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Research

A comparative approach to quantify the heterarchical structures of complex systems

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ABSTRACT. The dynamics and adaptive capacity of social-ecological systems are heavily contingent on system structure, which is established through geography, institutions, interactions, and movement. Contrasting views of system structure, as hierarchies and single-level networks respectively, have tended to emphasize the role of either top-down or lateral (peer-to-peer) connections. The concept of a heterarchy aims to capture both top-down and lateral connections on orthogonal axes and has been proposed as a way of unifying alternative approaches to measuring structure, but it has not been fully operationalized for quantifying and comparing system structures. We developed a simple approach to consistently quantifying heterarchical structure across different kinds of networks. We first calculated suitable metrics, including modularity and a hierarchy score, for a wide range of both simulated and real-world systems including food webs, biological, infrastructure, and social networks. Metrics were corrected for differences in size and magnitude. The results were then visualized as a heterarchy matrix. We compared the angle (degrees) and Euclidian distance of each simulated and real-world network from the center of the matrix between network groups. All networks showed distinct placement on the heterarchy matrix. Relative to one another, food webs were laterally polycentric, social networks were mainly pyramidal and coordinated polycentric, and biological networks were pyramidal and laterally polycentric. Our test of concept, although relatively basic, provides strong evidence that system structure cannot be fully understood as purely laterally connected or purely hierarchical. System resilience requires a trade-off between modularity, aiding redundancy and collaboration; and hierarchy, aiding efficient action. Our approach has the potential to provide a robust, accessible methodology to quantify system structure that allows for universal contextualization, a key step within fields such as resilience and sustainability science.

Key Words: *heterarchy; hierarchy; modularity; network; resilience*

INTRODUCTION

The complex interactions between the components of societies and ecosystems can be described as networks in which system elements (nodes, e.g., animals, locations, or people) are linked by a range of different kinds of interactions (e.g., predation, competition, information sharing, or flows of materials). From a network perspective, the core agenda of social-ecological systems (SES) research focuses on understanding and managing both the nodes and the interactions that comprise the SES (Ostrom 2009), and their emergent properties (e.g., persistence, resilience, sustainability). For example, the harvest of wild fish stocks for food involves, at a minimum, ecological networks (structured by trophic interactions and habitat suitability); human social networks (structured by dynamics of power, kinship, and information sharing); and socioeconomic networks (structured by spatially variable dynamics of supply and demand). Understanding how these different networks operate and interact is central to managing them sustainably and building desirable resilience. For instance, if economic or social demands place too much pressure (and/or provide too strong incentives) on a fisher to harvest fish, an individual may be tempted to over-harvest the fish stock, leading to changes in the ecological network that in turn reduce fish availability.

Unlike many classical social and ecological models, network analysis provides a method for describing the structure—both graphic and relational—of interactions between individual components of a SES. The answers to many important questions in sustainability and resilience science depend heavily on the details of system structure. For example, how long will a degraded ecosystem take to be re-colonized from nearby habitat patches? How does proximity to markets influence social-ecological dynamics? Do particular institutional and governance structures improve the sustainability of interactions between people and nature? To address these questions, which are structural in nature, we need to know not only about the processes and flows occurring within the system, but also about how the relative arrangements and different levels of connectivity of different nodes within the system influence the social-ecological processes in which we are interested.

The basis of network structure is the number and nature of nodes and interactions between them. Importantly, the same structural elements, i.e., the nodes and links, can be arranged (structured) in nearly endlessly different ways, each with potentially different consequences for system function. Many SES studies seek to develop general theories about how system structure interacts with resilience. For example, different approaches to natural resource governance may involve different kinds of social structures and power dynamics, with some kinds of institutional structure (e.g., polycentric governance) being proposed as more effective than alternatives. It is generally agreed, however, that no single structural design offers an optimal compromise between efficiency and resilience in a variable environment (Pimm 1984, Anderies and Norberg 2008, Bodin and Crona 2009, Bodin 2017).

Although SES research has already made substantial progress in understanding social-ecological dynamics, several recent articles have called for a greater emphasis on comparative research as a way of generalizing and extending existing knowledge (Maire et

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al. 2016, Bodin et al. 2019, Darling et al. 2019). To test and further develop theories about how SES structure influences general system dynamics, we require measures that allow relevant elements of the structure of qualitatively different systems (or the same system through time) to be compared directly. This quest thus complements other research efforts where the focus is to more precisely study specific systems, and/or certain aspects or parts of a SES. There are two critical structural properties that are particularly relevant in SESs: lateral or peer-to-peer connectedness, which occurs within a single hierarchical level; and top-down or hierarchical connectedness, which crosses hierarchical levels. Hierarchies tend to arise when flows are directional in nature.

Interactions between components of a complex system are critical for internal processes and thus for SES function and resilience (Cumming 2011). Many previous studies have explored elements of network structure and their relationship to SES resilience. In ecosystems, for example, higher biodiversity within functional groups of ecologically similar species, increasing the degree of lateral connectivity, results in a higher capacity to buffer stress due to the system relying less on a few functional pathways (Hirata and Ulanowicz 1984, Fath et al. 2019); whereas hierarchical organization, such as predator–prey–primary producer relationships, creates potential for a fast and efficient response to stress (Friesen et al. 2014). However, these studies have often struggled to measure relevant structural properties of social-ecological systems in a way that is replicable, interpretable, and comparable between systems of quite different kinds. The structures of many systems do not fall cleanly into categories. Terms such as "polycentric" or "hierarchical" are often used loosely to lump together systems with different kinds of structure. In practice, system structure is multi-modal and occurs along a continuum of different dimensions; we do not fully understand how location along a structural continuum influences the pattern–process or structure–function relationships that drive system-level resilience and sustainability. For example, imagine a group of equals in which decision making for natural resource management is entirely based on community consensus; and then imagine that hierarchical elements and inequalities are slowly introduced, until such time as there is a rigid hierarchy with a single leader who makes all decisions. At what point(s) along this trajectory would we expect to see changes in decision-making speed, efficiency, innovation, and flexibility?

