Finding the major descriptors of species networks

Tanya Strydom [1]; Andrew P. Beckerman [1]

Abstract: TODO

Keywords: food web, structure, dimensionality reduction

1 Introduction

To bridge the gap between the original paper and your new objectives, your introduction could follow this logical flow:

The Evolution of Ecological Network Theory

The Hook: Acknowledge the foundational shift from viewing biodiversity as a simple "species count" to viewing it as a complex web of interactions.

The Baseline: Summarize the core findings of the paper you're expanding on—specifically, how the architecture (e.g., compartmentalization vs. nestedness) affects stability differently in mutualistic vs. trophic networks.

The Need for Dimensionality

The Gap: Argue that while "connectance" and "nestedness" are vital, they don't capture the full resolution of ecosystem dynamics.

The Expansion: Introduce the necessity of more nuanced metrics (e.g., motifs, centrality, modularity, and beta-diversity of interactions) to capture the "hidden" stability of diverse networks.

Linking Structure to Ecosystem Function (EF)

The Framework: Explicitly connect structural metrics to the "Stability-Complexity" debate.

The Hypothesis: Propose how specific structural arrangements (like high modularity) act as "firewalls" to prevent the spread of perturbations, thereby maintaining ecosystem function under stress.

Objectives

The overarching goal of this study is to move beyond bipartite generalizations and define a comprehensive "structural fingerprint" of ecosystem stability. To achieve this, we address two primary objectives:

Identification of a Core Structural Subset

Ecological networks are characterized by a high degree of collinearity among structural descriptors. We aim to determine whether the 31 metrics analyzed in this study can be reduced to a **Minimum Sufficient Set**—a small, non-redundant group of indicators that capture the essential topological features of an ecosystem. By employing multivariate techniques such as **Variable Clustering** and **SVD Complexity**, we seek to move away from arbitrary metric selection toward a data-driven framework for network characterization.

Mapping the Multi-dimensional Stability Landscape

Building on the "stability-complexity" debate (McCann 2000, Ives & Carpenter 2007), we aim to map how these diverse structural metrics correlate with different facets of ecosystem health. Specifically, we test the following hypotheses:

- **The Robustness Hypothesis:** Metrics of redundancy (e.g., *Connectance, MaxSim*) will be the primary predictors of resistance to primary species loss.
- **The Containment Hypothesis:** Modular structures (e.g., *Clust, Modularity*) will correlate with system-wide resilience by preventing the propagation of local perturbations.
- **The Dynamic Capacity Hypothesis:** Information-theoretic measures (e.g., *SVD Complexity, Spectral Radius*) will provide a superior bridge between static topology and the dynamic ability of the system to return to equilibrium.

Clearly state that this study expands the taxonomic and structural scope of previous models to provide a generalized rulebook for network-mediated stability.

Synthesis: Linking to "Stability"

In your manuscript, you can group these metrics into **three functional categories**:

1. **Robustness Metrics:** (Richness, Connectance, Robustness, MaxSim) — These describe how many "hits" the network can take before collapsing.
2. **Efficiency/Flow Metrics:** (Path, ChLen, TL, Diameter) — These describe how quickly energy or perturbations move through the system.
3. **Organization Metrics:** (, Complexity, Modularity/Clust, Intervality) — These describe the "logic" of the arrangement, which dictates whether the system behaves predictably or chaotically.

Blah blah blah Vermaat et al. (2009)

"It is incumbent on network ecologists to establish clearly the independence and uniqueness of the descriptive metrics used." - Lau et al. (2017)

Table 1: Stuff

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)
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 Heterogeneity	SVD Complexity, LinkSD	**Positive:** Diverse interaction strengths prevent "resonant" instabilities.	Ulanowicz (2001)

