

Multiple dimensions of network structure underlie ecological stability

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Abstract: Ecological network structure is widely invoked to explain patterns of biodiversity and stability, yet decades of research have produced little consensus on which structural descriptors matter most. We argue that this apparent inconsistency arises not from methodological disagreement, but from a conceptual mismatch: network structure encodes multiple, hierarchically organised aspects of energy flow, each relating to different components of stability. Using a compilation of food webs from XXX, we quantified 31 commonly used structural metrics spanning species roles, interaction pathways, network geometry, and emergent system behaviour. We first used variable clustering and dimensionality reduction to identify dominant axes of structural variation and a non-redundant subset of descriptors. We then interpreted these axes through an energy-flow framework linking structural scale to distinct stability mechanisms: persistence (maintenance of energy flow following species loss), resistance (attenuation of perturbation propagation), and return (reorganisation of pathways following disturbance). Our analyses show that metrics often treated as competing predictors of ‘stability’ instead load onto different structural dimensions and relate to different stability components. Redundancy and species-role metrics primarily align with persistence, pathway and motif-based metrics with resistance, and global organisational measures with return dynamics. By explicitly mapping network structure to stability mechanisms, our results reconcile conflicting findings in the structure–stability literature and provide a principled framework for selecting network metrics based on ecological question and scale, rather than convention.

Keywords: food web, structure, dimensionality reduction

¹ 1 Introduction

² Which metrics best represent the distinct stages of the energy-flow hierarchy, and do they capture
³ different components of stability?

⁴ Ecological networks are commonly characterised using a large and diverse set of structural metrics, yet there
⁵ remains little consensus on how these metrics should be interpreted or compared across studies (Vermaat
⁶ et al. 2009; Lau et al. 2017). We argue that this difficulty arises because network structure is not a single
⁷ property, but a hierarchy of interrelated components that encode different aspects of how energy moves
⁸ through an ecosystem (Ulanowicz 1986; Thompson et al. 2012). Metrics derived at different structural scales
⁹ therefore capture different ecological processes and, consequently, relate to different components of stability.
¹⁰ Making these distinctions explicit is essential for interpreting patterns of structure–stability relationships.

¹¹ 1.0.1 Structural scale and the organisation of energy flow

¹² We conceptualise food-web structure as organised across four hierarchical structural scales: node-level, path-
¹³ level, network geometry, and emergent system behaviour (Pimm 1982; Cohen et al. 1990; Vermaat et al. 2009).
¹⁴ These scales reflect increasing levels of integration, progressing from individual species roles to whole-network
¹⁵ dynamics.

¹⁶ **Node-level structure:** describes the properties and roles of individual species within the network. Metrics
¹⁷ such as trophic position, basal and top species proportions, centrality, and trophic similarity capture how
¹⁸ energy enters the system, which species process or redistribute that energy, and the degree of functional
¹⁹ redundancy among taxa (Yodzis & Winemiller 1999; Estrada 2007; Allesina & Pascual 2009). At this scale,
²⁰ structure primarily reflects who participates in energy transfer and whether alternative species can compensate
²¹ for local losses, a long-standing mechanism proposed to underpin persistence in complex ecosystems (McCann
²² 2000).

²³ **Path-level structure:** describes how energy is routed through sequences of interactions linking species.
²⁴ Metrics such as food chain length, omnivory, motifs, loops, and prey–predator ratios capture the coupling of
²⁵ energy channels and the multiplicity of pathways connecting basal resources to higher trophic levels (Pimm &
²⁶ Lawton 1977; McCann et al. 1998; Stouffer & Bascompte 2011). This scale reflects how energy moves through
²⁷ the network and how perturbations may be transmitted across species, with particular pathway configurations
²⁸ either amplifying or diffusing disturbance effects (Neutel et al. 2002; Rooney et al. 2006).

²⁹ **Network geometry:** captures the global arrangement and constraints of interactions, including link density,
³⁰ connectance, clustering, modularity, intervality, and network distances (Dunne et al. 2002; Stouffer et al. 2006;

³¹ Delmas et al. 2019). These properties define the overall “shape” of the food web and constrain which
³² pathways are available for energy flow. Geometric organisation has been shown to influence the containment
³³ of perturbations, for example through compartmentalisation that limits the spread of local disturbances
³⁴ (Stouffer & Bascompte, 2011).

³⁵ **Emergent system-level behaviour:** reflects the collective dynamical properties that arise from the
³⁶ interaction of nodes, paths, and geometry. Metrics such as spectral radius, SVD complexity, and robustness
³⁷ capture properties that cannot be attributed to individual species or interactions alone, but instead describe
³⁸ the system’s overall capacity to absorb, reorganise, or amplify perturbations (May 1972; Staniczenko et
³⁹ al. 2013; Strydom et al. 2021).

⁴⁰ Together, these structural scales form a causal hierarchy: species roles give rise to interaction pathways, which
⁴¹ are embedded within a global network geometry, from which emergent dynamical behaviour arises.

⁴² 1.0.2 Stability as a multi-component property

⁴³ Stability is often treated as a single outcome, yet ecological theory has long recognised that it comprises
⁴⁴ multiple, distinct components (Pimm 1984; Ives & Carpenter 2007). Here, we focus on three complementary
⁴⁵ stability mechanisms that are directly interpretable in terms of energy flow: persistence, resistance, and
⁴⁶ return.

⁴⁷ **Persistence:** refers to the continued ability of the system to sustain energy flow following species loss or
⁴⁸ disturbance. Structures that promote redundancy, multiple basal inputs, and functional overlap among species
⁴⁹ enhance persistence by ensuring that energy can continue to enter and circulate within the network even when
⁵⁰ individual components are removed (McCann 2000; Dunne et al. 2002; Jonsson et al. 2015).

⁵¹ **Resistance:** describes the extent to which perturbations are attenuated or contained rather than propagating
⁵² through the network. Path-level structures such as omnivory, short chains, motifs, and modular organisation
⁵³ can diffuse or localise disturbances, reducing the likelihood that local perturbations escalate into system-wide
⁵⁴ effects (McCann et al. 1998; Neutel et al. 2002; Stouffer & Bascompte 2011).

⁵⁵ **Return:** captures the capacity of the system to reorganise or recover following disturbance, including the
⁵⁶ re-establishment of interaction pathways and the damping of oscillations. Emergent properties linked to
⁵⁷ global organisation and heterogeneity, such as spectral radius and structural complexity, reflect constraints on
⁵⁸ system-wide dynamics and influence the speed and manner with which a system returns to equilibrium or a
⁵⁹ new stable configuration (May 1972; Ulanowicz 2001; Staniczenko et al. 2013).

⁶⁰ Crucially, these stability components operate at different structural scales and are not expected to respond

⁶¹ uniformly to the same network properties.