Here, we explore the potential of the heterarchy concept in providing a simple but operational measure that combines different structural system properties for comparative research on SESs. Heterarchies were originally introduced to anthropological research by Crumley (1995) to describe social systems in which components could be ordered in several individually consistent ways that nonetheless appeared to contradict each other when adopting a single perspective on power and other directional relationships in social networks. An individual near the top of a governance hierarchy, for example, might be socially either quite isolated (weak or few peer-to-peer or lateral connections) or strongly integrated (strong or many lateral connections) independently of their hierarchical position, suggesting a need to consider social structure on two dimensions rather than one. However, much past research in societies, economies, and ecosystems has focused on a single dimension (i.e., either lateral

or hierarchical structures, rather than both together). Cumming (2016) reviewed and extended the heterarchy concept to propose that measures of lateral and hierarchical aspects of complex systems can be treated as orthogonal (right-angled) axes that capture different elements of system structure; and furthermore, that they can be used to position a given system on a structural continuum. We extend Cumming's (2016) conceptual approach by developing an operational measure of the heterarchical dimensions of a complex system from a singular structural perspective (Fig. 1). We use this measure to explore the potential benefits and applications of a relatively simple interpretation of heterarchical structure as a combination measure of lateral and hierarchical measures of system structure. Our analysis suggests that evaluating network typology through a heterarchy lens can facilitate the development of generalities about structure–function relationships and support a deeper understanding of system-level resilience.

Fig. 1. The heterarchy continuum, adapted from Cumming (2016) for a horizontal axis that measures compartmentalization. In this operational schematic, the upper-right quadrant contains "coordinated polycentric" systems that consist of different modules or sub-systems that are linked by an overarching coordinating function that leaves scope for localized hierarchical organization. The upper-left quadrant, originally described as "reticulated" networks, here resembles a polycentric system but without any overarching coordinating structure (i.e., a lack of hierarchy). In this quadrant, inter-center coordination would rely on lateral connection between the different centers, implying "laterally polycentric" organization. The lower-right quadrant captures "pyramidal" organization in the form of highly hierarchical systems lacking clearly distinguishable modules. Such pyramidal systems resemble a highly bureaucratic organization as well as a very centralized system where a few nodes have disproportionally more links than other more peripheral nodes. The final quadrant, the lower left, was originally described as "individualistic" organization with few connections between nodes. Using a compartmentalization axis, the lower-left quadrant now describes a potentially more connected system without hierarchies or different modules, describing "lateral/ flat" organization. This is similar to the original concept of reticulated structure, but here the system could still be quite dense. This kind of network might be found in networks where most nodes are on an equal standing with no signs of strong structuring mechanisms or divisions between clusters of nodes.
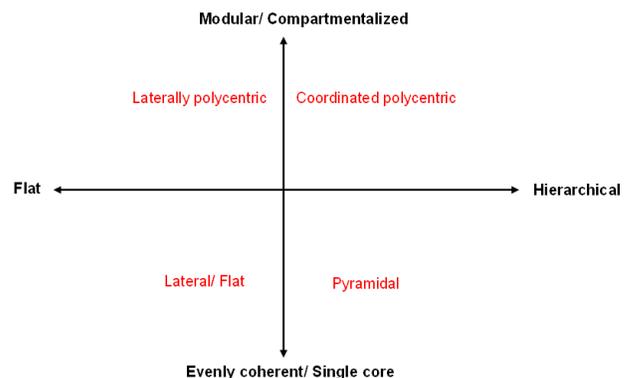
## OVERVIEW OF APPROACH AND METHODOLOGY

Approach

Our goal was to provide a test of concept rather than a highly sophisticated solution. Desirable properties of this first test of concept included transparency in how the measures were calculated and compared; relative simplicity; and a focus on metrics that capture the general characteristics of the entire network (this differs from other approaches which have, for example, focused on characteristics at the meso-level, see, e.g., Faust and Skvoretz 2002). Furthermore, we also aimed for metrics defined at the level that a competent user of R could easily replicate our methods using existing software; and transparent interpretability of measures within the conceptual framework proposed by Cumming (2016). All analyses and visualizations were undertaken in R software (R Core Team 2013) using the code provided online (https://github.com/amyshurety/Shurety-et-al.-Heterarchy-Code).

As summarized in Fig. 2, our first step was to randomly generate a range of networks that differed in their intensity of both lateral and hierarchical characteristics. We generated networks in igraph (Csardi and Nepusz 2006) using the Erdős-Rényi model, which adds links at random between a set number of nodes. One hundred networks were generated each with ten nodes and each pair of nodes had a fixed probability 0.33 of being connected. This was then repeated, increasing the number of nodes in increments of ten up until 100 nodes. In total, we generated 1,000 networks containing 10–100 nodes. The random networks represented different possible structures for networks of the same size (number of nodes), and the set of random networks covers a range of structural characteristics (cf. an inverted U-shaped distribution around a mean value where any two networks at opposite tails of the distribution would have quite different structural characteristics). To objectively measure the degree to which each generated network was respectively lateral and hierarchical, we calculated two metrics: network modularity, and the probability hierarchy score (PHS).