2 Materials and Methods

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	Ecological Significance	Reference (for maths), can make footnotes probs
Basal	Percentage of basal taxa, defined as species who have a vulnerability of zero	Measures the energy entry points; high basal % suggests a bottom-heavy, potentially more stable energy base.	
Connectance	L/S^2, where S is the number of species and L the number of links		
Cannibal	Percentage of species that are cannibals		
ChLen	Mean food chain length, averaged over all species (where a food chain is defined as a continuous path from a 'basal' to a 'top' species)	Reflects energy transfer efficiency. Longer chains may be more prone to top-down trophic cascades.	
ChSD	Standard deviation of ChLen	High SD indicates a mix of energy pathways, which can buffer the system	
ChNum	log number of food chains		
Clust	mean clustering coefficient (probability that two taxa linked to the same taxon are also linked)	Quantifies local redundancy; high clustering can buffer the network against the loss of specific interaction pathways.	**TODO** Watts & Strogatz (1998)
GenSD	Normalized standard deviation of generality of a species standardized by L/S	Interaction asymmetry. High variance in how links are distributed often points to the presence of 'hubs' (highly connected species), which makes the network robust to random loss but vulnerable to targeted 'keystone' removal.	Williams & Martinez (2008)

Label	Definition	Ecological Significance	Reference (for maths), can make footnotes probs
Herbivore	Percentage of herbivores plus detritivores (taxa that feed only on basal taxa)		
Intermediate	Percentage of intermediate taxa (with both consumers and resources)		
LinkSD	Normalized standard deviation of links (number of consumers plus resources per taxon)	Interaction asymmetry. High variance in how links are distributed often points to the presence of 'hubs' (highly connected species), which makes the network robust to random loss but vulnerable to targeted 'keystone' removal.	
Loop	Percentage of taxa in loops (food chains in which a taxon occurs twice)	High percentages of loops can lead to feedback cycles (positive or negative) that either amplify or dampen oscillations, directly impacting local stability.	
L/S	links per species		
MaxSim	Mean of the maximum trophic similarity of each taxon to other taxa, the number of predators and prey shared by a pair of species divided by their total number of predators and prey	Indicates functional redundancy; high similarity suggests species are replaceable, increasing robustness to individual extinctions.	**TODO** Yodzis & Winemiller (1999)

Label	Definition	Ecological Significance	Reference (for maths), can make footnotes probs
Omnivory	Percentage of omnivores (taxa that feed on ≥ 2 taxa with different trophic levels)	Links to coupling of energy channels; historically debated, but often found to stabilize food webs by diffusing top-down pressure.	McCann (2000)
Path	characteristic path length, the mean shortest food chain length between species pairs		
Richness	Number of nodes in the network		
TL	Prey-weighted trophic level averaged across taxa		Williams & Martinez (2004)
Top	Percentage of top taxa (taxa without consumers)		
VulSD	Normalized standard deviation of vulnerability of a species standardized by L/S	Interaction asymmetry. High variance in how links are distributed often points to the presence of 'hubs' (highly connected species), which makes the network robust to random loss but vulnerable to targeted 'keystone' removal.	
Links	The number of links in the network		
Diameter	Diameter can also be measured as the average of the distances between each pair of nodes in the network		Delmas et al. (2019)

Label	Definition	Ecological Significance	Reference (for maths), can make footnotes probs
ρ	Spectral radius is a a conceptual analog to nestedness. It is defined as the absolute value of the largest real part of the eigenvalues of the *undirected* adjacency matrix	Acts as a proxy for system-wide resilience; captures the speed at which a system returns to equilibrium after a small pulse perturbation.	Staniczenko et al. (2013)
Complexity	SVD complexity of a network, defined as the Pielou entropy of its singular values	Captures structural heterogeneity; distinguishes between a truly complex system and one that is merely large or 'random'.	Strydom et al. (2021)
Centrality	Centrality is a measure of how 'influential' a species is, under various definitions of 'influence'.	Centrality can help in quantifying the importance of species in a network	Estrada & Bodin (2008)
S1	Number of linear chains	Building blocks of stability (compartmentalisation, Stouffer and Bascompte?)	Stouffer et al. (2007) Milo et al. (2002)
S2	Number of omnivory motifs	Building blocks of stability (compartmentalisation, Stouffer and Bascompte?)	Stouffer et al. (2007) Milo et al. (2002)
S4	Number of apparent competition motifs	Building blocks of stability (compartmentalisation, Stouffer and Bascompte?)	Stouffer et al. (2007) Milo et al. (2002)
S5	Number of direct competition motifs	Building blocks of stability (compartmentalisation, Stouffer and Bascompte?)	Stouffer et al. (2007) Milo et al. (2002)
Intervality	The degree to which the prey in a food web can be ordered so that all species can be placed along a single dimension	Measures niche dimension; high intervality suggests a simpler organization where species feeding habits are constrained by a single trait (like body size).	Stouffer et al. (2006)