⁶² 1.0.3 Implications for interpreting network metrics

⁶³ Within this framework, metrics that are often treated as competing predictors of ‘stability’ instead emerge
⁶⁴ as complementary descriptors of different stability mechanisms (Thompson et al., 2012). Node-level metrics
⁶⁵ primarily relate to persistence, path-level metrics to resistance, and global organisational metrics to return
⁶⁶ dynamics. Some descriptors span multiple scales, reflecting the coupling between structural organisation and
⁶⁷ emergent behaviour (Allesina & Tang 2012).

⁶⁸ This perspective provides a mechanistic explanation for why studies using different network metrics frequently
⁶⁹ report contrasting structure–stability relationships. Rather than reflecting inconsistency or redundancy,
⁷⁰ these differences arise because different metrics implicitly target different components of stability (Lau et al.,
⁷¹ 2017). By explicitly linking structural scale, energy flow, and stability mechanism, this framework provides a
⁷² principled basis for interpreting network metrics and for selecting descriptors that align with specific ecological
⁷³ questions.

Table 1: Words

Structural scale	What it encodes	Energy-flow interpretation	Stability component
Node	Species roles and redundancy	Who handles energy	Persistence (can energy still enter and move?)
Path	Energy routing and coupling	How energy moves	Resistance (does disturbance spread?)
Geometry	Network constraints and organisation	Where energy can go	Containment / buffering
Behaviour	Emergent dynamics	How energy reorganizes	Return / reassembly

⁷⁴ 2 Materials & Methods

⁷⁵ 2.1 Data Compilation

⁷⁶ We compiled quantitative network data from XX, resulting in a total of XX ecological networks. Each
⁷⁷ network was characterized using a suite of XX structural metrics Table 2, including classic descriptors such as
⁷⁸ richness, connectance, and modularity, as well as information-theoretic measures like spectral radius and SVD

⁷⁹ complexity. Prior to analysis, networks with missing values were omitted, and all metrics were standardized
⁸⁰ (mean = 0, SD = 1) to account for differences in scale and units across descriptors.

Table 2: An informative caption about the different network properties. We use a combination of metrics from both the original Vermaat et al. (2009) paper as well as including those that have been identified by Thompson et al. (2012) and have been linked to emerging ecosystem properties such as stability

Label	Definition	Structural interpretation	Reference
Basal	Proportion of taxa with zero vulnerability (no consumers).	Quantifies the proportion of species representing basal energy inputs to the network.	
Top	Proportion of taxa with zero generality (no resources).	Describes the relative prevalence of terminal consumers in the network.	
Intermediate	Proportion of taxa with both consumers and resources.	Captures the proportion of species participating in both upward and downward energy transfer.	
Richness (S)	Number of taxa (nodes) in the network.	Describes network size.	
Links (L)	Total number of trophic interactions (edges).	Describes interaction density independent of network size.	
Connectance	L/S^2 , where S is the number of species and L the number of links	Measures the proportion of realised interactions relative to all possible interactions.	Dunne et al. 2002
L/S	Mean number of links per species.	Captures average interaction density per taxon.	
Cannibal	Proportion of taxa with self-loops.	Quantifies the prevalence of cannibalistic interactions.	
Herbivore	Proportion of taxa feeding exclusively on basal species.	Describes the representation of primary consumers.	

Label	Definition	Structural interpretation	Reference
Intermediate	Percentage of intermediate taxa (with both consumers and resources)		
Trophic level (TL)	Prey-weighted trophic level averaged across taxa.	Captures the vertical organisation of energy transfer.	Williams & Martinez (2004)
MaxSim	Mean maximum trophic similarity of each taxon to all others.	Quantifies functional similarity based on shared predators and prey.	Yodzis & Winemiller (1999)
Centrality	Node centrality averaged across taxa (definition-dependent).	Captures the distribution of influence or connectivity among species.	Estrada & Bodin (2008)
ChLen	Mean length of all food chains from basal to top taxa.	Describes the average number of steps in energy-transfer pathways.	
ChSD	Standard deviation of food chain length.	Captures variability in pathway lengths.	
ChNum	Log-transformed number of distinct food chains.	Quantifies the multiplicity of alternative energy pathways.	
Path	Mean shortest path length between all species pairs.	Describes the average distance between taxa within the network.	
Diameter	Maximum shortest path length between any two taxa.	Captures the largest network distance between species.	
Omnivory	Proportion of taxa feeding on resources at multiple trophic levels.	Describes vertical coupling of energy channels.	McCann (2000)

Label	Definition	Structural interpretation	Reference
Loop	Proportion of taxa involved in trophic loops.	Quantifies the prevalence of cyclic interaction pathways.	
Prey:Predator	Ratio of prey taxa (basal + intermediate) to predator taxa (intermediate + top).	Describes the overall shape of the trophic structure.	
Diameter	Diameter can also be measured as the average of the distances between each pair of nodes in the network		
Clust	Mean clustering coefficient.	Measures the tendency for taxa sharing interaction partners to also interact with each other.	Watts & Strogatz (1998)
GenSD	Normalised standard deviation of generality.	Captures heterogeneity in the number of resources per taxon.	Williams & Martinez (2004)
VulSD	Normalised standard deviation of vulnerability.	Captures heterogeneity in the number of consumers per taxon.	Williams & Martinez (2004)
LinkSD	Normalised standard deviation of total links per taxon.	Quantifies variation in species connectivity.	
Intervality	Degree to which taxa can be ordered along a single niche dimension.	Measures the extent of niche ordering in trophic interactions.	Stouffer et al. (2006)
(Spectral radius)	Largest real part of the eigenvalues of the undirected adjacency matrix.	Captures a global property of network organisation related to interaction strength aggregation.	

Label	Definition	Structural interpretation	Reference
Complexity (SVD)	Shannon entropy of the singular value decomposition of the adjacency matrix.	Quantifies heterogeneity in interaction structure.	Strydom et al. (2021)
Robustness	Proportion of secondary extinctions following primary species removal.	Operational measure of tolerance to node loss.	Jonsson et al. (2015)
S1 (Linear chain)	Frequency of three-node linear chains ($A \rightarrow B \rightarrow C$) with no additional links.	Captures the prevalence of simple, unbranched energy-transfer pathways.	Stouffer et al. (2007) Milo et al. (2002)
S2 (Omnivory)	Frequency of three-node motifs forming a feed-forward loop ($A \rightarrow B \rightarrow C, A \rightarrow C$).	Describes vertical coupling of trophic levels within small subnetworks.	Stouffer et al. (2007) Milo et al. (2002)
S4 (Apparent competition)	Frequency of motifs where one consumer feeds on two resources ($A \rightarrow B \leftarrow C$).	Captures the prevalence of shared-predator structures among resources.	Stouffer et al. (2007) Milo et al. (2002)
S5 (Direct competition)	Frequency of motifs where two consumers share a single resource ($A \leftarrow B \rightarrow C$).	Describes the occurrence of shared-resource structures among consumers.	Stouffer et al. (2007) Milo et al. (2002)

81 2.2 Statistical Characterisation of Network Space

82 To identify the dominant axes of structural variation within our dataset, we expanded upon the dimensionality
 83 reduction approach established by Vermaat et al. (2009). We quantified 31 structural metrics for each food

⁸⁴ web, categorising them into four hierarchical scales of energy flow: Node-level (e.g., trophic roles), Path-level
⁸⁵ (e.g., energy sequences), Network Geometry (e.g., global shape), and Emergent Behaviour (e.g., system-wide
⁸⁶ complexity).