Lateral connectedness is the degree of horizontal exchanges/interactions within a network, which is also (indirectly) related to network density (the number of interactions relative to the number of possible interactions). As randomly adding more links to a network increases its density as well as its lateral connectedness, lateral connectedness is a characteristic that is hard to adequately single out in modeling methodology aimed to facilitate comparisons across networks that inherently differ in their overall level of connectivity (density). We therefore chose to operationalize the dimension "evenly coherent vs. modular" (Fig. 1), that captures the extent of system connectedness within hierarchical levels (Cumming 2016), using a measure of system compartmentalization into different subsystems (also referred to as groups, factions, cliques, or modules). Compartmentalization as measured by network modularity describes the degree to which densely connected groups of nodes can be adequately separated into individual communities, or clusters, that function as semi-independent groups (Newman 2006). In that sense, compartmentalization indirectly captures lateral connectedness, while being less dependent on overall network connectedness. In a social-ecological system, a highly compartmentalized system might contain social cliques or specific user groups at similar

Fig. 2. A flow diagram summarising the methodological steps undertaken in our approach to operationalise the heterarchical dimensions of network structure. The yellow compartments are steps that make use of the theoretical networks, the green compartments use the real-world networks, and the blue use both the theoretical and real-world networks.
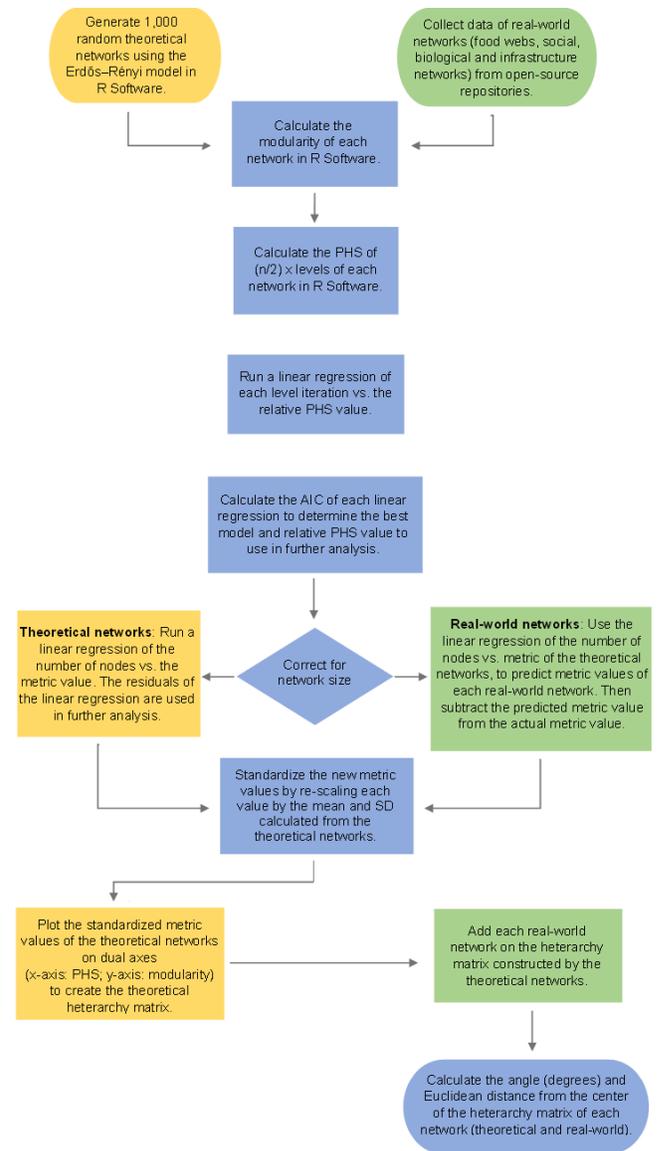
income levels (e.g., farmers, who interact in different fora from fishers); distinct ecological communities (e.g., grassland vs. forest species); or clusters of interacting firms (e.g., Silicon Valley-type technological developments). At the other end of the scale, a network with low compartmentalization is more structurally homogeneous, and its elements may be more interchangeable; it might represent, for example, a human community in which each or most members play an equivalent role in decision making or an ecological community in which there is high substitutability of one prey type by another, leading to relatively homogeneous

levels of predation across species (low compartmentalization does, however, not necessarily mean that all nodes are equally connected—there could, for example, be a core of more densely connected nodes to some extent signifying a hierarchical organization, but it means that there are not clearly observable factions of the network). Compartmentalization is also relevant for dynamic processes; both perturbations and innovations, for example, travel faster through less compartmentalized networks.

We estimated the compartmentalization (modularity) of all 1,000 random networks using the standard *modularity* function in the igraph package. Community membership, which is needed to calculate modularity, was calculated using the *cluster_walktrap* function. The modularity metric showed a normal distribution with a range between negative one and one.

