3	0.10±0.23	7.7	0.2±0.19
K4: Mixed	K41	29	225.3	5.6±4.53	28.6	0.7±0.28	4.5	0.11±0.26	8.5	0.2±0.17
	K42	23	168.6	5.0±3.65	24.9	0.7±0.32	3.4	0.10±0.22	9.5	0.3±0.17
	K43	14	118.5	4.7±2.51	18.4	0.7±0.32	3.5	0.14±0.23	10.1	0.4±0.21

Note: *) The normalized C_B values

The accumulation and average C_B values in ecosystems indicate species' importance in maintaining relationships within food webs. Trophic level composition and interspecific competition exert more influence on C_B values than species presence. Ecosystems with high C_B value accumulation typically feature numerous species acting as critical connectors in energy flow, such as in ecosystem type K11 (Table 2). Conversely, a high average of C_B values suggests a scarcity of species acting as disconnectors, such as mammalian predator species in ecosystems K13, K22, K23, and K43 (Tables 1 and 2). This applies at the level of interspecific association as the roles species play within different trophic levels and their interactions (predation and competition) shape energy transfer and ecosystem stability. Critical connectors link multiple trophic levels, ensuring efficient energy flow. Competition for resources influences species distribution and the overall structure of the food web. Ecosystems with high C_B values have species that facilitate robust energy transfer and support resilience. Conversely, a high average C_B value indicates fewer disruptions in energy flow. Thus, interspecific interactions are key to understanding C_B values and their impact on ecosystem stability.

The accumulation and average C_E values are inversely related to species diversity within the ecosystem (Table 2). An ecosystem's larger accumulation and average C_E values indicate that each species has a significant C_E or is concentrated on specific species. Conversely, lower accumulation and average C_E values indicate a more even distribution of values among species. C_E values serve as an indication of vulnerability to ecosystem stability. An increase in C_E values indicates increasing vulnerability, as the ecosystem relies more heavily on specific species (Swift et al. 2023; Zhao et al. 2023).

The centrality values of mammal species within the food web of an ecosystem

Degree centrality species (C_D)

The degree of centrality of species reflects the extent of interconnection of a species with others within the food web. Species with high C_D indicate a more significant number of species linked to them. This association may signify species serving as sources of energy or food (out-degree-OC_D) and species as consumers of energy/predators (in-degree, IC_D). The C_D value is the summation of IC_D and OC_D. Analysis of food networks in each ecosystem type reveals that high species CD may arise from either significant IC_D or OC_D, or both having equal magnitudes. Species with large IC_Ds suggest their connection to numerous energy sources, while high OC_D suggests species linked to many predators. Typically, species with large IC_{Ds} are carnivores and big omnivores, whereas those with high OC_D are smaller-sized species (Table 3). Mammalian species tend to exhibit similar IC_D and OC_D values. These species function as energy sources for other species while also serving as predators. They are generally small-sized (<5 kg) and occupy omnivore and carnivore trophic levels (Roemer et al. 2009; Tucker and Rogers 2014).

In the context of mammalian species' food webs within ecosystems, analysis reveals that approximately one-third of the cumulative C_D values in each ecosystem originate from the top 3-5 species (Table 3). Most of these species exhibit higher IC_D values than OC_D values, showing significant gradients. Species with high C_D values include both large omnivores and carnivores (Lai et al. 2012; Sun et al. 2020). Large omnivorous species such as *Helarctos malayanus*, *Paradoxurus hermaphroditus*, and *Sus scrofa*, and carnivores such as *Viverra tangalunga*, *Prionailurus bengalensis*, *Pardofelis marmorata*, *Neofelis diardi*, and *Prionailurus planiceps* are among them. Small omnivorous species like *Ratufa affinis*, *Nycticebus menagensis*, and *Herpestes brachyurus* exhibit high C_D values, with approximately 50% stemming from OC_D. These species position themselves within the food web as predators and prey for other species.

The C_D values within each ecosystem provide insights into the extent of species' interactions or relationships with others within the food web. Interpreting these values also offers an understanding of the availability and diversity of food sources within an ecosystem (Table 3 and Figure 2). A higher value indicates a greater abundance of food sources in the ecosystem and higher species diversity (Feng et al. 2019; Ng et al. 2021). Higher average and cumulative C_D values lead to more stable ecosystems with lower vulnerability to disturbances or changes. Species with high C_D values have a more significant impact on ecosystem stability if disrupted or lost, while species with low C_D values have a more localized influence.

Table 3. Species contribute 0.33 to the cumulative C_D values in the food web of each ecosystem

Ecosystem types	Code (∑ species)	Species	IC_D	OC_D	C_D
K1: Plantation and industrial forest plantation	K11 (32 species)	*Helarctos malayanus*	15.67	0.00	15.67
		Prionailurus bengalensis	11.29	0.26	11.55
		Pardofelis marmorata	9.21	1.04	10.26
		Prionailurus planiceps	8.97	0.79	9.76
		Ratufa affinis	4.00	2.80	6.80
	K12 (21 species)	*Helarctos malayanus*	13.39	0.00	13.39
		Prionailurus bengalensis	8.08	0.44	8.52
		Paradoxurus hermaphroditus	5.82	1.36	7.18
		Prionodon linsang	4.35	1.46	5.81
	K13 (12 species)	*Helarctos malayanus*	7.74	0.00	7.74
		Prionailurus bengalensis	5.80	0.37	6.17
		Paradoxurus hermaphroditus	3.51	1.47	4.98
K2: Bushes and shrubss	K21 (33 species)	*Viverra tangalunga*	17.40	1.32	18.72
		Helarctos malayanus	18.34	0.00	18.34
		Neofelis diardi	14.21	0.40	14.61
		Arctogalidia trivirgata	10.02	3.85	13.87
		Prionailurus bengalensis	12.30	1.16	13.46
	K22 (22 species)	*Viverra tangalunga*	15.66	0.00	15.66
		Arctogalidia trivirgata	8.52	2.25	10.76
		Prionailurus bengalensis	10.02	0.49	10.51
		Paradoxurus hermaphroditus	7.67	1.58	9.24
	K23 (13 species)	*Helarctos malayanus*	8.53	0.00	8.53
		Herpestes brachyurus	5.75	1.37	7.12
		Prionailurus bengalensis	5.41	0.17	5.58
K3: Forest	K3 (31 species)	*Helarctos malayanus*	16.73	0.00	16.73
		Lutra sumatrana	13.88	0.32	14.19
		Sus scrofa	13.55	0.00	13.55
		Prionailurus bengalensis	12.08	0.94	13.02
		Paradoxurus hermaphroditus	9.88	1.85	11.73
K4: Mixed	K41 (29 species)	*Helarctos malayanus*	17.47	0.00	17.47
		Prionailurus bengalensis	13.00	0.38	13.39
		Herpestes brachyurus	11.51	1.83	13.34
		Paradoxurus hermaphroditus	10.33	1.20	11.54
	K42 (23 species)	*Helarctos malayanus*	15.11	0.00	15.11
		Prionailurus bengalensis	9.97	0.47	10.44
		Paradoxurus hermaphroditus	6.97	1.51	8.47
		Nycticebus menagensis	4.00	2.12	6.12
	K43 (14 species)	*Viverra tangalunga*	9.23	0.59	9.82
		Helarctos malayanus	9.01	0.00	9.01
		Herpestes brachyurus	5.75	2.03	7.78

Closeness centrality species

The C_C measure in food webs reflects the efficiency of species in accessing food resources and transmitting energy. Species with high C_C tend to have shorter access and act as connectors of energy flow. Conversely, species with low C_C indicate isolation from other mammalian species and lack connectivity in energy flow (Jordán et al. 2007). Model results indicate that species acting as connectors in the ecosystem's energy flow have $C_C>0$ and vice versa. Species without predators in the food web have C_C approaching 0, for instance, *H. malayanus*, *Sus barbatus*, *S. scrofa*, *Rusa unicolor*, and *Pongo pygmaeus*. These are large-sized species with minimal chances of being preyed upon by carnivorous mammals in the ecosystem under study. C_C is related to C_D values. The mentioned species above have significantly higher IC_D than OC_D, resulting in low C_C. These species only serve as final energy recipients without reconnecting with other species. Higher chances of a species being preyedon and acting as an energy flow connector for other species will result in high C_C.