Label	Definition	Ecological Significance	Reference (for maths), can make footnotes probs
Prey:predator	Ratio of prey (basal + intermediate) to predators (top + intermediate)	A measure of food web 'shape'. Values <1 imply an inverted structure and might indicate instability	
Robustness	Minimum level of secondary extinction that occurs in response to a particular perturbation		Jonsson et al. (2015)

Table 3: Here is a table showing the correlation of the different network properties with the first three dimensions of the PCA

Property	PCA 1 (30%)	PCA 2 (20%)	PCA 3 (17%)
richness	0.3	**0.89**	-0.16
links	0.62	**0.72**	0.04
connectance	0.52	-0.62	0.49
diameter	**0.74**	0.38	-0.3
complexity	-0.52	0.09	-0.49
distance	0	0.3	0.18
basal	-0.47	0.29	**0.75**
top	-0.58	0.2	-0.24
intermediate	**0.69**	-0.35	-0.52
predpreyRatio	-0.26	0.27	**0.76**
herbivory	-0.54	0.22	0.07
omnivory	**0.78**	-0.23	-0.21
cannibal	**0.72**	0.07	0.31
l_S	**0.83**	0.47	0.23
GenSD	-0.4	0.58	0.45
VulSD	-0.41	0.58	-0.26
TL	0.52	-0.24	**-0.77**

Table 3: Here is a table showing the correlation of the different network properties with the first three dimensions of the PCA

Property	PCA 1 (30%)	PCA 2 (20%)	PCA 3 (17%)
ChLen	0.51	-0.41	-0.62
ChSD	0.32	0.2	-0.45
ChNum	-0.2	**0.8**	-0.3
path	0.26	0.4	-0.26
LinkSD	-0.27	**0.74**	-0.23
S1	**0.9**	0.03	0.03
S2	**0.84**	-0.07	0.36
S4	0.61	0.49	0.28
S5	**0.67**	0.39	0.49
	0.57	-0.43	0.48
centrality	-0.24	**-0.67**	0.18
loops	**0.8**	0.32	0.12
robustness	0.05	-0.05	0.66
intervals	0.45	**0.7**	-0.05
MaxSim	-0.03	-0.17	0.6
Clust	**0.69**	-0.33	0.06

Source: Article Notebook

[Figure 1 about here.]

[Figure 2 about here.]

References

Delmas, E., Besson, M., Brice, M.-H., Burkle, L. A., Riva, G. V. D., Fortin, M.-J., Gravel, D., Guimarães, P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2019). Analysing ecological networks of species interactions. *Biological Reviews*, *94*(1), 16–36. https://doi.org/10.1111/brv.12433

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences*, *99*(20), 12917–12922.

https://doi.org/10.1073/pnas.192407699

Estrada, E., & Bodin, Ö. (2008). Using Network Centrality Measures to Manage Landscape Connectivity. *Ecological Applications*, *18*(7), 1810–1825. https://doi.org/10.1890/07-1419.1

Jonsson, T., Berg, S., Pimenov, A., Palmer, C., & Emmerson, M. (2015). The reliability of R50 as a measure of vulnerability of food webs to sequential species deletions. *Oikos*, *124*(4), 446–457. https://doi.org/10.1111/oik.01588

Lau, M. K., Borrett, S. R., Baiser, B., Gotelli, N. J., & Ellison, A. M. (2017). Ecological network metrics: Opportunities for synthesis. *Ecosphere*, *8*(8), e01900. https://doi.org/10.1002/ecs2.1900

McCann, K. S. (2000). The diversity–stability debate. *Nature*, *405*(6783), 228–233. https://doi.org/10.1038/35012234

Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network Motifs: Simple Building Blocks of Complex Networks. *Science*, *298*(5594), 824–827. https://doi.org/10.1126/science.298.5594.824

Neutel, A.-M., Heesterbeek, J. A. P., & De Ruiter, P. C. (2002). Stability in Real Food Webs: Weak Links in Long Loops. *Science*, *296*(5570), 1120–1123. https://doi.org/10.1126/science.1068326