We used PHS (Cheng et al. 2015) to measure the degree of hierarchy and operationalize the dimension "flat vs. hierarchical" (Fig. 1). We chose PHS over other alternatives because it is more sophisticated in considering the direction of connections, relatively insensitive to sample size, and allows networks with differing numbers of nodes and hierarchical levels to be more readily compared. The higher the PHS, the more hierarchical the network is considered to be. In a real-world social-ecological system, for example, higher values of PHS might equate to having more layers of bureaucracy; higher social inequality and power differentials between individuals; tighter feedbacks between trophic levels, leading to a higher potential for trophic cascades in an ecosystem; or more centralized administration of resources. These concepts are expanded upon later, within the Discussion.

Probability hierarchy score was calculated for every possible number of hierarchical levels within each network. As the number of levels within a given network was not known a priori, PHS was calculated for different potential numbers of hierarchical levels ranging from 2 to (n/2), where n is the number of nodes within the network (real networks are unlikely to have more than n/2 levels). To objectively select a single value for the PHS metric, we used the log likelihood for each level iteration of the PHS metric to calculate its Akaike Information Criterion (AIC). The PHS value for the model with the lowest AIC was used as the "correct" value (best estimate) for that network. For the random networks, PHS showed a normal distribution with a range from 1.99 up to 34.03.

The metrics (modularity and PHS) were chosen for the following desired properties: (1) a continuous scale; (2) being reliable and quick to implement without subjective choices; (3) being normally or lognormally distributed, for ease of further calculations; (4) providing reasonable but not excessive sensitivity to detect differences between different systems; (5) some degree of independence from system size; and (6) some degree of independence from construction method (i.e., method by which random networks were generated).

The next step was to correct for the relative influence of network size (number of nodes) on each metric (Mones et al. 2012, de Jonge and Schückel 2021). This is necessary as the number of nodes in a system can influence the behavior of individual nodes (e.g., Sparrowe et al. 2001). We approached this issue by fitting a linear regression to a plot of the metric against the number of

nodes within the network and then using the residuals of the linear regression (i.e., the variance in each metric that was independent of sample size) in place of the original data for further analysis. The impact of network size after the adoption of the residuals was tested using a Pearson correlation test. The relationship to network size (number of nodes) was weak for PHS (correlation coefficient = -0.149; $p < 0.05$) and moderate for modularity (correlation coefficient = 0.492; $p < 0.05$).

To achieve true structural comparability, we also had to correct for differences in magnitude between the two metrics (given that the range of PHS is much greater than that of modularity). To do so, we standardized the residuals using data from the 1,000 Erdős-Rényi (theoretical) networks. The results were re-scaled for each metric independently, subtracting the mean and dividing by the standard deviation, to translate metrics to deviation units with a zero mean. We then compared these results as a two-axis heterarchy matrix following the updated heterarchy framework form originally proposed by Cumming (2016) (Fig. 3).

Fig. 3. The heterarchy matrix using PHS (x) and modularity (y) of the 1,000 theoretical networks (black points). The heterarchy matrix delineates four quadrants whereby networks that have both a high PHS and modularity have a coordinated polycentric structure (top right), those with a low modularity but high PHS a pyramidal structure (bottom right), those with both high PHS and modularity a lateral/ flat structure (bottom left), and those with low PHS but high modularity a laterally polycentric structure (top left).
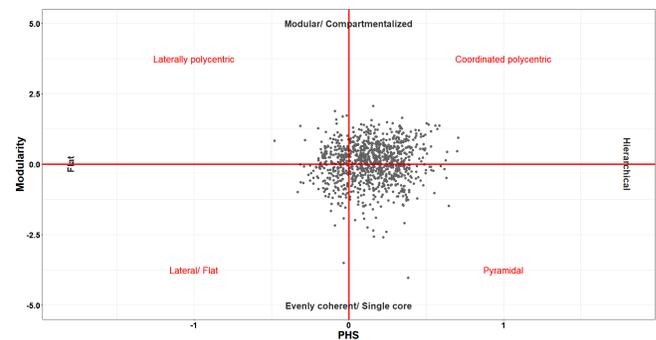

Test of Concept Using Real Data
Our approach so far operationalized the heterarchy concept by plotting theoretical random networks on orthogonal axes. We next used the same approach to describe the structures of a range of existing real-world networks, including ecological food webs, biological networks, social networks, and infrastructure networks (see Appendix, Table A1.1). The real-world network data were taken from open-source data repositories such as igraphdata, networkdata, and the Swedish National Data Service. The modularity and PHS metrics were calculated, using the same methodology for the theoretical networks, for each real-world network (as described in Fig. 2). To correct for the impact of size, the linear regression of the number of nodes and the metric values of the theoretical networks were used to predict expected metrics for each real-world network (based on the number of nodes). The predicted value was then subtracted from the actual value.

The corrected real-world metric values were then standardized using the mean and standard deviation previously calculated from the random theoretical networks (i.e., adjusting each real-world metric based on the counterfactual of a random network) to directly compare how different real-world networks were on both axes relative to what might be expected by chance. We chose to use the random rather than the actual data to correct for size and magnitude because our approach needed to be robust to comparing networks that might have arisen through different mechanisms; corrections using the actual data risk altering these relative signals. The standardized metric values of the real-world networks were plotted on the heterarchy matrix as for the theoretical networks (Fig. 4).