Species with low C_C can also indicate their vulnerability level due to their dependence on other species within an ecosystem. Conversely, high C_C can indicate their role in maintaining ecosystem stability and sustainability. These species are more responsive to environmental changes within the ecosystem, as they have quick access to resources and other species, enabling them to adapt better to changing environmental conditions. High C_C species, being more integrated and central within the ecosystem, play a crucial role in supporting the flow of energy and nutrients. Their ability to interact with multiple species efficiently significantly contributes to the overall resilience and health of the ecosystem.

Among the mammalian species analyzed in this study, those with high C_C include *P. bengalensis, P. marmorata, P. planiceps, P. hermaphroditus, Macaca fascicularis, Macaca nemestrina, Emballonura alecto, Muntiacus muntjak, Tragulus napu, Hystrix crassispinis, Presbytis rubicunda, Presbytis frontata, Hylobates muelleri, Hystrix brachyura, Hipposideros cineraceus*, and *Manis javanica*. In each ecosystem, the number of species with C_C>0.5 averages above ±75% of its total species count (See Figure 3).

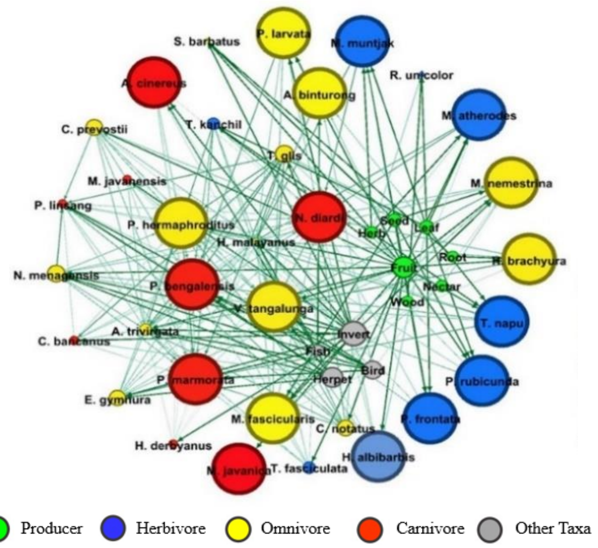
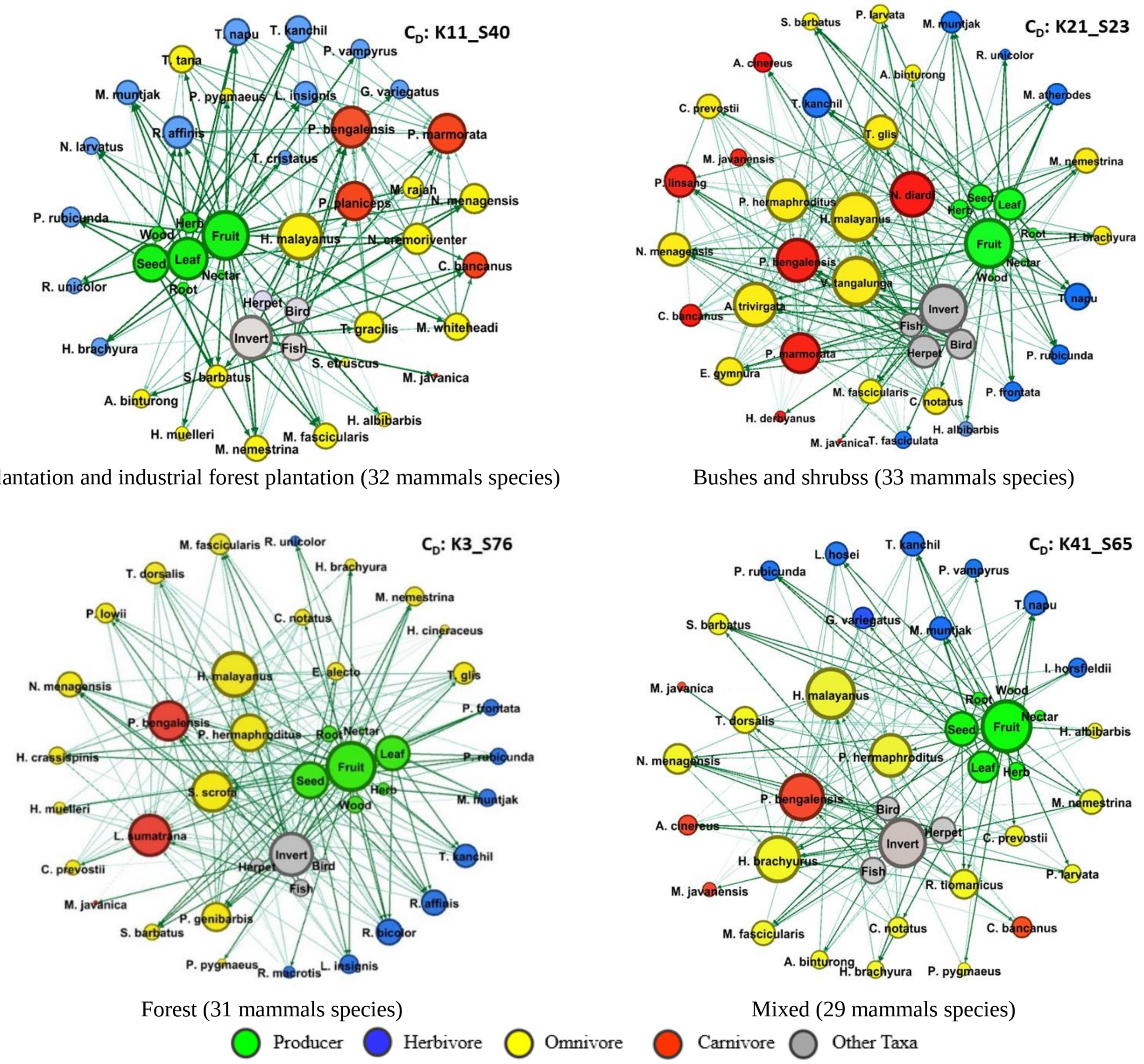


Figure 3. An example of closeness centrality values in the Bushes and shrubss ecosystem food web (K21). (Note: Larger circle sizes indicate higher values)



Plantation and industrial forest plantation (32 mammals species)

Bushes and shrubss (33 mammals species)

Forest (31 mammals species)

Mixed (29 mammals species)

Figure 2. The degree centrality measure of each species in the food web of each ecosystem

Betweenness centrality

The C_B values in a food web within an ecosystem measure how frequently a species lies on the shortest paths between pairs of other species. These species act as conduits for energy flow between species in the ecosystem. Species with high C_B values serve as primary connectors for interactions among species in the ecosystem across various trophic levels to facilitate the flow of energy and matter between these species. This function makes them controllers of energy flow in the ecosystem. In this context, the relative contribution of mammalian species ranges from 8-23.2% (see Table 4 and Figure 4), and species in other taxa, such as birds, herpetofauna, invertebrates, and fish, contribute the remainder. The influence of species composition in trophic levels on this relative contribution is greater than the number of species present.