Staniczenko, P. P. A., Kopp, J. C., & Allesina, S. (2013). The ghost of nestedness in ecological networks. *Nature Communications*, *4*(1), 1391. https://doi.org/10.1038/ncomms2422

Stouffer, D. B., & Bascompte, J. (2011). Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(9), 3648–3652. https://doi.org/10.1073/pnas.1014353108

Stouffer, D. B., Camacho, J., & Amaral, L. A. N. (2006). A robust measure of food web intervality. *Proceedings of the National Academy of Sciences*, *103*(50), 19015–19020. https://doi.org/10.1073/pnas.0603844103

Stouffer, D. B., Camacho, J., Jiang, W., & Nunes Amaral, L. A. (2007). Evidence for the existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1621), 1931–1940. https://doi.org/10.1098/rspb.2007.0571

Strydom, T., Dalla Riva, G. V., & Poisot, T. (2021). SVD Entropy Reveals the High Complexity of Ecological Networks. *Frontiers in Ecology and Evolution*, *9*. https://doi.org/10.3389/fevo.2021.623141

Thompson, R. M., Brose, U., Dunne, J., Hall, R. O., Hladyz, S., Kitching, R. L., Martinez, N. D., Rantala, H., Romanuk, T. N., Stouffer, D. B., & Tylianakis, J. M. (2012). Food webs: Reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution*, *27*(12), 689–697. https://doi.org/10.1016/j.tree.2012.08.005

Ulanowicz, R. E. (2001). Information theory in ecology. *Computers & Chemistry*, *25*(4), 393–399. https://doi.org/10.1016/S0097-8485(01)00073-0

Vermaat, J. E., Dunne, J. A., & Gilbert, A. J. (2009). Major dimensions in food-web structure properties. *Ecology*, *90*(1), 278–282. https://doi.org/10.1890/07-0978.1

Watts, D. J., & Strogatz, S. H. (1998). Collective dynamics of "small-world" networks. *Nature*, *393*(6684), 440–442. https://doi.org/10.1038/30918

Williams, R. J., & Martinez, N. D. (2004). Limits to Trophic Levels and Omnivory in Complex Food Webs: Theory and Data. *The American Naturalist*, *163*(3), 458–468. https://doi.org/10.1086/381964

Williams, R. J., & Martinez, N. D. (2008). Success and its limits among structural models of complex food webs. *The Journal of Animal Ecology*, *77*(3), 512–519. https://doi.org/10.1111/j.1365-2656.2008.01362.x

Yodzis, P., & Winemiller, K. O. (1999). In Search of Operational Trophospecies in a Tropical Aquatic Food Web. *Oikos*, *87*(2), 327–340. https://doi.org/10.2307/3546748