⁸⁷ **2.2.1 Dimensionality Reduction and Metric Selection**

⁸⁸ To identify a non-redundant subset of structural descriptors, we performed a Principal Component Analysis
⁸⁹ (PCA) on the scaled structural metrics. We excluded stability-related outcomes (*e.g.*, robustness, , and SVD
⁹⁰ complexity) from the PCA to ensure the resulting dimensions represented pure physical architecture.

⁹¹ We determined the number of significant structural dimensions using Kaiser's Criterion (eigenvalues >1) and
⁹² an analysis of the scree plot 'elbow'. To select a representative anchor for each significant dimension, we
⁹³ programmatically identified the metric with the highest contribution percentage (\cos^2) to each Principal
⁹⁴ Component (PC). In cases where a single metric dominated multiple dimensions, the next highest unique
⁹⁵ contributor was selected to ensure a parsimonious yet comprehensive subset of predictors.

⁹⁶ **2.3 Linking Structure to Stability Components**

⁹⁷ To test the hypothesis that different hierarchical structural scales govern distinct aspects of ecological stability,
⁹⁸ we employed Random Forest (RF) models. We defined three response variables representing components of
⁹⁹ Stability:

- ¹⁰⁰ • Persistence: Quantified as structural Robustness (secondary extinction resistance).
- ¹⁰¹ • Dampening: Quantified as the Spectral Radius (), representing local stability.
- ¹⁰² • Organization: Quantified as SVD Complexity, representing the informational diversity of energy channels.

¹⁰³ **2.3.1 Model Specification and Importance**

¹⁰⁴ Each stability component was modelled as a function of the six 'Structural Pillars' identified in the PCA
¹⁰⁵ phase (S1, Richness, PredPreyRatio, Distance, Herbivory, and MaxSim). We used 1,000 trees per forest
¹⁰⁶ to ensure stable importance estimates. We quantified the relative influence of each structural pillar using
¹⁰⁷ Percentage Increase in Mean Squared Error (%IncMSE), which identifies the metrics most indispensable for
¹⁰⁸ model accuracy.

¹⁰⁹ **2.3.2 Directional Effects**

¹¹⁰ To interpret the ecological nature of these relationships, we generated Partial Dependence Plots (PDPs).
¹¹¹ These plots visualize the marginal effect of a winning structural pillar on its associated stability component

₁₁₂ while accounting for the average effects of all other predictors.

₁₁₃ 2.4 Validation of Structural Modularity

₁₁₄ To assess the redundancy and independence of the 31 structural metrics, we performed a Hierarchical Variable
₁₁₅ Clustering analysis using the hclust algorithm in R. We used 1– Correlation as the distance metric to group
₁₁₆ variables based on the strength of their relationship, regardless of the direction of the correlation.

₁₁₇ To determine the optimal number of structural modules, we calculated Average Silhouette Widths for k=2 to
₁₁₈ 10. Additionally, we performed multiscale bootstrap resampling (n=1000) using the pvclust package to assign
₁₁₉ Approximately Unbiased (AU) p-values to each cluster, ensuring that the identified modules were statistically
₁₂₀ robust and not artifacts of the specific dataset.

₁₂₁ 3 Results

₁₂₂ 3.1 The Six Dimensions of Food Web Architecture

₁₂₃ The PCA revealed a high-dimensional structural space where the first six principal components accounted for
₁₂₄ 84.9% of the total structural variation (Table 1). This indicates that while food web structure is complex, it
₁₂₅ can be effectively distilled into six primary axes of architectural variation.

- ₁₂₆ • Dimension 1 (31.6% variance) was anchored by S1 (the number of pathways from basal species),
₁₂₇ representing the total volume of energy entry points.
- ₁₂₈ • Dimension 2 (21.6% variance) was dominated by Richness (S), representing the overall scale of the
₁₂₉ network.
- ₁₃₀ • Dimension 3 (15.5% variance) was defined by the Predator-Prey Ratio, capturing the balance of trophic
₁₃₁ roles (Node-level).
- ₁₃₂ • Dimension 4 (6.8% variance) was driven by Mean Distance, reflecting the efficiency or tightness of the
₁₃₃ wiring (Path-level).
- ₁₃₄ • Dimension 5 (5.2% variance) was anchored by Herbivory, identifying the functional dominance of specific
₁₃₅ energy channels.
- ₁₃₆ • Dimension 6 (4.4% variance) was represented by MaxSim (Maximum Similarity), a measure of trophic
₁₃₇ redundancy and functional overlap.

138 **3.2 Alignment with the Energy-Flow Hierarchy**

139 The distribution of these representative metrics across the PCA dimensions suggests that no single hierarchical
140 scale dominates food-web variation. Instead, the network space is composed of a mixture of Path-level (S1,
141 Distance), Geometry (Richness), and Node-level (PredPreyRatio, Herbivory, MaxSim) properties. Notably, S1
142 (a Path-level metric) explained more variance than Richness, suggesting that the arrangement of energy flow
143 pathways is a more fundamental structural signature than simple species counts.

144 **3.2.1 Differential Drivers of Ecological Stability**

145 The Random Forest models revealed a clear partitioning of structural influence, with different ‘pillars’ emerging
146 as the dominant predictors for each stability component (Table 2).

147 Persistence (Robustness) was primarily governed by PredPreyRatio (%IncMSE = 15.98) and Herbivory
148 (%IncMSE = 10.23). Surprisingly, network Richness had no predictive power for persistence (%IncMSE =
149 -2.49), suggesting that the balance of trophic roles is more critical for preventing extinction cascades than the
150 total number of species.

151 Dampening () was most sensitive to Herbivory (%IncMSE = 17.28). This indicates that the strength and
152 proportion of energy flow originating from the basal-consumer interface is the primary regulator of a network’s
153 local stability.

154 Organization (SVD Complexity) was uniquely driven by MaxSim (%IncMSE = 13.12) and S1 (%IncMSE =
155 12.56). This supports the view that informational complexity emerges from a combination of unique species
156 roles (low similarity) and the total volume of energy entry pathways.

157 **3.2.2 Directionality and Trophic Control**

158 Partial dependence analysis provided a mechanistic look at how these pillars operate:

159 Trophic Balance: Persistence showed a [direction] response to the PredPreyRatio, indicating an optimal
160 balance between consumers and resources is required to maintain structural integrity.

161 Basal Channels: The system’s ability to dampen perturbations () improved as Herbivory [increased/decreased],
162 suggesting that basal-heavy webs act as a buffer for energy surges.