The food web analysis results across various ecosystems reveal that small mammal species occupying herbivorous and omnivorous trophic levels exhibit high C_B (Table 5 and Figure 4). These species with high C_B values were selected using a fitting curve method with constraints when changes in the curve's curvature from the value sequence occur. The results demonstrate that species composition is more influential than species richness (Mello et al. 2015; Astudillo et al. 2020). Species composition refers to the types and functional roles of species present in an ecosystem, emphasizing the identity and interactions of these species. Species with high C_B values play a key role as connectors in the food web of an ecosystem. These species ensure efficient energy and nutrient flow and maintain ecosystem stability. Species richness denotes the quantity of various species within an ecosystem without considering the functional roles or interactions of the species. Species richness alone is insufficient to guarantee the ecosystem's connectivity and stability. Even though an ecosystem may have many species, without species that serve as key connectors with high C_B, the ecosystem may be less stable and more vulnerable to disturbances. For instance, the presence of 29 species in ecosystem K41 includes only two species with high C_B values. In contrast, ecosystems K13, K23, and K43, with lower species presence, have 5, 4, and 4 species with high C_B values, respectively. Most species with high C_B values are found in ecosystem K3, totaling eight species. The presence of species with substantial C_B within each ecosystem profoundly impacts its stability and sustainability. A reduction in species with high C_B heightens ecosystem vulnerability, as their absence could disrupt energy flow within the food web, exerting a dominant influence on the extinction dynamics of other species. Thus, species exhibiting high C_B value may bolster ecosystem resilience against environmental disturbances or changes.

The results of this study also indicate that in every ecosystem, there are species with low CB values, which tend to approach zero. These species play a less significant role in the flow of energy and nutrients within the ecosystem's food web. They do not function as key connectors between other species in the ecosystem, so their presence or absence has a minor impact on the stability and connectivity of the ecosystem. These species are likely more dependent on other species rather than acting as critical connectors within the ecosystem network. In contrast to other species in the food web, this species is rarely involved in food pathways or energy transfer. Several factors contribute to this phenomenon, including (i) highly specific or restricted dietary specialization, such as observed in *M. javanica*, (ii) habitat isolation or specificity limits interactions between these species and others in the food web, as seen in *Lutra sumatrana* and *Aonyx cinereus*, (iii) size, reducing their susceptibility to predation by other mammals in the ecosystem, as observed in *P. pygmaeus*, *R. unicolor*, *S. barbatus*, and *S. scrofa*, (iv) species positioned at the apex of the food pyramid in an ecosystem, such as *H. malayanus*, and (v) species with small or limited populations result in constrained interactions with other species. However, species with low C_B may play more specific roles in maintaining ecosystem balance, albeit not actively engaged in direct inter-species connections.

Eigenvector centrality species

The C_E value of a species indicates the strength of its connections within the food web. Species with high C_E are typically crucial for maintaining ecosystem equilibrium, as this metric also considers the importance of other species connected to them. In this study, the highest C_E was determined using a fitting curve approach, with the constraint of the curve's inflection point. Analysis across each ecosystem revealed that omnivorous and carnivorous species tend to exhibit high C_E values (Table 6).

Table 4. The relative contribution of mammal species as connectors and controllers of energy flow in the food web of an ecosystem

Ecosystem types	**Code (∑ species)**	**∑ C_B*)**	**Mammal contribution**
K1:Plantation	K11 (32 species)	5.3	12.9 %
andindustrial forest	K12 (22 species)	3.9	13.0 %
plantation	K13 (12 species)	3.7	13.4 %
K2:Bushes and	K21 (33 species)	4.1	23.2 %
shrubss	K22 (22 species)	4.7	12.1 %
	K23 (13 species)	3.4	9.7 %
K3:Forest	K3 (31 species)	4.3	11.6 %
K4:Mixed	K41 (29 species)	4.5	10.8 %
	K42 (23 species)	3.4	8.0 %
	K43 (14 species)	3.5	10.7 %

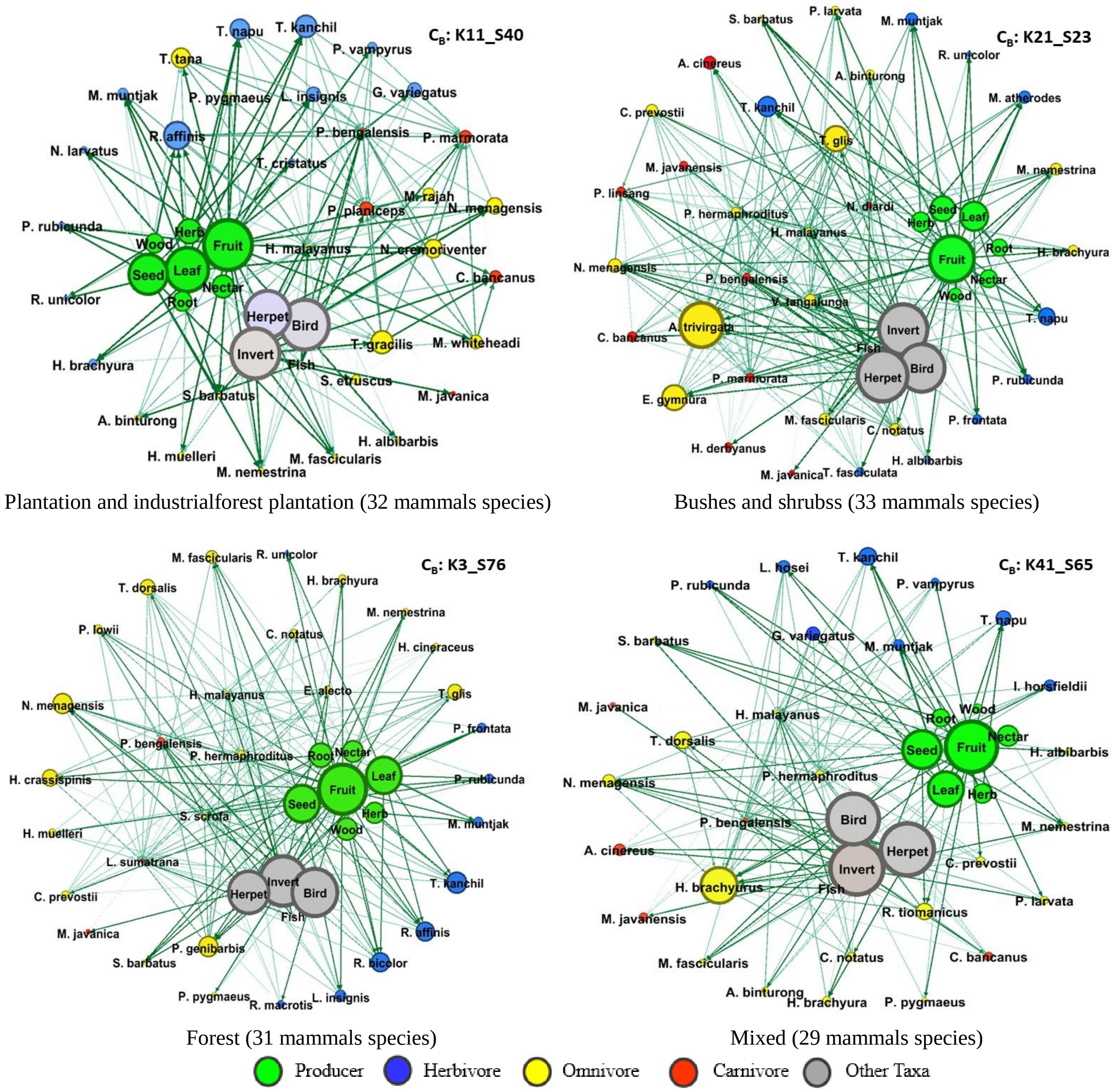
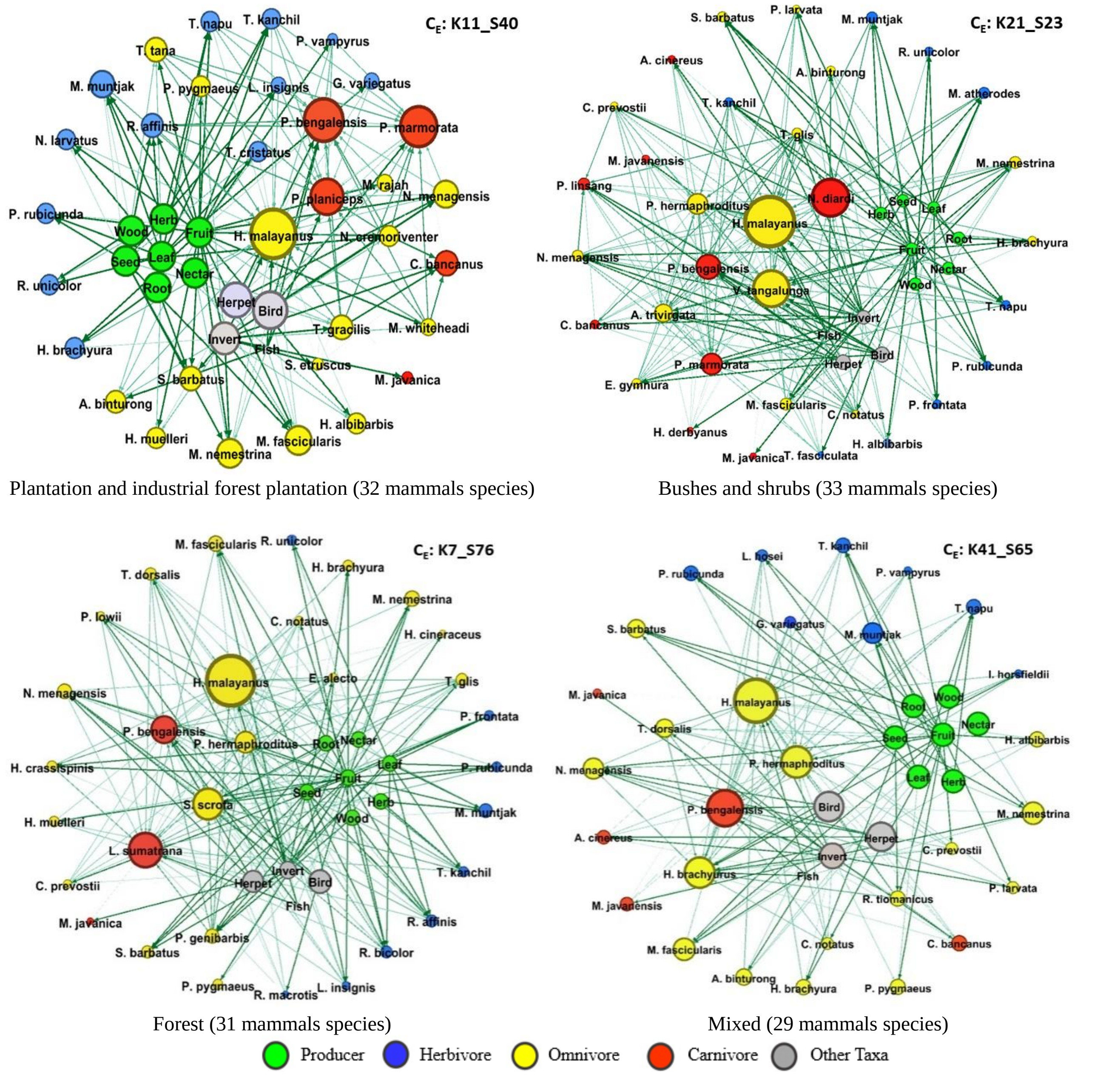