Fig. 4. The heterarchy matrix, using PHS (x) and modularity (y) including both theoretical and real-world networks. After the theoretical networks (gray) were used to construct the matrix (see Fig. 1) a range of real-world networks including food webs (green), biological (blue), infrastructure (purple) and social (yellow) networks were plotted onto the dual axes using their relative PHS and modularity metrics, that were corrected for the impact of network size and standardized.
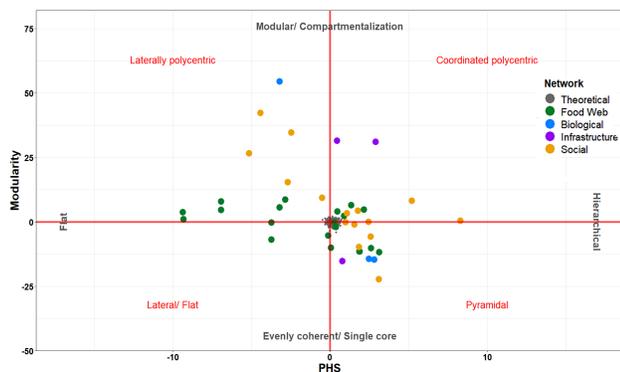
We tested for fundamental differences in structure between all network groups (theoretical, food webs, biological, social and infrastructure), based on their placement within the heterarchy matrix. First, we calculated the angle (degrees) of each network point from the center of the heterarchy matrix. The angle was calculated clockwise with the positive y-axis being 0° from center. Second, we calculated the Euclidean distance between all real-world network points and the center of the heterarchy matrix. The results were visualized on boxplots, providing insight into how the structures of the different network groupings relate to each other. As the angles (degrees) from the center of the heterarchy matrix were circular data (e.g., values of 350 and 10 are more similar than 250 and 300), a Hermans-Rasson test was used to determine whether the angles from center (degrees) were statistically different between the networks used. We used the average absolute angular distance between all network groups to compare how far away on average each network group was from each other.

We used a Kruskal-Wallis test to determine whether the Euclidean distance from the center of the heterarchy matrix was statistically different between different network groups. This non-parametric test was used as the data variance was found to be unequal. A

Dunn test was then used to determine which network groups were different from one another.

RESULTS

Analysis of theoretical, randomly generated networks provided a first proof of concept for our proposed approach. Across a large sample, metrics were regularly distributed and could be displayed and potentially compared along axes of compartmentalization and hierarchical structure. Food webs were present in all four quadrants but had generally low PHS, with the majority being found in quadrant four (Figs. 4 and 5). Therefore, according to the heterarchy measure of network structure, food webs are somewhat laterally polycentric in comparison with social and economic networks, not highly hierarchical, and with a varying degree of modularity. Interestingly, our results show that food webs were the most similar to the random networks (Figs. 4 and 6). Although social networks were found within three quadrants, they showed higher PHS values, causing a higher presence in quadrants one (coordinated polycentric) and two (pyramidal) (Figs. 4 and 5). Similarly, infrastructure networks were only found in quadrants one (coordinated polycentric) and two (pyramidal) (Figs. 4 and 5) with higher PHS values. Biological networks were only found in quadrants two (pyramidal) and four (laterally polycentric) (Figs. 4 and 5), suggesting an inverse relationship between the degree of modularity and hierarchy within biological networks.

Fig. 5. A boxplot indicating the angle from the centre (degrees) of the heterarchy matrix of each network group. The angle was calculated clockwise with the positive y axis being zero degrees from centre. Zero to 90 degrees delineates the co-ordinated polycentric (top-right) quadrant, 90 to 180 degrees delineates the pyramidal (bottom right) quadrant, 180 to 270 degrees delineates the lateral/ flat (bottom left) quadrant, and 270 to 360 degrees delineated the laterally polycentric (top left) quadrant.
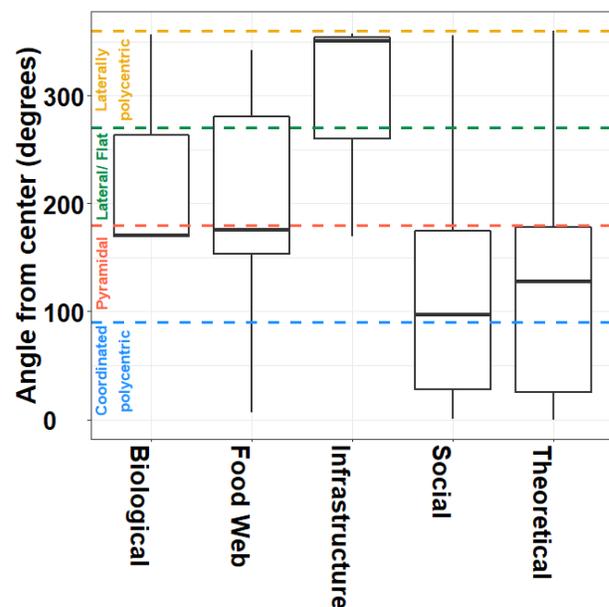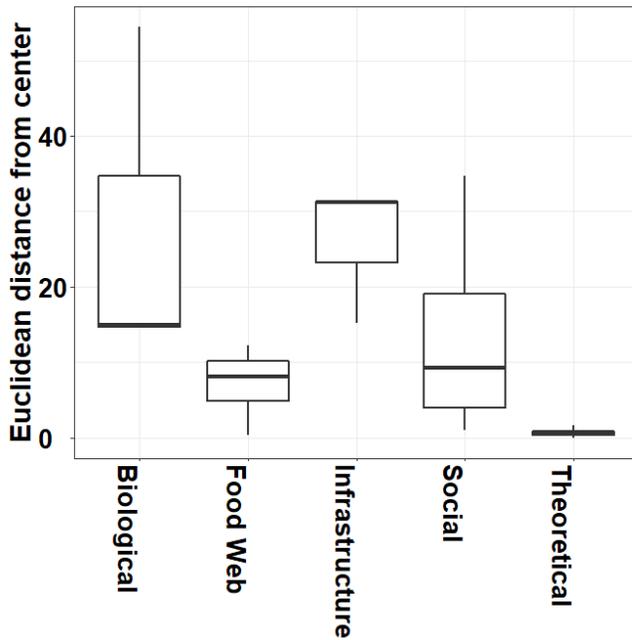
Fig. 6. A boxplot indicating the Euclidean distance from the centre of the heterarchy matrix of each network group.