163 Specialization: SVD Complexity increased as MaxSim decreased, confirming that organised networks are
164 those where species occupy distinct, non-overlapping trophic niches rather than redundant ones.

165 Our multi-stage analysis reveals that food web stability is governed by a hierarchical architecture where

166 structural modules serve as specialized functional levers. While Principal Component Analysis and Silhouette
167 validation ($k=10$) confirm the high dimensionality of network space, the hierarchical clustering identifies
168 four robust, independent modules (AU 0.94) that dictate system behaviour. We find a clear decoupling
169 of network scale from network persistence; specifically, the Geometric Scale module (containing Richness
170 and Connectance) accounts for significant structural variance but fails to predict any component of stability.
171 Instead, the Energy Flow Engine (Module 3) and Trophic Redundancy (Module 4) emerge as the primary
172 controllers. Specifically, node-level balance within the flow engine (PredPreyRatio and Herbivory) determines
173 persistence and dampening, while the isolation of species roles (MaxSim) dictates organizational complexity.
174 This suggests that the stability of an ecosystem is not a product of its size, but of the specific configuration of
175 its energy channels and the redundancy of its functional roles.

- 176 • Redundancy / persistence
177 • Pathway coupling / resistance
178 • Organizational constraint / return
179 • Reduced metric sets retain these axes

180 4 Discussion

181 4.1 Why consensus on “the best metric” has remained elusive

182 For more than four decades, the structure–stability debate has oscillated between competing structural
183 descriptors, from connectance and complexity to modularity, omnivory, and trophic redundancy. Early
184 theoretical work, most notably by May, suggested that increasing complexity should destabilise large systems,
185 placing global descriptors such as connectance and interaction density at the centre of the debate. Subsequent
186 empirical and theoretical studies, however, demonstrated stabilising roles for omnivory, weak links, and
187 compartmentalisation (e.g. McCann; Dunne), shifting attention toward pathway-level and geometric properties.
188 Our results suggest that this apparent inconsistency does not arise because some metrics are “wrong,” but
189 because they capture different dimensions of a fundamentally multi-layered architecture. Food-web structure
190 is not a single axis ranging from simple to complex; it is a high-dimensional space in which node composition,
191 pathway routing, geometric constraint, and emergent organisation vary semi-independently. Metrics that
192 have historically been treated as competitors—such as richness, connectance, omnivory, and redundancy—are
193 in fact anchors of distinct structural dimensions. This explains why no single metric consistently predicts
194 “stability” across studies: stability itself is not singular. When studies measure persistence (e.g. secondary
195 extinctions), node-level balance and redundancy dominate. When they measure local stability or damping,

196 path-level coupling and basal channel dominance matter more. When they measure recovery or informational
197 organisation, global heterogeneity and role differentiation become decisive. The search for a universal structural
198 predictor of stability has therefore been misguided—not because structure is unimportant, but because both
199 structure and stability are multidimensional.

200 **4.2 Reconciling contrasting structure–stability relationships**

201 A persistent challenge in the literature has been that similar metrics sometimes show opposite associations
202 with stability. For example, omnivory has been reported as stabilising in some contexts and destabilising
203 in others. Within our framework, this variability is expected. Path-level coupling (e.g. omnivory motifs)
204 primarily relates to resistance—the containment or diffusion of perturbations—rather than persistence per
205 se. A structure that dampens oscillations may not prevent extinction cascades, and vice versa. Similarly,
206 our finding that richness contributes substantially to structural variance but fails to predict any stability
207 component underscores an important decoupling: network size is not synonymous with robustness. This
208 result aligns with empirical syntheses showing that species richness alone poorly predicts secondary extinction
209 resistance unless accompanied by trophic balance or redundancy. In our analyses, the predator–prey ratio and
210 herbivory—metrics reflecting trophic shape and basal channel dominance—were far stronger determinants of
211 persistence and damping than richness itself. This helps reconcile why biodiversity–stability studies sometimes
212 find positive, neutral, or context-dependent relationships. Richness operates primarily as a geometric scaling
213 variable. Its effect on stability depends on how additional species alter the configuration of energy channels—
214 whether they add redundancy, elongate chains, skew trophic balance, or increase coupling. Without specifying
215 which structural dimension richness modifies, its stability effect is indeterminate.

216 **4.3 Implications for biodiversity–stability theory**

217 Our results contribute to a long-standing tension between the “complexity begets instability” argument and
218 more recent views that diversity enhances resilience. The resolution lies in recognising that different dimensions
219 of complexity influence different stability components. Redundancy and trophic similarity (low MaxSim
220 heterogeneity) enhance persistence by providing functional compensation following species loss. Pathway
221 multiplicity and basal channel dominance regulate resistance by shaping how perturbations propagate. Global
222 organisational heterogeneity (captured by SVD complexity and spectral properties) influences return dynamics
223 by constraining system-wide oscillations and reassembly patterns. In this sense, complexity is neither inherently
224 stabilising nor destabilising. Instead, distinct forms of complexity map onto distinct dynamical outcomes.
225 Connectance, motif structure, redundancy, and informational heterogeneity are not interchangeable proxies

226 for “complexity,” but structurally and mechanistically distinct attributes. By explicitly embedding food-web
227 metrics within an energy-flow hierarchy, our framework reframes biodiversity–stability theory. Stability emerges
228 not from species number alone, but from the configuration of energy channels and the distribution of functional
229 roles across those channels. A bottom-heavy web with balanced predator–prey ratios and differentiated trophic
230 niches may achieve both persistence and damping, even at moderate richness. Conversely, a species-rich but
231 top-heavy or weakly differentiated web may remain fragile.

232 **4.4 Structural modularity and the minimum sufficient set**

233 A key practical outcome of our analysis is the identification of six structural pillars that capture nearly
234 85% of the variation in network architecture. Despite starting with 31 commonly used metrics, much of
235 their variance collapses into a smaller number of independent axes. Hierarchical clustering further revealed
236 robust modules corresponding to trophic balance, pathway structure, geometric scale, and redundancy. This
237 dimensional reduction has two important implications. First, it demonstrates that many commonly reported
238 metrics are statistically redundant. Reporting both connectance and L/S, or multiple correlated distance
239 measures, adds little new information. Second, it provides a principled route toward a minimum sufficient
240 descriptor set tailored to ecological questions. Rather than selecting metrics by convention, researchers can
241 select representatives of the relevant structural scale.

242 **4.5 Guidance for metric choice based on ecological question**

243 If the question concerns extinction cascades or tolerance to species loss (persistence): prioritise node-level
244 balance and redundancy metrics (e.g. predator–prey ratio, herbivory, similarity). If the question concerns
245 perturbation propagation or damping (resistance): focus on path-level and basal-channel metrics (e.g. pathway
246 multiplicity, omnivory, mean distance). If the question concerns recovery dynamics or organisational reassembly
247 (return): emphasise global heterogeneity and spectral measures (e.g. SVD complexity, spectral radius). If
248 the question concerns comparative architecture across systems: use geometric anchors (e.g. richness) but
249 interpret them as scale descriptors rather than stability predictors. This scale-explicit approach shifts the
250 emphasis from asking “Which metric best predicts stability?” to “Which structural dimension corresponds to
251 the stability mechanism of interest?”