Figure 4. The betweenness centrality measure of each species in the food web of each ecosystem

High C_E value among omnivores stems from the diversity of their dietary preferences. Notable species in this category include *H. malayanus*, *P. hermaphroditus*, and *Arctogalidia trivirgata*. On the other hand, high C_E value in carnivores arises from the diverse range of mammalian species they prey upon such species include *N. diardi*, *V. tangalunga*, *P. bengalensis*, and *P. marmorata* (Figure 5). Besides their dietary diversity, these species are also linked to other pivotal mammalian species; both prey and predator (refer to Table 3). Species with elevated C_E wield considerable influence over ecosystem stability. Their presence or absence significantly impacts biodiversity and trophic equilibrium within the ecosystem, affecting the distribution of energy and nutrient flow across the food web.

Ecosystem stability and key species

The stability of ecosystems within the framework of food web analysis is evaluated based on the robustness of the network (Rn). The assessment of network robustness integrates centrality values derived from the food web. In this study, the network centrality values under scrutiny are C_D, C_C, C_B, and C_E. Factor analysis yields two factors (F1 and F2) for each ecosystem. Each ecosystem exhibits distinct factor weights and centrality variables (Table 7). Equations incorporating constant values in factor and centrality weights will be utilized to compute the food web's robustness, stability, and sustainability.



Plantation and industrial forest plantation (32 mammals species)

Bushes and shrubs (33 mammals species)

Forest (31 mammals species)

Mixed (29 mammals species)

Figure 5. The eigenvector centrality measure of each species in the food web of each ecosystem

The robustness of the food web depends on the availability of food resources, the diversity of species, and the structure of the community within the ecosystem, as these factors collectively determine the stability and resilience of ecological interactions. On average, food webs within Bushes and shrubs ecosystems demonstrate the highest robustness compared to other ecosystems, especially those characterized by heightened species diversity (see Table 8). Bushes and shrubs ecosystems boast more significant biomass growth than other ecosystems, ensuring ample food resource availability. Within such ecosystems, species that uphold stability and regulate populations wield a more dominant presence than other ecosystems, notably in ecosystem K21. These species typically comprise mammalian predators. Conversely, species contributing to sustainability and connectivity assume a more prominent role in ecosystems characterized by slower biomass growth, such as K1 and K3.

A greater number of mammal species correlates with more resilient food webs. Ecosystems with a rich diversity of mammal species generally show higher resilience than ecosystems with fewer species. However, community structure across trophic levels also influences food web resilience. Compared with herbivores and carnivores, the prevalence of omnivorous animals contributes to the increase in Rn values. For example, despite fewer species, the K42 ecosystem is more resilient than K41.

Table 5. Mammal species with influential C_B values in the food web of a specific ecosystem

Ecosystem types	Code (∑ species)	Species	C_B (x 10^{-2})
K1: Plantation and industrial forest plantation	K11 (32 species)	*Ratufa affinis*	0.34
		Tupaia gracilis	0.22
		Tragulus kanchil	0.21
		Tragulus napu	0.16
		Tupaia tana	0.16
		Niviventer cremoriventer	0.13
		Nycticebus menagensis	0.10
	K12 (22 species)	*Tragulus kanchil*	0.38
		Rattus exulans	0.36
		Rattus argentiventer	0.36
		Tragulus napu	0.24
		Aonyx cinereus	0.19
		Callosciurus notatus	0.18
		Prionodon linsang	0.16
	K13 (12 species)	*Tragulus kanchil*	0.80
		Aonyx cinereus	0.72
		Tragulus napu	0.53
		Callosciurus notatus	0.19
		Paradoxurus hermaphroditus	0.14
K2: Bushes and shrubs	K21 (33 species)	*Arctogalidia trivirgata*	2.29
		Tupaia glis	0.52
		Echinosorex gymnura	0.51
		Tragulus kanchil	0.29
		Tragulus napu	0.20
	K22 (22 species)	*Arctogalidia trivirgata*	0.83
		Ratufa bicolor	0.53
		Tragulus kanchil	0.31
		Tragulus napu	0.17
	K23 (13 species)	*Tragulus napu*	0.61
		Herpestes brachyurus	0.59
		Callosciurus notatus	0.20
		Muntiacus muntjak	0.15
K3: Forest	K3 (31 species)	*Tragulus kanchil*	0.20
		Petinomys genibarbis	0.19
		Nycticebus menagensis	0.18
		Ratufa affinis	0.16
		Ratufa bicolor	0.16
		Hystrix crassispinis	0.12
		Tupaia dorsalis	0.10
		Tupaia glis	0.10
K4: Mixed	K41 (29 species)	*Herpestes brachyurus*	0.98
		Tragulus kanchil	0.17
	K42 (23 species)	*Tragulus kanchil*	0.27
		Tragulus napu	0.18
		Nycticebus menagensis	0.18
		Aonyx cinereus	0.14
		Galeopterus variegatus	0.13
		Muntiacus muntjak	0.06
	K43 (14 species)	*Tragulus napu*	0.64
		Herpestes brachyurus	0.55
		Callosciurus notatus	0.18
		Muntiacus muntjak	0.14