The real-world networks compared with the random networks and with each other in several interesting ways. The angle from center (Fig. 5) was significantly different between network groups (theoretical, food web, biological, social, and infrastructure; (Herman-Rasson T = 444.86, p < 0.05, n = 1,053)), suggesting that different kinds of networks dominantly fell into particular quadrants. Network groupings that were found to be on average more than 90° (i.e., one quadrant) apart from one another were biological and theoretical networks (105.68°), infrastructure and theoretical networks (165.83°), food webs and infrastructure networks (106.1°), and lastly, social and biological networks (96.02°). As discussed below, these differences appear to make sense based on what we know about differences in the fundamental organizing principles of each kind of network, although the details will take further research to clarify.

The Euclidean distance (Fig. 6) from the center of the heterarchy matrix to each network point (Fig. 4) was also significantly different between network groups (Kruskal-Wallis $\chi2$ = 107.05, df = 4, p < 0.05, n = 1,053), indicating that network groups fell at distinct distances from the center of the plot.

The Dunn test revealed that the Euclidean distances from the center of the theoretical networks were on average significantly different (Dunn's statistic = 3.067; 6.074; 3.075; 6.477, p < 0.05) from all other network groups (food web, biological, social, and infrastructure). Thus, real-world networks contained greater magnitudes of structure than would be expected in randomly generated Erdős-Rényi networks. In addition, the distance of infrastructure networks from the center of the plot differed significantly (Dunn's statistic = -0.05; 0.147, p < 0.05) from those observed in both the food webs and the social networks; and the distance to center was significantly different between food webs (Dunn's statistic = 0.14, p < 0.05) and biological networks.

DISCUSSION

Empirical studies have found that real-world networks are seldom completely random and show clear structural trends (Jeong et al. 2000, Strogatz 2001, Albert and Barabási 2002, Alm and Arkin 2003, Newman 2003, Mones et al. 2012). This generalization was supported by our results; all real-world networks were statistically different from random networks in their Euclidean distance from center. Furthermore, all network groups showed distinct placement on the heterarchy matrix. This finding is useful to validate our test of concept as it illustrates that vastly different networks show a continuum of both lateral and hierarchical measures.

For food webs, our results illustrate a relatively low degree of hierarchical organization. This result matches contemporary theoretical expectations because the depth of a trophic hierarchy is limited by energy flow (Pimm 1982, Elton 2001). Losses of energy at each hierarchical level mean that there is insufficient energy available to support additional higher layers. Classical energetics perspectives of pyramidal food webs gloss over the relevance of interactions within the same level; species richness at each level presumably reflects non-trophic influences on niche partitioning (e.g., structural complexity in the environment) and is only weakly correlated with energy availability (Storch et al. 2018). In addition, many predators have evolved to use multiple prey sources from the same trophic level, meaning that the substitutability of nodes within the same level of a food web may be higher than expected by chance. In all systems, not just food webs, a rigid hierarchical approach leads to less flexibility in flow currency, be it energy, information, transport, or genetic information, making them vulnerable to top-heavy mechanisms of collapse (Cumming and Peterson 2017). Studies have found that food webs show increased resilience to overfishing when they are not strictly hierarchical as commercial fishing disproportionately removes top predators (Bascompte et al. 2005). Food webs on either end of the hierarchical x-axis (low PHS Florida Bay wet season and high PHS Chrystal River Creek) were both estuarine food webs, which could be a reflection of their highly variable (hence, far from an energetic equilibrium) abiotic and biotic estuarine environments (Vinagre and Costa 2014, Tecchio et al 2015).

Modularity is also known to vary considerably between different ecological communities, conditional on the nature of energy flows and perturbations to which the community is subjected to (Montoya et al. 2015, Takemoto and Kajihara, 2016, Ho et al. 2019). For example, previous work on the Chesapeake Bay food web showed that the network was separated into distinct pelagic and benthic communities (Girvan and Newman 2002). Keystone species also add a degree of modularity by adding "hubs" of resource use (Albert and Barabási 2002, Krause et al. 2003). Studies suggest that when food webs form clusters of species, also known as functional groups, the system as a whole is more resilient to perturbation (Bascompte et al. 2003, Moody and White 2003, Stouffer and Bascompte 2011, Cumming 2016). As many species are performing the same function, if one were to be removed, it would enable the continuation of system function, providing adaptive capacity (Fath et al. 2019).