252 **4.6 Limitations and future directions**

253 While our framework clarifies structural dimensionality, it remains grounded in static network topology. Real
254 ecosystems exhibit interaction strengths, temporal variability, adaptive rewiring, and environmental forcing.

255 Incorporating weighted networks and dynamic simulations would strengthen the mechanistic link between
256 structural axes and realised dynamics. Additionally, the separation of persistence, resistance, and return is
257 analytically useful but biologically intertwined. For example, structures that enhance resistance may indirectly
258 support persistence by preventing large cascades. Future work could explore how these components interact
259 across environmental gradients and disturbance regimes. Finally, extending this framework beyond trophic
260 networks to mutualistic, host–parasite, or multilayer networks would test its generality. The energy-flow
261 hierarchy proposed here may represent a broader organising principle of ecological interaction systems.

262 5 Conclusion

263 Food-web stability is not governed by a single structural property, but by multiple, hierarchically organised
264 dimensions of network architecture. Node composition, pathway routing, geometric constraint, and emergent
265 organisation each represent distinct levers through which ecosystems maintain persistence, resist perturbation,
266 and reorganise following disturbance.

267 By explicitly mapping structural scale to stability mechanism, we reconcile decades of seemingly conflicting
268 findings in the structure–stability literature. The key insight is not that one metric is superior, but that
269 different metrics answer different ecological questions. Recognising and embracing this multidimensionality
270 provides a coherent foundation for future biodiversity–stability research and a practical framework for selecting
271 network descriptors based on mechanism rather than tradition.

Table 3: Network properties used for analysis.

Dimension	Key Metrics	Expected Effect on Stability	Supporting Literature
Complexity & Redundancy	Connectance, MaxSim, Links	Positive: High redundancy allows for ‘functional compensation’ if one species is lost.	Dunne et al. (2002); McCann (2000)
Compartmentalization	Clust, Modularity,	Positive: Limits the spread of perturbations; local collapses don’t become global.	Stouffer & Bascompte (2011)

Dimension	Key Metrics	Expected Effect on Stability	Supporting Literature
Feedback & Coupling	Omnivory (S2), Loop, ChLen	Variable: Omnivory can stabilize by diffusing energy, but long chains can amplify oscillations.	McCann (2000); Neutel et al. (2002)
Hierarchy & Shape	Prey:Predator, Basal, Top	Critical: ‘Bottom-heavy’ systems are generally more stable; inverted pyramids are fragile.	
Information	SVD Complexity,	Positive: Diverse interaction strengths prevent ‘resonant’	Ulanowicz (2001)
Heterogeneity	LinkSD	instabilities.	

272 To better link network structure to ecosystem function, we grouped commonly used food web metrics into
 273 four functional categories reflecting their ecological interpretation. Node-level metrics (e.g., basal, top,
 274 intermediate, herbivory, cannibal, trophic level, centrality, MaxSim) capture the roles and properties of
 275 individual species. Path-level metrics (*e.g.*, food chain lengths, motifs, omnivory, loops, prey-to-predator
 276 ratios) describe how energy and interactions flow through the network. Geometry metrics (e.g., connectance,
 277 link density, clustering, variation in links, diameter, intervality, spectral radius, SVD complexity) quantify the
 278 overall network arrangement and topological organization. Finally, behavioural/system-level metrics (e.g.,
 279 robustness, spectral radius, SVD complexity) capture emergent properties such as resilience, redundancy,
 280 and dynamic stability. This framework provides a transparent, ecologically interpretable mapping from
 281 species-level roles and interaction paths to system-level behaviour, facilitates identification of a Minimum
 282 Sufficient Set of descriptors, and links network structure to long-standing questions in the stability–complexity
 283 debate.

Table 4: Classification of food web metrics into functional categories. Node-level metrics capture species roles; path-level metrics capture energy or interaction flows; geometry metrics describe network structure; and behaviour/system-level metrics capture emergent stability and resilience.

Category	Metrics	Rationale
Node-level	basal, top, intermediate, herbivory, cannibal, TL, centrality, MaxSim	Metrics describing individual species and their roles in the network, including trophic position (TL), feeding type (basal, herbivory, cannibal), influence (centrality), and functional redundancy (MaxSim).
Path level	ChLen, ChSD, ChNum, path, S1, S2, S4, S5, omnivory, loops, predpreyRatio, distance	Metrics describing energy flow or interaction paths through the network, including food chain lengths, motifs, omnivory, loops, and prey-predator ratios. Capture how energy and interactions move across nodes.
Geometry/topology	connectance, l_S, links, richness, Clust, GenSD, VulSD, LinkSD, diameter, intervals	Metrics describing overall network structure , including density (connectance, links, L/S), size (richness), local clustering, link asymmetry, network distances (diameter), and niche structure (intervals). Capture the ‘shape’ of the network.

Category	Metrics	Rationale
Behaviour/system-level	, complexity, robustness	Metrics describing emergent properties of the network, including system-wide stability, resilience, and structural complexity. Capture how the network responds to perturbations or organizes itself at a global level.

Table 5: Here is a table showing the correlation of the different network properties with the first three dimensions of the PCA

Property	dimension	quanti.correlation	quanti.p.value
richness	Dim.1	0.38	NA
richness	Dim.2	0.84	NA
richness	Dim.3	-0.27	NA
richness	Dim.4	0.04	NA
richness	Dim.5	-0.05	NA
links	Dim.1	0.68	NA
links	Dim.2	0.68	NA
links	Dim.3	0.01	NA
links	Dim.4	0.03	NA
links	Dim.5	0.12	NA
connectance	Dim.1	0.40	NA
connectance	Dim.2	-0.56	NA
connectance	Dim.3	0.60	NA
connectance	Dim.4	-0.04	NA
connectance	Dim.5	0.10	NA
diameter	Dim.1	0.80	NA
diameter	Dim.2	0.27	NA
diameter	Dim.3	-0.24	NA
diameter	Dim.4	0.02	NA

Table 5: Here is a table showing the correlation of the different network properties with the first three dimensions of the PCA