Key species within food webs are guardians of stability and sustainability in ecosystem energy flow. Different ecosystem characteristics yield distinct key species (Hooper et al. 2005; Correia and Lopes 2023). In Bushes and shrubs ecosystems, key species are predominantly mammalian predators, spanning both carnivore and omnivore trophic levels. These species uphold ecosystem stability by regulating the populations of prey species. Conversely, in other ecosystems, key species are primarily connectors, ensuring the sustained energy flow. Typically, these species inhabit herbivore and omnivore trophic levels and possess relatively smaller body sizes than their predators.

Table 6. Mammal species with influential C_E in the food web of each ecosystem

Ecosystem types	Code (∑ species)	Species	C_E
K1: Plantation and industrial forest plantation	K11 (32 species)	*Helarctos malayanus*	1.00
		Prionailurus bengalensis	0.53
		Pardofelis marmorata	0.45
		Prionailurus planiceps	0.35
	K12 (22 species)	*Helarctos malayanus*	1.00
	K13 (12 species)	*Helarctos malayanus*	1.00
		Macaca fascicularis	0.57
K2: Bushes and shrubs	K21 (33 species)	*Helarctos malayanus*	1.00
		Neofelis diardi	0.72
		Viverra tangalunga	0.70
		Prionailurus bengalensis	0.43
		Pardofelis marmorata	0.36
		Paradoxurus hermaphroditus	0.35
		Arctogalidia trivirgata	0.28
	K22 (22 species)	*Viverra tangalunga*	1.00
		Prionailurus bengalensis	0.49
		Paradoxurus hermaphroditus	0.43
		Arctogalidia trivirgata	0.42
	K23 (13 species)	*Helarctos malayanus*	1.00
K3: Forest	K3 (31 species)	*Helarctos malayanus*	1.00
		Lutra sumatrana	0.66
		Sus scrofa	0.57
		Prionailurus bengalensis	0.49
		Paradoxurus hermaphroditus	0.36
K4: Mixed	K41 (29 species)	*Helarctos malayanus*	1.00
		Prionailurus bengalensis	0.55
		Paradoxurus hermaphroditus	0.43
		Herpestes brachyurus	0.41
	K42 (23 species)	*Helarctos malayanus*	1.00
		Prionailurus bengalensis	0.42
	K43 (14 species)	*Helarctos malayanus*	1.00
		Viverra tangalunga	0.80

Table 7. Weighting factors and centrality variables in food web networks in each ecosystem

Ecosystem types	Code	φF1	φF2	ρC_D	ρC_C	ρC_B	ρC_E	Q2	Q3
K1: Plantation and industrial forest plantation	K11	0.478	0.275	-0.319*)	-0.149**)	1.134*)	0.026*)	0.029	0.054
	K12	0.507	0.285	-0.040*)	0.062**)	-0.061*); -1.116**)	0.274*)	0.023	0.046
	K13	0.414	0.302	-0.065*)	-0.065**)	-0.190*)	0.194*); -0.105**)	0.009	0.014
K2: Bushes and shrubs	K21	0.457	0.259	-0.552*)	0.015**)	0.164*)	1.335*)	0.137	0.199
	K22	0.48	0.285	-0.184*)	1.037**)	1.071*); -0.078**)	-0.046*)	0.301	0.318
	K23	0.433	0.305	-0.036*)	0.038**)	0.170*)	-0.202*)	0.009	0.012
K3: Forest	K3	0.47	0.301	-0.306*)	0.211**)	1.122*); 0.077**)	0.064*)	0.035	0.057
K4: Mixed	K41	0.485	0.277	-0.225*)	-0.169 **)	1.090*)	-0.039*)	0.019	0.031
	K42	0.496	0.295	-0.281*)	-1.062**)	1.129*)	-0.034*)	0.339	0.355
	K43	0.426	0.306	-0.178*)	1.055**)	1.078*)	-0.078*)	0.029	0.077

Note: φF1: Weighting of F1; φF2: Weighting of F2; ρC_D: Weighting of degree centrality; ρC_C: Weighting of closeness centrality; ρC_B: Weighting of betweenness centrality; ρC_E: Weighting of variables with eigenvalues >0; Q2 and Q3 are quartile values for classifying important mammal species in ecosystems *) weight values of centrality variables in Factor 1; **) weight values of centrality variables in Factor 2

Table 8. Key species and robustness of food webs in each ecosystem

Ecosystem type	Code (∑ species)	Key species	Kf	Function	Rn (Robustness)
K1: Plantation and industrial plantation forest	K11 (32 species)	*Ratufa affinis*	0.095	Kb	3.91
		Tupaia gracilis	0.067	Kb	
		Tragulus kanchil	0.060	Kb	
		Tragulus napu	0.052	Kb	
		Tupaia tana	0.050	Kb	
		Niviventer cremoriventer	0.047	Kb	
	K12 (22 species)	*Tragulus kanchil*	0.042	Kb	1.80
		Rattus exulans	0.041	Kb	
		Rattus argentiventer	0.041	Kb	
		Helarctos malayanus	0.039	St	
	K13 (12 species)	*Helarctos malayanus*	0.017	St	0.26
K2: Bushes and shrubs	K21 (33 species)	*Helarctos malayanus*	0.936	St	8.43
		Viverra tangalunga	0.694	St,Kb	
		Neofelis diardi	0.680	St	
		Prionailurus bengalensis	0.436	St	
		Pardofelis marmorata	0.367	St	
		Paradoxurus hermaphroditus	0.364	St,Kb	
		Arctogalidia trivirgata	0.327	St,Kb	
		Prionodon linsang	0.173	St,Kb	
	K22 (22 species)	*Tragulus napu*	0.333	Kb	9.76
		Aonyx cinereus	0.328	Kb	
		Paradoxurus hermaphroditus	0.320	St,Kb	
		Prionailurus bengalensis	0.318	St	
		Macaca nemestrina	0.315	Kb	
		Hystrix brachyura	0.309	Kb	
	K23 (13 species)	*Helarctos malayanus*	0.018	St	0.25
		Callosciurus notatus	0.015	Kb	
K3: Forest	K3 (31 species)	*Petinomys genibarbis*	0.061	Kb	3.44
		Nycticebus menagensis	0.059	Kb	
		Tragulus kanchil	0.059	Kb	
		Ratufa bicolor	0.052	Kb	
		Ratufa affinis	0.052	Kb	
K4: Mixed	K41 (29 species)	*Herpestes brachyurus*	0.148	St,Kb	3.05
		Tupaia dorsalis	0.033	Kb	
		Rattus tiomanicus	0.031	Kb	
		Tragulus kanchil	0.031	Kb	
		Tragulus napu	0.028	Kb	
	K42 (23 species)	*Tragulus napu*	0.367	Kb	10.77
		Aonyx cinereus	0.359	St,Kb	
		Prionailurus bengalensis	0.356	St	
		Paradoxurus hermaphroditus	0.356	St,Kb	
		Muntiacus muntjak	0.350	Kb	
	K43 (14 species)	*Tragulus napu*	0.067	Kb	2.19
		Herpestes brachyurus	0.063	St,Kb	