Our results for social systems similarly reflect contemporary human social structures, which use different levels of hierarchical control to achieve societal outcomes across a range of different

scales; ecosystems do not have a national or provincial government, or its equivalent. Previous studies have found that social networks often demonstrate clear hierarchical organization (Newman 2003, Ravasz and Barabási 2003). However, in our study, social networks were shown to be both pyramidal and laterally polycentric, meaning that the degree of hierarchy and modularity varied in the examples that were tested. The social network of Enron email was laterally polycentric, suggesting that emails within the company were mostly sent within company departments and not across company management. In the opposite quadrant (pyramidal), a network of interactions between preschool children was highly hierarchical. This could potentially be due to age-based groupings of the preschool children. With fewer fundamental energetic limits to network properties, we would expect human societies to form a more diverse range of possible structures than ecological networks.

Social networks can benefit from a reasonably compartmentalized structure that supports effective in-group collaboration (Bodin et al. 2006), as very high degrees of lateral connectivity can create overheads (e.g., increased transaction costs or the transmission of pathogens). Modularity in social groups creates clusters of social entities that normally have similar functions and therefore prompt collaboration (Guimera and Amaral 2005), for example, in community structures such as fishermen who formed groups according to the type of equipment used (Alexander et al. 2018). Conversely, perturbations can be extinguished by a hierarchical organization as a system can respond with both efficiency and innovation (Cumming 2016). Preliminary results from our (albeit small) social network sample suggest that their degree of lateral collaboration ranges from weak to strong, but their hierarchical organization is relatively strong in comparison with biological networks. Mechanisms that are hypothesized to lead to collapse in pyramidal and coordinated polycentric systems are top-heavy and mismatch mechanisms (Cumming and Peterson 2017), which appear to create key vulnerabilities in social systems.

The results for infrastructure networks presumably reflect the underlying differences in the mechanisms that drive their structures. Our findings again make intuitive sense if the origins and development of each kind of network are considered. Infrastructure networks are often created to channel people or resources to key locations (the "all roads lead to Rome" approach), leading initially through preferential attachment to a more radial structure, like a bicycle wheel, in which the central node may be particularly dominant. For instance, air travel networks and power distribution networks are often organized hierarchically around central hubs belonging to a particular airline or power station (Zhang 1996, Zhang and Zhang 2006), whereas road networks gradually achieve a more laterally polycentric structure (Xie and Levinson 2007). By contrast, biological networks are organized by such processes as energy metabolism, competition, predation, niche differentiation, and mutualism to form more compartmentalized, interactive structures (Peterson et al. 1998). Finally, and as our results indicate, social networks can often be organized more "freely," i.e., being less constrained by certain energetic or functional limitations, although for example there might be cognitive limits to the number of deeper social relations a person is able to maintain (Dunbar 1992).

Biological networks showed a trade-off between a hierarchical and laterally connected structure. Hierarchical structure is not expected in biological networks due the overall aim of reliability and stability, which results in a high number of feedbacks and interacting processes (Mones et al. 2012). Modules acting as functional hubs are a common feature in biological networks, such as regulatory networks and protein–protein interaction networks (Alm and Arkin 2003, Ravasz and Barabási 2003). We found support for this claim in our analysis, with a network of brain areas and interactions positioned in the laterally polycentric quadrant.

Overall, our results also show that the use of two or more axes against which to quantify network structure as a continuous variable should be encouraged. Using a single indicator to infer a system's structure does not adequately describe the complexity of real-world systems. Complex real-world networks typically show degrees of both module clustering and hierarchical organization (Levin 1992, Ravasz and Barabási 2003, Mones et al. 2012), as indicated by our results; no example networks were purely laterally connected or purely hierarchical. The distinct placement of networks on the orthogonal axes of the heterarchy matrix highlights the need to incorporate a continuum of network structures along both axes in future network research, which has historically involved a strong focus on either top-down or peer-to-peer controls without incorporating both dimensions together (Simon 1991, Cumming 2016).

Our analysis provides a clear demonstration of both the feasibility and the potential value of combining relatively simple compartmentalization and hierarchical measures to quantify heterarchical structure in comparative analyses of complex systems. The analysis using random networks suggests that existing measures (modularity and the PHS metric) have suitable properties for this purpose. Application of the approach to real-world data permitted us to compare quite different kinds of networks in an objective manner; identify structural differences between groups of networks; and reflect on similarities and differences within our sample. Thus, although this is not yet a fully developed or widely tested approach, the methods that we have developed here have considerable potential for use in hypothesis testing and comparative studies as a way of bringing together structural observations from different systems both within and between disciplines.

Tracking structural changes in heterarchies over time using our approach has potential value for exploring whether and why systems shift between different structural quadrants. It is widely accepted that no single system structure fits all circumstances to guarantee resilience (Levin 1992, Albert and Barabási 2000, Cumming 2016, Cumming and Peterson 2017), but the degree to which system collapse or reorganization are caused by endogenous or exogenous factors remains unclear. A system is thought to achieve resilience through a range of internal trade-offs (Schneider and Kay 1994, Ulanowicz 2009, Cumming 2016, Folke 2016, Fath et al. 2019). If a social-ecological system favors rigid organization, it risks becoming fragile; conversely, by favoring increased adaptability and redundancy, it could lack the required efficiency to persist. For example, the degree of lateral connectivity in ecological networks such as food webs and predator–prey networks is known to change as a result of climate

change, due to increased dispersal and generalist species found in higher temperatures (Bartley et al. 2019, Kortsch et al. 2019, Pecuchet et al. 2020). Therefore, one would expect the placement of impacted systems on the heterarchy matrix to change through time, providing multi-dimensional evidence of the impact of climate change on system structure.