Property	dimension	quanti.correlation	quanti.p.value
diameter	Dim.5	0.11	NA
distance	Dim.1	-0.01	NA
distance	Dim.2	0.33	NA
distance	Dim.3	0.08	NA
distance	Dim.4	0.59	NA
distance	Dim.5	0.40	NA
basal	Dim.1	-0.52	NA
basal	Dim.2	0.44	NA
basal	Dim.3	0.65	NA
basal	Dim.4	0.22	NA
basal	Dim.5	-0.19	NA
top	Dim.1	-0.54	NA
top	Dim.2	0.21	NA
top	Dim.3	-0.38	NA
top	Dim.4	-0.55	NA
top	Dim.5	0.09	NA
intermediate	Dim.1	0.72	NA
intermediate	Dim.2	-0.48	NA
intermediate	Dim.3	-0.35	NA
intermediate	Dim.4	0.10	NA
intermediate	Dim.5	0.11	NA
predpreyRatio	Dim.1	-0.31	NA
predpreyRatio	Dim.2	0.39	NA
predpreyRatio	Dim.3	0.71	NA
predpreyRatio	Dim.4	0.31	NA
predpreyRatio	Dim.5	-0.27	NA
herbivory	Dim.1	-0.51	NA
herbivory	Dim.2	0.27	NA
herbivory	Dim.3	0.02	NA

Table 5: Here is a table showing the correlation of the different network properties with the first three dimensions of the PCA

Property	dimension	quanti.correlation	quanti.p.value
herbivory	Dim.4	-0.17	NA
herbivory	Dim.5	0.55	NA
omnivory	Dim.1	0.77	NA
omnivory	Dim.2	-0.31	NA
omnivory	Dim.3	-0.14	NA
omnivory	Dim.4	0.05	NA
omnivory	Dim.5	-0.15	NA
cannibal	Dim.1	0.69	NA
cannibal	Dim.2	0.07	NA
cannibal	Dim.3	0.40	NA
cannibal	Dim.4	-0.39	NA
cannibal	Dim.5	0.00	NA
l_S	Dim.1	0.84	NA
l_S	Dim.2	0.45	NA
l_S	Dim.3	0.26	NA
l_S	Dim.4	-0.09	NA
l_S	Dim.5	0.03	NA
GenSD	Dim.1	-0.39	NA
GenSD	Dim.2	0.67	NA
GenSD	Dim.3	0.33	NA
GenSD	Dim.4	0.21	NA
GenSD	Dim.5	-0.32	NA
VulSD	Dim.1	-0.34	NA
VulSD	Dim.2	0.56	NA
VulSD	Dim.3	-0.42	NA
VulSD	Dim.4	-0.46	NA
VulSD	Dim.5	0.17	NA
TL	Dim.1	0.57	NA
TL	Dim.2	-0.40	NA

Table 5: Here is a table showing the correlation of the different network properties with the first three dimensions of the PCA

Property	dimension	quanti.correlation	quanti.p.value
TL	Dim.3	-0.66	NA
TL	Dim.4	-0.05	NA
TL	Dim.5	-0.08	NA
ChLen	Dim.1	0.54	NA
ChLen	Dim.2	-0.54	NA
ChLen	Dim.3	-0.49	NA
ChLen	Dim.4	0.12	NA
ChLen	Dim.5	-0.16	NA
ChSD	Dim.1	0.37	NA
ChSD	Dim.2	0.11	NA
ChSD	Dim.3	-0.45	NA
ChSD	Dim.4	0.40	NA
ChSD	Dim.5	-0.10	NA
ChNum	Dim.1	-0.11	NA
ChNum	Dim.2	0.76	NA
ChNum	Dim.3	-0.47	NA
ChNum	Dim.4	-0.24	NA
ChNum	Dim.5	-0.15	NA
path	Dim.1	0.31	NA
path	Dim.2	0.34	NA
path	Dim.3	-0.36	NA
path	Dim.4	0.54	NA
path	Dim.5	0.35	NA
LinkSD	Dim.1	-0.19	NA
LinkSD	Dim.2	0.72	NA
LinkSD	Dim.3	-0.39	NA
LinkSD	Dim.4	-0.05	NA
LinkSD	Dim.5	-0.29	NA
S1	Dim.1	0.90	NA

Table 5: Here is a table showing the correlation of the different network properties with the first three dimensions of the PCA

Property	dimension	quanti.correlation	quanti.p.value
S1	Dim.2	-0.03	NA
S1	Dim.3	0.14	NA
S1	Dim.4	-0.07	NA
S1	Dim.5	0.08	NA
S2	Dim.1	0.79	NA
S2	Dim.2	-0.06	NA
S2	Dim.3	0.47	NA
S2	Dim.4	-0.26	NA
S2	Dim.5	-0.06	NA
S4	Dim.1	0.62	NA
S4	Dim.2	0.48	NA
S4	Dim.3	0.28	NA
S4	Dim.4	-0.26	NA
S4	Dim.5	0.18	NA
S5	Dim.1	0.66	NA
S5	Dim.2	0.42	NA
S5	Dim.3	0.52	NA
S5	Dim.4	-0.08	NA
S5	Dim.5	0.00	NA
centrality	Dim.1	-0.30	NA
centrality	Dim.2	-0.61	NA
centrality	Dim.3	0.26	NA
centrality	Dim.4	0.07	NA
centrality	Dim.5	0.46	NA
loops	Dim.1	0.81	NA
loops	Dim.2	0.28	NA
loops	Dim.3	0.17	NA
loops	Dim.4	-0.09	NA
loops	Dim.5	0.12	NA

Table 5: Here is a table showing the correlation of the different network properties with the first three dimensions of the PCA

Property	dimension	quanti.correlation	quanti.p.value
intervals	Dim.1	0.51	NA
intervals	Dim.2	0.65	NA
intervals	Dim.3	-0.11	NA
intervals	Dim.4	0.24	NA
intervals	Dim.5	0.18	NA
MaxSim	Dim.1	-0.12	NA
MaxSim	Dim.2	-0.07	NA
MaxSim	Dim.3	0.57	NA
MaxSim	Dim.4	-0.14	NA
MaxSim	Dim.5	0.21	NA
Clust	Dim.1	0.64	NA
Clust	Dim.2	-0.35	NA
Clust	Dim.3	0.16	NA
Clust	Dim.4	0.01	NA
Clust	Dim.5	-0.40	NA
S1	Dim.1	0.90	0.0000000
l_S	Dim.1	0.84	0.0000000
loops	Dim.1	0.81	0.0000000
diameter	Dim.1	0.80	0.0000000
S2	Dim.1	0.79	0.0000000
omnivory	Dim.1	0.77	0.0000000
intermediate	Dim.1	0.72	0.0000004
cannibal	Dim.1	0.69	0.0000015
links	Dim.1	0.68	0.0000030
S5	Dim.1	0.66	0.0000077
Clust	Dim.1	0.64	0.0000170
S4	Dim.1	0.62	0.0000282
TL	Dim.1	0.57	0.0001879
ChLen	Dim.1	0.54	0.0005272

Table 5: Here is a table showing the correlation of the different network properties with the first three dimensions of the PCA