Note: Kf: Importance value of species in the food web. Rn: Robustness value of the food web in an ecosystem. St: Role of mammal species for stabilityof food web, including population control. Kb: Role of mammal species in sustainability and connectivity of energy flow in the food web

Discussion

Network analysis for the food web within the ecosystem serves as a valuable tool for identifying pivotal species and assessing stability. It is important to note that this study does not consider various external factors that could potentially impact the availability of food for different species, including social influences, hunting activities, land cover changes, and the effects of climate change. Nonetheless, through this study, we gain insights into species interactions and their roles within the food web using centrality metrics such as degree centrality, closeness centrality, betweenness centrality, and eigen centrality. Each species within the ecosystem fulfils a distinct function; however, some species have roles and influences more significant for the ecosystem's stability and sustainability than others. These roles and influences can be quantitatively assessed using food web centrality metrics. The centrality metric values of each species within an ecosystem's food web can be used to identify key species within that food web. These key species play critical roles in maintaining the stability of the food web, including population control and ensuring the sustainability and connectivity of energy flow within the food web.

The major mammal species in a food web can be classified into two categories: key to stability and key to sustainability. Species important for ecosystem stability are closely involved in population regulation such as *H. malayanus, V. tangalunga, N. diardi, P. bengalensis, P. marmorata, P. hermaphroditus, H. brachyurus.* Species that exhibit high levels of closeness and eigenvector centrality contribute significantly to maintaining ecosystem stability, often acting as predators across carnivore and omnivore trophic levels. The closeness centrality measure in food webs reflects the efficiency of species in accessing food resources and transmitting energy. The eigenvector centrality of a species indicates the strength of its connections within the food web. Species with high eigenvector centrality are typically crucial for maintaining ecosystem equilibrium (Allesina and Pascual 2009), as this metric also considers the importance of other species connected to them. In contrast, species with high betweenness centrality values play an important role in ensuring ecosystem sustainability by facilitating energy flow between species, thereby preventing flow disturbances and protecting other species from the risk of extinction. Species with relatively high betweenness and closeness centrality values within a community are more important than others in the food web processes and thus can be considered as key species (González et al. 2010; Lai et al. 2012). Sequential removal modes of these species significantly affect the decreasing connectivity robustness (Cagua et al. 2019; Fengzhen and Yi 2019). It indicates that key species play a crucial role in maintaining the robust connectivity of the food web.

Centrality indices in food webs offer a way to measure the resilience of food webs in a given ecosystem. Complex food webs characterized by interactions of multiple species tend to show greater stability and resilience in the face of environmental disturbances (Vallina and Le Quéré 2011; Johnson et al. 2014; Fengzhen and Yi 2019; Gellner et al. 2023). Classical ecosystem resilience theory predicts that food web stability will decrease as complexity increases. Longer negative feedback loops resulting from interactions among numerous species can disrupt food web stability as complexity rises. Disturbances to one species can have broader and more unpredictable effects on other species (Rodriguez et al. 2022; Lever et al. 2023). However, this condition only sometimes occurs (Vallina and Le Quéré 2011; Lever et al. 2023). The strength of food webs in various ecosystem types depends on several important factors, including resource availability, species diversity, and community structure (Gruner et al. 2008; Canning et al. 2014). Bushes and shrubs ecosystems tend to have higher resilience than other ecosystems due to abundant food sources and the prevalence of mammal species as population regulators (Canning and Death 2019). Several studies have shown that Bushes and shrubs ecosystems can rapidly recover and maintain their biodiversity and ecological functions following disturbances. For instance, Mediterranean shrublands (Pausas and Keeley 2009), African savannas (Bond and Keeley 2005), and shrub and prairie communities in Orange County, CA, USA (Kimball et al. 2018) have all demonstrated high resilience in the face of disturbances. Moreover, omnivorous species' substantial presence further bolsters the food webs' robustness, even in ecosystems with fewer species (McLeod and Leroux 2021). Hence, a comprehensive understanding of community structure and the roles of key species, particularly mammals and omnivores, is paramount in maintaining ecosystem stability and sustainability by preserving the resilience of food webs.

Network analysis can contribute significantly to species and ecosystem conservation efforts. This analysis deeply explains interactions between species, food web structure, and ecosystem dynamics (Staniczenko et al. 2010; D'Alelio et al. 2016; Kéfi 2020). Understanding the complex relationships between species in food webs can help conservationists identify key species important in maintaining ecosystem stability. Additionally, this analysis helps in planning effective conservation strategies, such as restoring disturbed ecosystems and managing populations of endangered species (Strydom et al. 2021). Some examples of the use of network analysis include understanding the role of keystone species in the recovery of degraded mangrove ecosystems (O'Connell et al. 2022), studying habitat connectivity for endangered species (Yamaki 2015; Pfeifer et al. 2017), controlling invasive species (Escobar et al. 2019; Runghen et al. 2023), spesies management of protected area (Chaput-Bardy et al. 2017; Smith and Wollman 2021), and understanding plant-pollinator interactions to enhance biodiversity and ecosystem services (González et al. 2010)

Conclusion, network analysis in food webs can reveal that each ecosystem has different key mammal species. Centrality measures in the food web can be used to identify species that play crucial roles in maintaining ecosystem stability and sustainability. This approach provides deeper insights by considering species' relationships and positions within the food web's overall structure. The function of these major mammal species, as identified through research, is to ensure the stability and sustainability of the food web; a higher diversity of mammal species in an ecosystem resulting a stronger food web. Ecosystems with mixed land cover, including forests, shrubs, and plantations, have the most resilient food webs compared to other ecosystems. In contrast, the most fragile food webs are found in plantation and industrial forest ecosystems. In addition, network analysis in ecosystem food webs can contribute significantly to the conservation of species and ecosystems by providing a deep understanding of interspecies interactions, food web structure, and ecosystem dynamics. This analysis can serve as an effective tool to conserve biodiversity and ensure ecosystem sustainability.

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REFERENCES

Agrawal A, Gopal K. 2013. Biomass production in food chain and its role at trophic levels. Biomonitoring of Water and Waste Water 59-70. DOI: 10.1007/978-81-322-0864-8_6.

Allesina S, Pascual M. 2009. Googling food webs: can an eigenvector measure species' importance for coextinctions?. PLoS Comput Biol 5 (9): e1000494. DOI: 10.1371/journal.pcbi.1000494.

Astudillo PX, Grass I, Siddons DC, Schabo DG, Farwig N. 2020. Centrality in species-habitat networks reveals the importance of habitat quality for high-andean birds in Polylepis Woodlands. Ardeola 67 (2): 307. DOI: 10.13157/arla.67.2.2020.ra5.

Baiser B, Whitaker N, Ellison AM. 2013. Modeling foundation species in food webs. Ecosphere 4 (12): art146. DOI: 10.1890/ES13-00265.1.

Bastian M, Heymann S, Jacomy M. 2009. Gephi: An open source software for exploring and manipulating networks. Proc Intl AAAI Conf Weblogs Soc Media 3 (1): 361-362. DOI: 10.1609/icwsm.v3i1.13937.

Bond WJ, Keeley JE. 2005. Fire as a global 'herbivore': The ecology and evolution of flammable ecosystems. Trends Ecol Evol 20 (7): 387-394. DOI: 10.1016/j.tree.2005.04.025.

Borrelli JJ, Ginzburg LR. 2014. Why there are so few trophic levels: Selection against instability explains the pattern. Food Webs 1 (1-4): 10-17. DOI: 10.1016/j.fooweb.2014.11.002.

Brandes U. 2001. A faster algorithm for betweenness centrality. J Math Sociol 25 (2): 163-177. DOI: 10.1080/0022250X.2001.9990249.