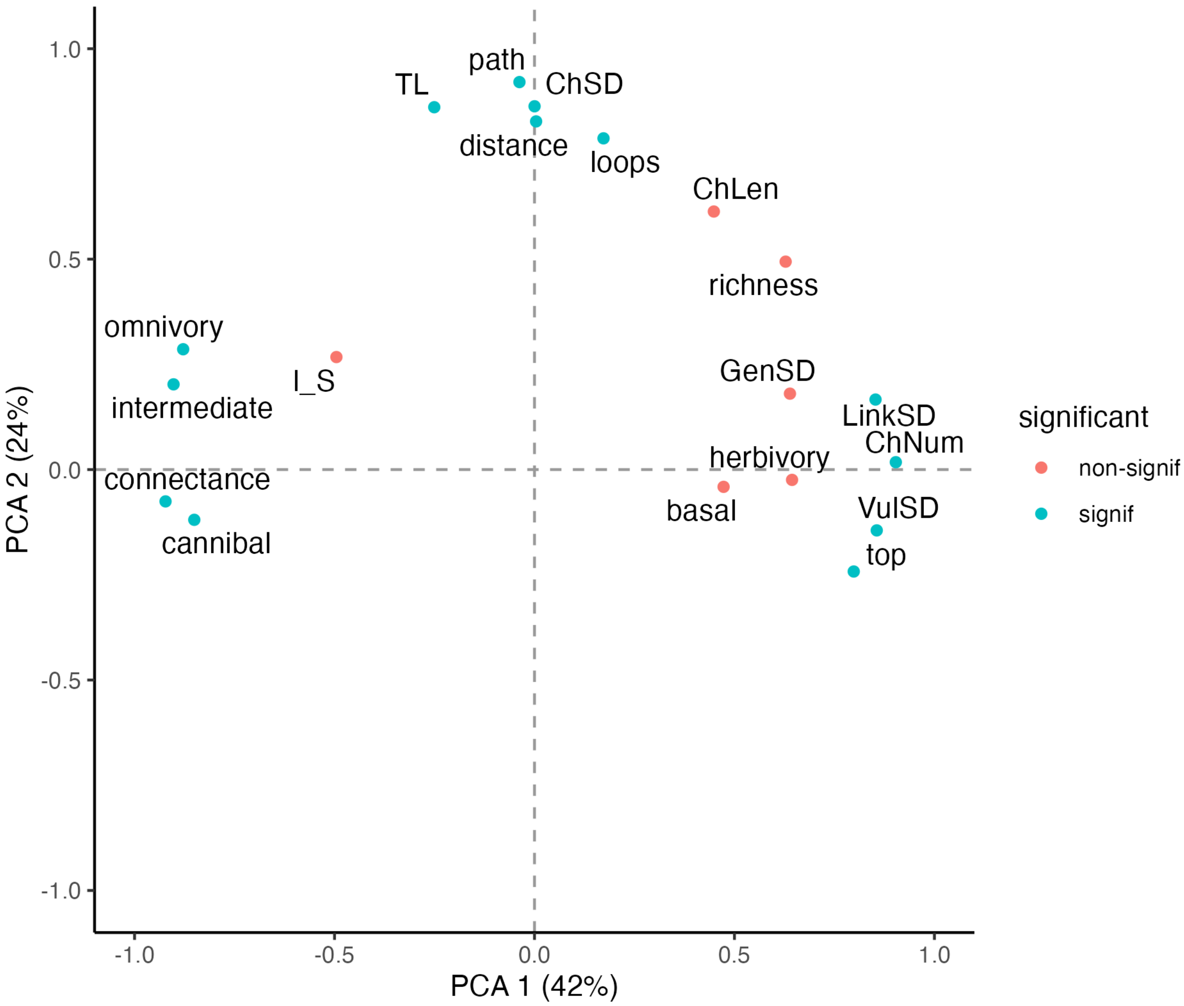
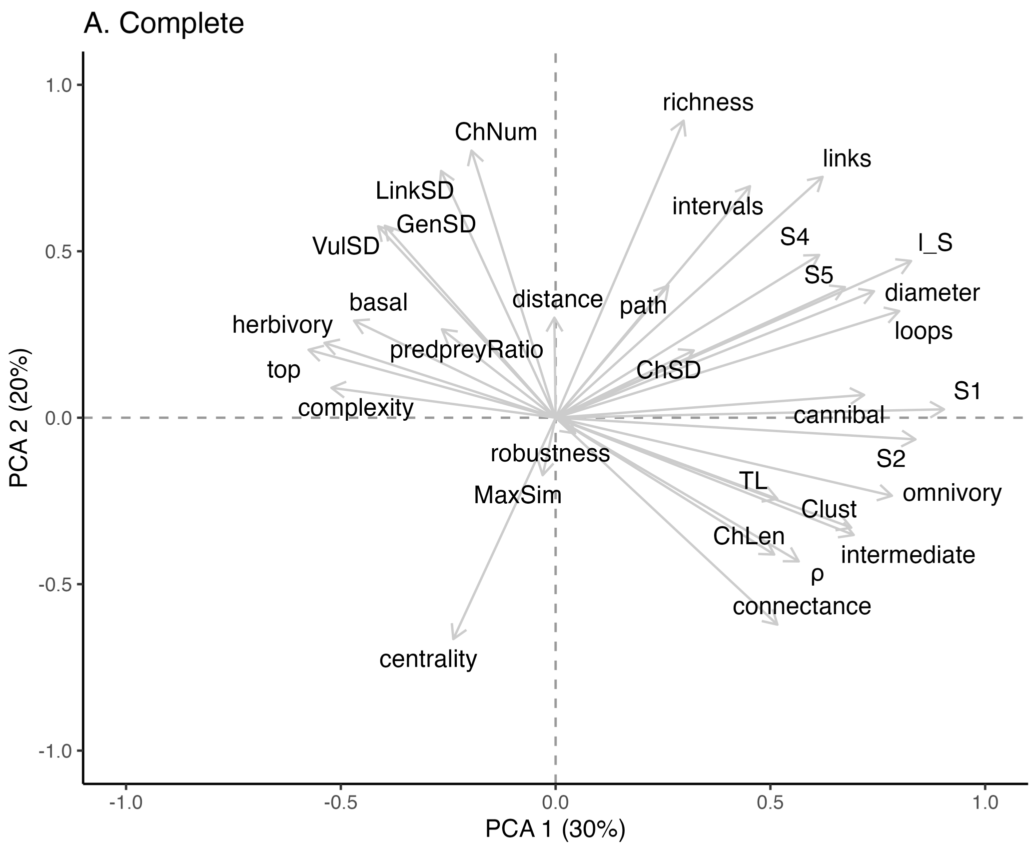