Property	dimension	quanti.correlation	quanti.p.value
intervals	Dim.1	0.51	0.0009658
connectance	Dim.1	0.40	0.0123944
richness	Dim.1	0.38	0.0182160
ChSD	Dim.1	0.37	0.0205346
VulSD	Dim.1	-0.34	0.0348758
GenSD	Dim.1	-0.39	0.0150597
herbivory	Dim.1	-0.51	0.0010542
basal	Dim.1	-0.52	0.0009130
top	Dim.1	-0.54	0.0004175
richness	Dim.2	0.84	0.0000000
ChNum	Dim.2	0.76	0.0000000
LinkSD	Dim.2	0.72	0.0000003
links	Dim.2	0.68	0.0000030
GenSD	Dim.2	0.67	0.0000051
intervals	Dim.2	0.65	0.0000111
VulSD	Dim.2	0.56	0.0002484
S4	Dim.2	0.48	0.0020815
1_S	Dim.2	0.45	0.0049841
basal	Dim.2	0.44	0.0062051
S5	Dim.2	0.42	0.0091132
predpreyRatio	Dim.2	0.39	0.0142971
path	Dim.2	0.34	0.0381102
distance	Dim.2	0.33	0.0426262
Clust	Dim.2	-0.35	0.0303883
TL	Dim.2	-0.40	0.0139488
intermediate	Dim.2	-0.48	0.0023996
ChLen	Dim.2	-0.54	0.0005074
connectance	Dim.2	-0.56	0.0002624
centrality	Dim.2	-0.61	0.0000504

Table 5: Here is a table showing the correlation of the different network properties with the first three dimensions of the PCA

Property	dimension	quanti.correlation	quanti.p.value
predpreyRatio	Dim.3	0.71	0.0000006
basal	Dim.3	0.65	0.0000122
connectance	Dim.3	0.60	0.0000804
MaxSim	Dim.3	0.57	0.0002078
S5	Dim.3	0.52	0.0008330
S2	Dim.3	0.47	0.0029951
cannibal	Dim.3	0.40	0.0122774
GenSD	Dim.3	0.33	0.0416849
intermediate	Dim.3	-0.35	0.0293668
path	Dim.3	-0.36	0.0276975
top	Dim.3	-0.38	0.0201240
LinkSD	Dim.3	-0.39	0.0148989
VulSD	Dim.3	-0.42	0.0094597
ChSD	Dim.3	-0.45	0.0047583
ChNum	Dim.3	-0.47	0.0026959
ChLen	Dim.3	-0.49	0.0018937
TL	Dim.3	-0.66	0.0000064

²⁸⁴ Source: [Article Notebook](#)

²⁸⁵ [Figure 1 about here.]

²⁸⁶ [Figure 2 about here.]

²⁸⁷ [Figure 3 about here.]

²⁸⁸ References

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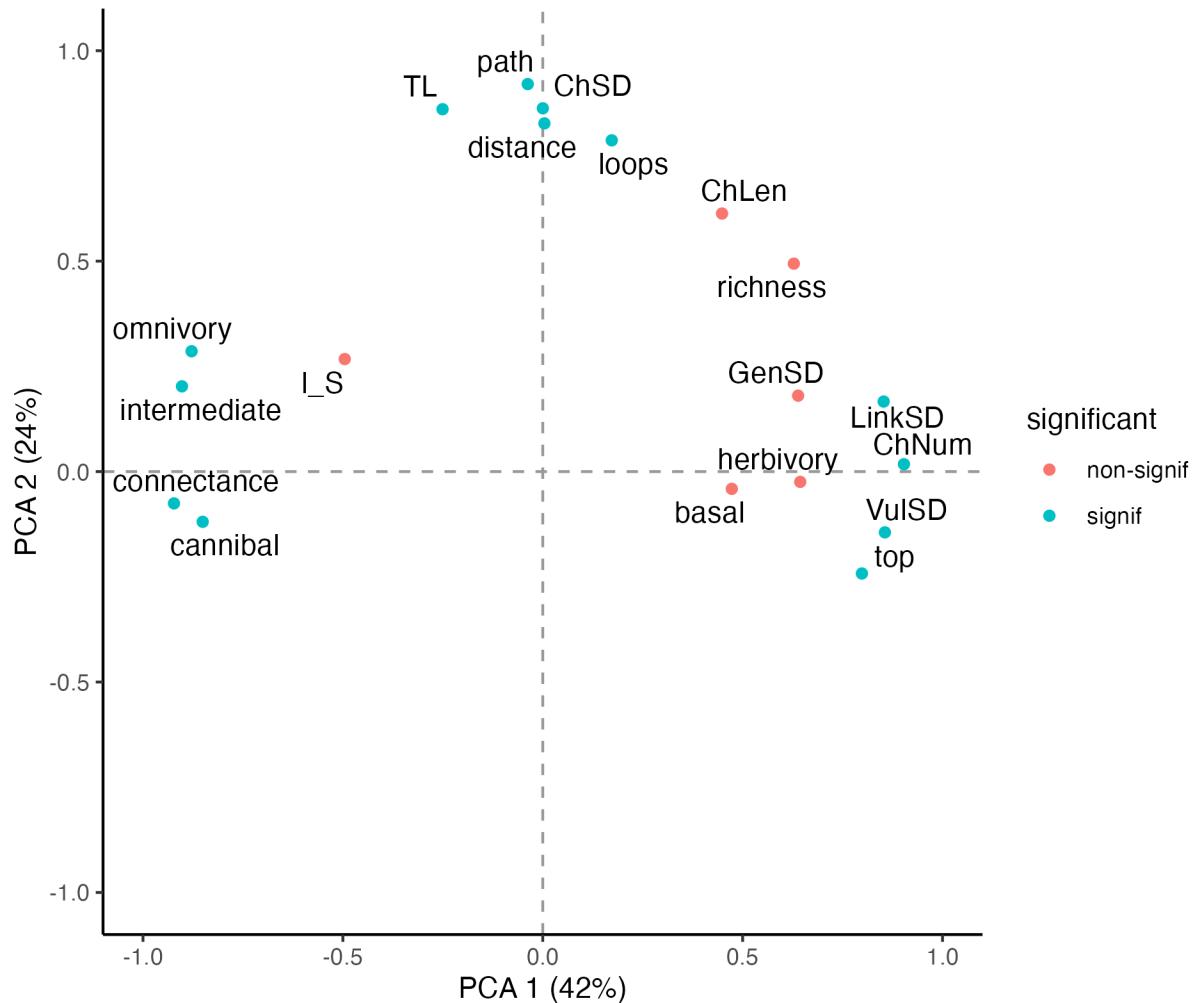