Cagua EF, Wootton KL, Stouffer DB. 2019. Keystoneness, centrality, and the structural controllability of ecological networks. J Ecol 107 (4): 1779-1790. DOI: 10.1111/1365-2745.13147.

Canning A, Death RG, Joy M. 2014. Predicting Food Web Structure and Robustness. Ecological Society of America, Sacramento, CA

Canning AD, Death RG. 2019. Food web structure but not robustness differ between rivers, lakes and estuaries. Oecol Aust 23 (1): 112-126. DOI: 10.4257/oeco.2019.2301.10.

Capocefalo D, Pereira J, Mazza T, Jordán F. 2018. Food web topology and nested keystone species complexes. Complexity 2018 (1): 1979214. DOI: 10.1155/2018/1979214.

Chaput-Bardy A, Alcala N, Secondi J, Vuilleumier S. 2017. Network analysis for species management in rivers networks: Application to the Loire River. Biol Conserv 210: 26-36. DOI: 10.1016/j.biocon.2017.04.003.

Chen JL, Zhang WJ. 2020. Parasites Govern the topological properties of food webs: A conclusion from network analysis. Appl Ecol Environ Res 18 (2): 3419-3437. DOI: 10.15666/aeer/1802_34193437.

Correia AM, Lopes LF. 2023. Revisiting biodiversity and ecosystem functioning through the lens of complex adaptive systems. Diversity 15 (8): 895. DOI: 10.3390/d15080895.

D'Alelio D, Libralato S, Wyatt T, Ribera d'Alcalà M. 2016. Ecological-network models link diversity, structure and function in the plankton food-web. Sci Rep 6 (1): 21806. DOI: 10.1038/srep21806.

Delmas E, Besson M, Brice M, Burkle LA, Dalla Riva GV, Fortin M, Gravel D, Guimarães PR, Hembry DH, Newman EA, Olesen JM, Pires MM, Yeakel JD, Poisot T. 2019. Analysing ecological networks of species interactions. Biol Rev 94 (1): 16-36. DOI: 10.1111/brv.12433.

Dunne JA. 2023. The network structure of food webs. Ecological Networks: 27-92. DOI: 10.1093/oso/9780195188165.003.0002.

Dunne JA, Williams RJ, Martinez ND. 2002. Network structure and biodiversity loss in food webs: Robustness increases with connectance. Ecol Lett 5 (4): 558-567. DOI: 10.1046/j.1461-0248.2002.00354.x.

Escobar LE, Romero-Alvarez D, Larkin DJ, Phelps NBD. 2019. Network analysis to inform invasive species spread among lakes. J Oceanol Limnol 37 (3): 1037-1041. DOI: 10.1007/s00343-019-7208-z.

Evans DM, Pocock MJO, Memmott J. 2013. The robustness of a network of ecological networks to habitat loss. Ecol Lett 16 (7): 844-852. DOI: 10.1111/ele.12117.

Feng G, Yan H, Yang X. 2019. Climate and food diversity as drivers of mammal diversity in Inner Mongolia. Ecol Evol 9 (4): 2142-2148. DOI: 10.1002/ece3.4908.

Fengzhen W, Yi T. 2019. Determination of key species in the food web and their impact on the robustness. Biodiv Sci 27 (10): 1132-1137. DOI: 10.17520/biods.2019208.

Fretwell SD. 1987. Food chain dynamics: The central theory of ecology? Oikos 50 (3): 291. DOI: 10.2307/3565489.

Funes M, Saravia LA, Cordone G, Iribarne OO, Galván DE. 2022. Network analysis suggests changes in food web stability produced by bottom trawl fishery in Patagonia. Sci Rep 12 (1): 10876. DOI: 10.1038/s41598-022-14363-y.

Galiana N, Arnoldi JF, Barbier M, Acloque A, de Mazancourt C, Loreau M. 2021. Can biomass distribution across trophic levels predict trophic cascades?. Ecol Lett 24 (3): 464-476. DOI: 10.1111/ele.13658.

Gellner G, McCann K, Hastings A. 2023. Stable diverse food webs become more common when interactions are more biologically constrained. Proc Natl Acad Sci 120 (31): e2212061120. DOI: 10.1073/pnas.2212061120.

Gouveia C, Móréh Á, Jordán F. 2021. Combining centrality indices: Maximizing the predictability of keystone species in food webs. Ecol Indic 126: 107617. DOI: 10.1016/j.ecolind.2021.107617.

González AM, Dalsgaard B, Olesen JM. 2010. Centrality measures and the importance of generalist species in pollination networks. Ecol Complex 7 (1): 36-43. DOI: 10.1016/j.ecocom.2009.03.008.

Gruner DS, Smith JE, Seabloom EW, Sandin SA, Ngai JT, Hillebrand H, Harpole WS, Elser JJ, Cleland EE, Bracken ME, Borer ET, Bolker BM. 2008. A cross-system synthesis of consumer and nutrient resource control on producer biomass. Ecol Lett 11: 740-755. DOI: 10.1111/j.1461-0248.2008.01192.x.

Hooper DU, Chapin III FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol Monogr 75 (1): 3-35. DOI: 10.1890/04-0922.

Jiang LQ, Zhang WJ. 2015. Determination of keystone species in CSM food web: A topological analysis of network structure. Netw Biol 5 (1): 13-33. DOI: 10.1016/j.fooweb.2015.07.002.

Johnson S, Domínguez-García V, Donetti L, Muñoz MA. 2014. Trophic coherence determines food-web stability. Proc Natl Acad Sci 111 (50): 17923-17928. DOI: 10.1073/pnas.1409077111.

Jordán F, Benedek Z, Podani J. 2007. Quantifying positional importance in food webs: A comparison of centrality indices. Ecol Model 205 (1-2): 270-275. DOI: 10.1016/j.ecolmodel.2007.02.032.

Kéfi S. 2020. Ecological networks: From structure to dynamics. In: McCann KS, Gellner G (eds). Theoretical Ecology: Concepts and Applications. Oxford University Press, Oxford. DOI: 10.1093/oso/9780198824282.003.0010.

Kimball S, Principe Z, Deutschman D, Strahm S, Huxman TE, Lulow M, Balazs K. 2018. Resistance and resilience: Ten years of monitoring shrub and prairie communities in Orange County, CA, USA. Ecosphere 9 (5): e02212. DOI: 10.1002/ecs2.2212.

Kolesnikov V, Anikin V, Mosolova E, Faizliev A, Mironov S, Zemlyanskaya M, Pleshakov M, Sidorov S. 2019. Food chain analysis based on graph centrality indicators. J Phys: Conf Ser 1334 (1): 12004. DOI: 10.1088/1742-6596/1334/1/012004.

Kones JK, Soetaert K, van Oevelen D, Owino JO. 2009. Are network indices robust indicators of food web functioning? A Monte Carlo approach. Ecol Model 220 (3): 370-382. DOI: 10.1016/j.ecolmodel.2008.10.012.

Kortsch S, Primicerio R, Fossheim M, Dolgov AV, Aschan M. 2015. Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. Proc R Soc B Biol Sci 282 (1814): 20151546. DOI: 10.1098/rspb.2015.1546.

Lai S-M, Liu W-C, Jordán F. 2012. On the centrality and uniqueness of species from the network perspective. Biol Lett 8 (4): 570-573. DOI: 10.1098/rsbl.2011.1167.

Landi P, Minoarivelo HO, Brännström Å, Hui C, Dieckmann U. 2018. Complexity and stability of ecological networks: A review of the theory. Popul Ecol 60 (4): 319-345. DOI: 10.1007/s10144-018-0628-3.

Lever JJ, Van Nes EH, Scheffer M, Bascompte J. 2023. Five fundamental ways in which complex food webs may spiral out of control. Ecol Lett 26 (10): 1765-1779. DOI: 10.1111/ele.14293.