Figure 1: VERMAAT networks only



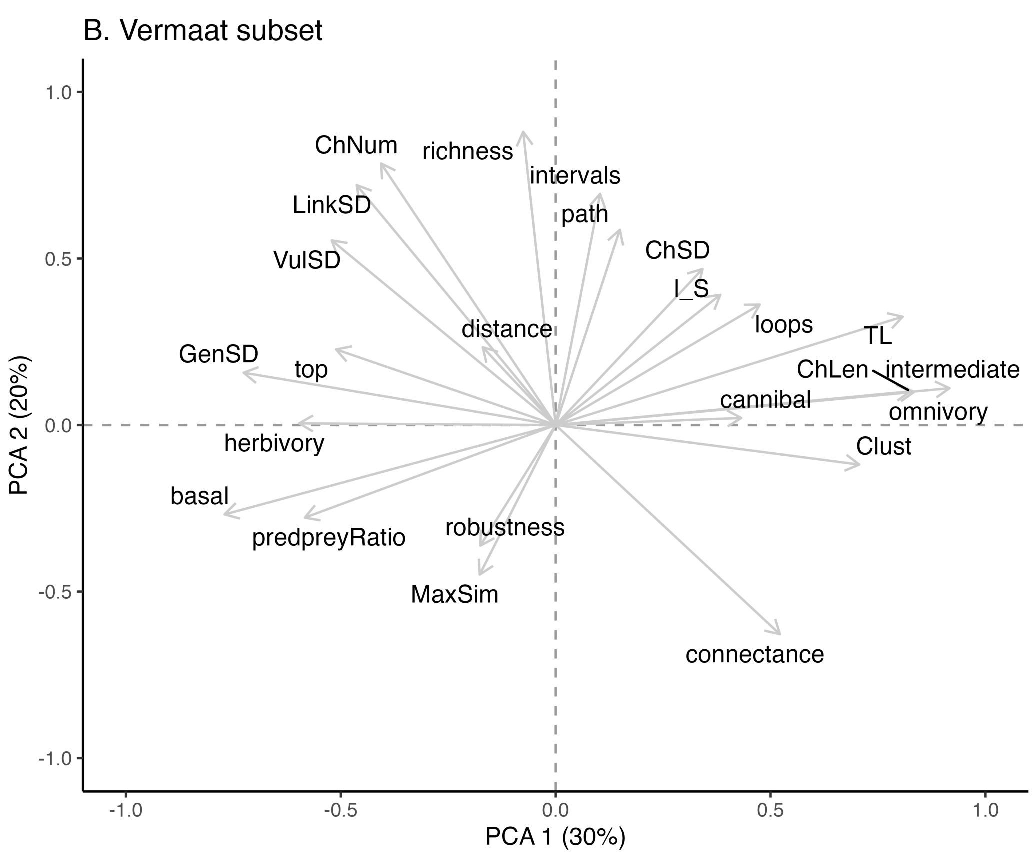


Figure 2: All networks. Vermaat subset = using only the structural measures from Vermaat