Figure 1: VERMAAT networks only

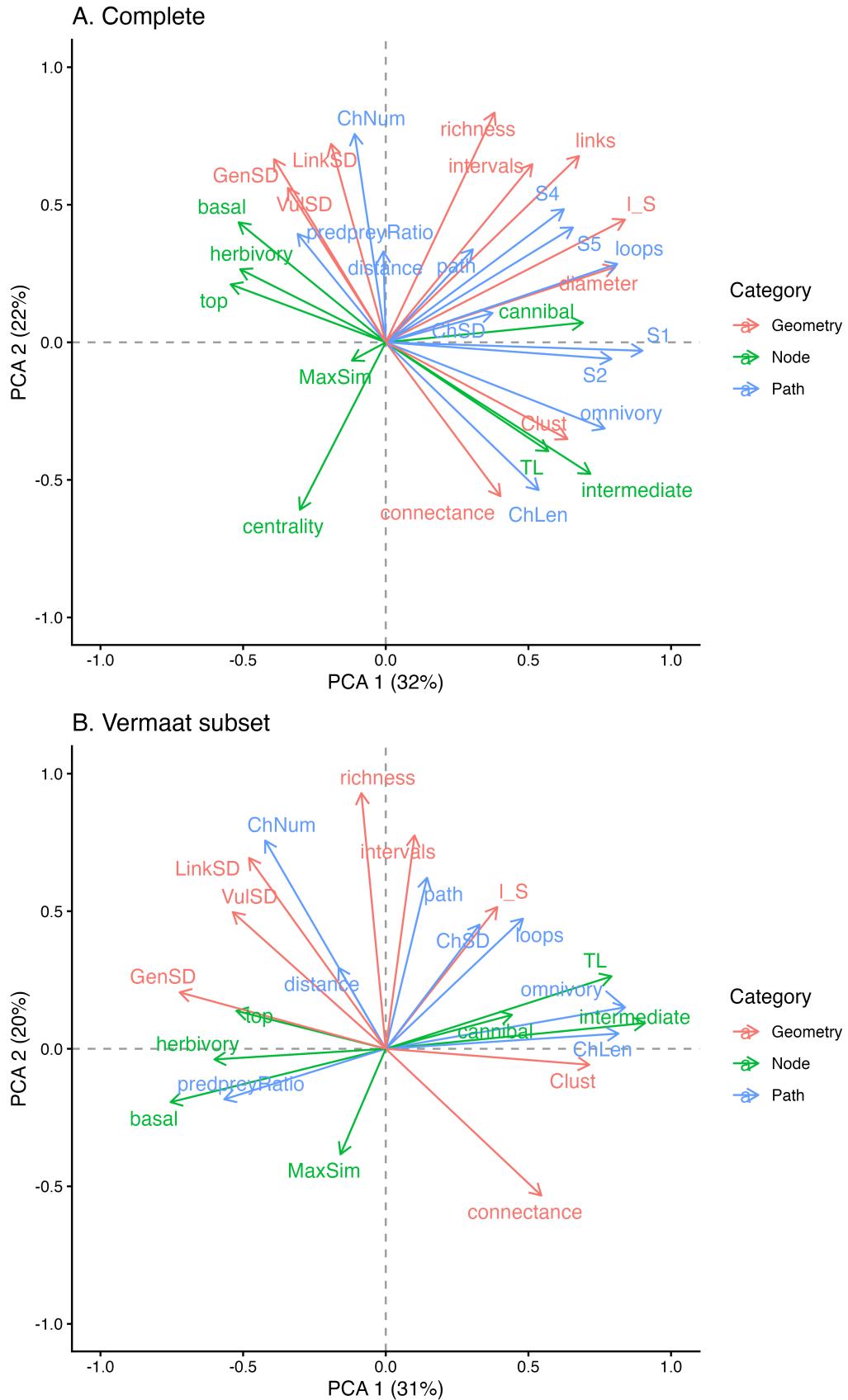


Figure 2: All networks. Vermaat subset = using only the structural measures from Vermaat
29

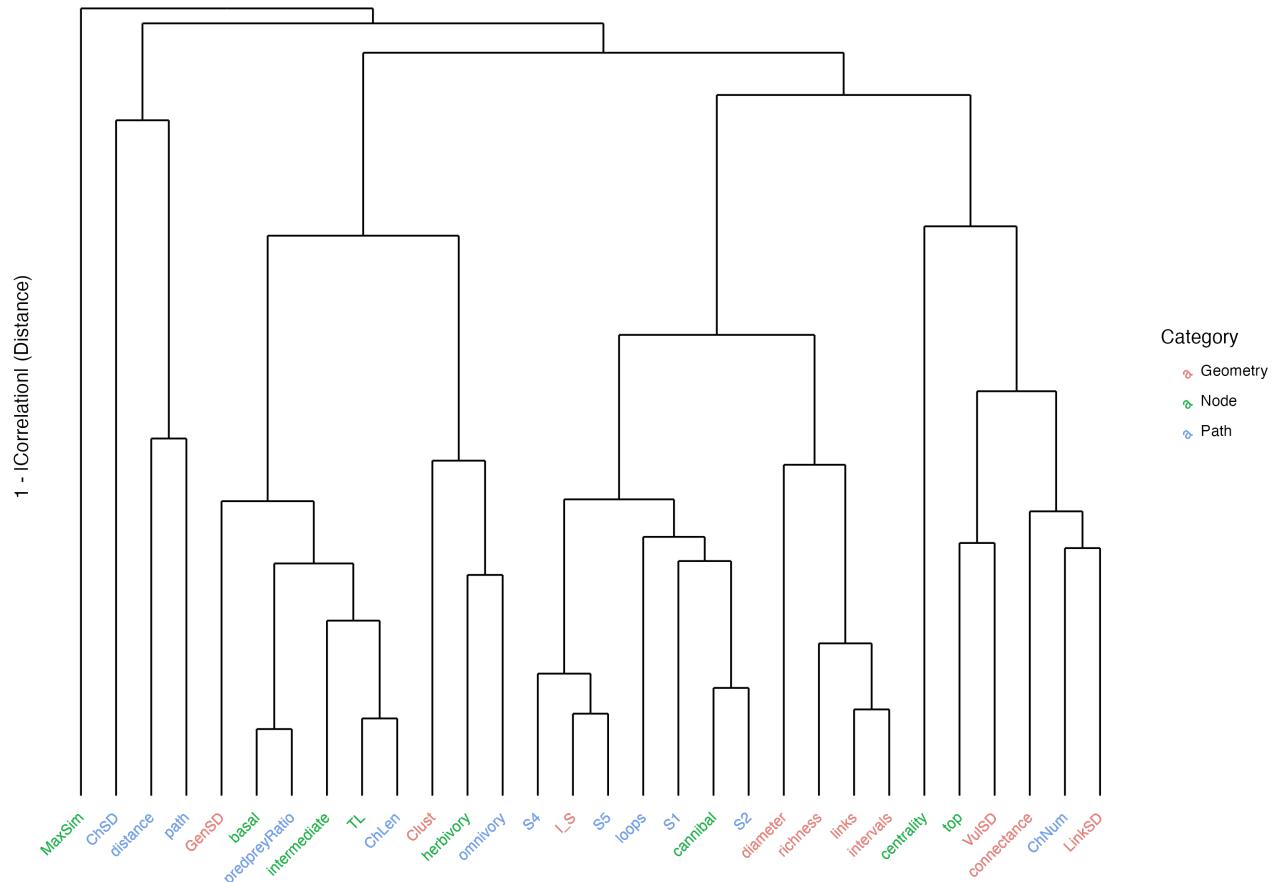


Figure 3: Cluster