Libralato S, Christensen V, Pauly D. 2006. A method for identifying keystone species in food web models. Ecol Model 195 (3-4): 153-171. DOI: 10.1016/j.ecolmodel.2005.11.029.

Matsuda H, Namba T. 1991. Food web graph of a coevolutionarily stable community. Ecology 72 (1): 267-276. DOI: 10.2307/1938920.
McLeod AM, Leroux SJ. 2021. The multiple meanings of omnivory influence empirical, modular theory and whole food web stability relationships. J Anim Ecol 90 (2): 447-459. DOI: 10.1111/1365-2656.13378.
Meilhac J, Durand J-L, Beguier V, Litrico I. 2019. Increasing the benefits of species diversity in multispecies temporary grasslands by increasing within-species diversity. Ann Bot 123 (5): 891-900. DOI: 10.1093/aob/mcy227.
Mello MAR, Rodrigues FA, Costa L da F, Kissling WD, Şekercioğlu ÇH, Marquitti FMD, Kalko EKV. 2015. Keystone species in seed dispersal networks are mainly determined by dietary specialization. Oikos 124 (8): 1031-1039. DOI: 10.1111/oik.01613.
Ng WP, van Manen FT, Sharp SP, Wong S Te, Ratnayeke S. 2021. Mammal species composition and habitat associations in a commercial forest and mixed-plantation landscape. For Ecol Manag 491: 119163. DOI: 10.1016/j.foreco.2021.119163.
O'Connell DP, Fusi M, Djamaluddin R, Rajagukguk BB, Bachmid F, Kitson JJN, Dunnett Z, Trianto A, Tjoa AB, Diele K, Evans DM. 2022. Assessing mangrove restoration practices using species-interaction networks. Restor Ecol 30 (4): e13546. DOI: 10.1111/rec.13546.
Ochoa-Hueso R, Delgado-Baquerizo M, Risch AC, Schrama M, Morriën E, Barmentlo SH, Geisen S, Hannula SE, Resch MC, Snoek BL, Putten WHvd. 2021. Ecosystem coupling: A unifying framework to understand the functioning and recovery of ecosystems. One Earth 4 (7): 951-966. DOI: 10.1016/j.oneear.2021.06.011.
Oehlers M, Fabian B. 2021. Graph metrics for network robustness-A survey. Mathematics 9 (8): 895. DOI: 10.3390/math9080895.
Pausas JG, Keeley JE. 2009. A burning story: The role of fire in the history of life. BioScience 59 (7): 593-601. DOI: 10.1525/bio.2009.59.7.10.
Pfeifer M, Lefebvre V, Peres CA et al. 2017. Creation of forest edges has a global impact on forest vertebrates. Nature 551 (7679): 187-191. DOI: 10.1038/nature24457.
Rodriguez ID, Marina TI, Schloss IR, Saravia LA. 2022. Marine food webs are more complex but less stable in sub-Antarctic (Beagle Channel, Argentina) than in Antarctic (Potter Cove, Antarctic Peninsula) regions. Mar Environ Res 174: 105561. DOI: 10.1016/j.marenvres.2022.105561.
Roemer GW, Gompper ME, Van Valkenburgh B. 2009. The ecological role of the mammalian mesocarnivore. BioScience 59 (2): 165-173. DOI: 10.1525/bio.2009.59.2.9.
Runghen R, Llopis-Belenguer C, McNeill MR, Dalla Riva GV, Stouffer DB. 2023. Using network analysis to study and manage human-mediated dispersal of exotic species. Biol Invasions 25 (11): 3369-3389. DOI: 10.1007/s10530-023-03122-3.
Smith JE, Pinter-Wollman N. 2021. Observing the unwatchable: Integrating automated sensing, naturalistic observations and animal social network analysis in the age of big data. J Anim Ecol 90 (1): 62-75. DOI: 10.1111/1365-2656.13362.
Staniczenko PPA, Lewis OT, Jones NS, Reed-Tsochas F. 2010. Structural dynamics and robustness of food webs. Ecol Lett 13 (7): 891-899. DOI: 10.1111/j.1461-0248.2010.01485.x.
Steele JH, He X. 2019. Network analysis of food webs. Encycloped Ocean Sci 1: 746-752. DOI: 10.1016/B978-0-12-409548-9.10802-4.
Strydom T, Catchen MD, Banville F, Caron D, Dansereau G, Desjardins-Proulx P, Forero-Muñoz NR, Higino G, Mercier B, Gonzalez A, Gravel D, Pollock L, Poisot T. 2021. A roadmap towards predicting species interaction networks (across space and time). Philos Trans R Soc B Biol Sci 376 (1837): 20210063. DOI: 10.1098/rstb.2021.0063.
Sun X, Zhao L, Zhao D, Huo Y, Tan W. 2020. Keystone species can be identified based on motif centrality. Ecol Indic 110: 105877. DOI: 10.1016/j.ecolind.2019.105877.
Sunaryo MSW, Salleh Z, Mamat M. 2013. Mathematical model of three species food chain with holling type-III functional response. Intl J Pure Appl Math 89 (5): 647-657. DOI: 10.12732/ijpam.v89i5.1.
Swift RJ, Anteau MJ, Ellis KS, Ring MM, Sherfy MH, Toy DL. 2023. Conspecific density and habitat quality affect breeding habitat selection: Support for the social attraction hypothesis. Ecosphere 14 (5): e4524. DOI: 10.1002/ecs2.4524.
Thompson RM, Brose U, Dunne JA, Hall RO, Hladyz S, Kitching RL, Martinez ND, Rantala H, Romanuk TN, Stouffer DB, Tylianakis JM. 2012. Food webs: Reconciling the structure and function of biodiversity. Trends Ecol Evol 27 (12): 689-697. DOI: 10.1016/j.tree.2012.08.005.
Trebilco R, Baum JK, Salomon AK, Dulvy NK. 2013. Ecosystem ecology: Size-based constraints on the pyramids of life. Trends Ecol Evol 28 (7): 423-431. DOI: 10.1016/j.tree.2013.03.008.
Tucker MA, Rogers TL. 2014. Examining predator-prey body size, trophic level and body mass across marine and terrestrial mammals. Proc R Soc B Biol Sci 281 (1797): 20142103. DOI: 10.1098/rspb.2014.2103.
Vallina SM, Le Quéré C. 2011. Stability of complex food webs: Resilience, resistance and the average interaction strength. J Theor Biol 272 (1): 160-173. DOI: 10.1016/j.jtbi.2010.11.043.
Van Dover CL. 2001. The ecology of Deep-Sea Hydrothermal Vents. Limnol Oceanogr 46 (8): 2094. DOI: 10.2307/j.ctv1zm2v35.12.
Webb P, Boltt G. 1990. Food chain to food web: A natural progression? J Biol Educ 24 (3): 187-190. DOI: 10.1080/00219266.1990.9655139.
Woodward G, Hildrew AG. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. J Anim Ecol 71 (6): 1063-1074. DOI: 10.1046/j.1365-2656.2002.00669.x.
Wu J, Liu Y, Sui H, Xu B, Zhang C, Ren Y, Xue Y. 2020. Using network analysis to identify keystone species in the food web of Haizhou Bay, China. Mar Freshw Res 71 (4): 469-481. DOI: 10.1071/MF18417.
Yamaki K. 2015. Network governance of endangered species conservation: A case study of Rebun Lady's-Slipper. J Nat Conserv 24: 83-92. DOI: 10.1016/j.jnc.2014.10.004.
Zhao J, Yu Q, Xu C, Ma J, Liu W, Sun W, Miao Y, Nawaz T. 2023. Integrated approach for ecological restoration and ecological spatial network optimization with multiple ecosystem functions in mining areas. Ecol Indic 156: 111141. DOI: 10.1016/j.ecolind.2023.111141.