For social networks, many factors can drive structural changes over time. For example, it has been suggested that groups of actors that maintain collaboration over time will become more prone to address common problems that are associated with higher risks and costs (Berardo and Scholz 2010). However, it is also suggested that when actors jointly address higher-risk problems, they tend to prefer bonding over bridging structures (Lubell et al. 2014), although recent research has elaborated that assumption by also taking overall levels of trust into account (Bodin et al. 2020). Bonding structures, i.e., when actors form close-knit local structures among their immediate network peers, can increase overall compartmentalization (e.g., Bodin and Crona 2009), whereas bridging structures could indirectly enhance lateral connectedness and/or the degree of hierarchical organization (Carlsson and Sandström 2008). Thus, by tracking the evolution of social networks over time, one could infer different exogenous and endogenous factors re-shaping the ways in which actors interact, and how these changes in aggregation could affect key systemic characteristics of social-ecological systems.

Tracking heterarchical changes over time may therefore provide a fruitful avenue for understanding cycles of change and periodic collapse that have been attributed to growing system rigidity and a loss of adaptive capacity (Holling 2001). These ideas have often remained largely conceptual, however, and non-operational for the purposes of social-ecological research. Analyses of Holling's adaptive cycle (Holling 2001) in particular have been largely qualitative. Our analysis suggests that with sufficient time-series data across a range of comparable networks, we could more easily measure structural change within complex systems and relate observed changes more directly to Holling's (2001) hypotheses about the causes of system cycles.

Reflecting on our approach and test of concept, one suggestion for future research is to enquire further into alternative null models that test a fuller range of potential theoretical networks. In this study, Erdős-Rényi random networks were used as the null model. The underlying assumptions of the Erdős-Rényi model add network links incrementally and treat all network links as being equally likely. Alternative null models could include those that explicitly account for other mechanisms, such as preferential attachment (Jeong et al. 2000) that skews the degree distribution, and/or when investigating social networks: micro-level social mechanisms like homophily (McPherson et al. 2001), geographical proximity (Belaire et al. 2011, Alexander et al. 2018, Jasny et al. 2019), resource access (Jenssen and Koenig 2002, Calanni et al. 2015), or policy preferences (Matti and Sandström 2011, Ingold and Fischer 2014). For future applications, we would encourage the adoption of the null model that best describes the general properties of the systems under consideration. Such extensions to the framework we provide here would allow the investigator to more clearly tease out particularities of any study systems that deviate from what could be expected of a simplified and "generic" representation of any such system (and also to help

in more precisely identifying and separating generic from specific characteristics of different types of systems). Benchmarking a range of real-world networks through time will further help in clarify any "fuzzy boundaries" by providing reference and threshold values over a range of contexts, an important step in bridging the gap between empirical and theoretical research.

Although we considered the influence of varying network sizes, we kept the network density constant when generating the random networks. To maintain a certain density when the network size is doubled, each node however needs to maintain four times as many links as they previously had. As there might be inherent limitations among the systems components to uphold many links (e.g., the number of prey species a predator is able to effectively target might differ significantly from the number of social media contacts a person can maintain), we encourage future applications also investigating any such scaling effects. Furthermore, some metrics do not scale well if the density increases or decreases substantially, such as degree centralization (Butts 2006).

CONCLUSION
The heterarchy concept acknowledges the complex role of system structure in social-ecological dynamics and the need to operationalize approaches to exploring different forms of regulation and control. The approach that we have outlined here, while still at a relatively early and potentially over-simplistic stage, offers the basis for an operational approach to measure changes in complex system structure and comparing structure between complex systems. We believe that further developing and grounding of this kind of approach, such as experimentation with different metrics, the density of networks and types of networks, is an essential step toward developing a universal but comparable and inclusive measure of system structure, with many potentially exciting and relevant applications in the study of SES stability and persistence.

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Appendix 1

Table A1.1: Descriptive information of the real-world networks used.

Open-source Repository	Network Group	Network	Details
igraphdata	Food Web	Bay dry	Food web of Florida Bay (dry season)
igraphdata	Food Web	Bay wet	Food web of Florida Bay (wet season)
igraphdata	Food Web	Chesap	Food web of Chesapeake
igraphdata	Food Web	ChesUp	Food web of Chesapeake Upper
igraphdata	Food Web	ChesLow	Food web of Chesapeake Lower
igraphdata	Food Web	ChesMid	Food web of Chesapeake Middle
igraphdata	Food Web	Chrys C	Food web of Chrystal River Creek
igraphdata	Food Web	Chrys D	Food web of Chrystal River Creek
igraphdata	Food Web	Cyp dry	Food web of Cypress (dry season)
igraphdata	Food Web	Cyp wet	Food web of Cypress (wet season)
igraphdata	Food Web	Maspal	Food web of Charca de Maspalomas
igraphdata	Food Web	Mich	Food web of Lake Michigan
igraphdata	Food Web	Mond	Food web of Modego Estuary
igraphdata	Food Web	Narra	Food web of Narragansett Bay
igraphdata	Food Web	Rhode	Food web of Rhode River Watershed
igraphdata	Food Web	St Marks	Food web of St Marks River
igraphdata	Food Web	Gram dry	Food web of Everglades Graminoids (dry season)
igraphdata	Food Web	Gram wet	Food web of Everglades Graminoids (wet season)
igraphdata	Food Web	Mang dry	Food web of Mangrove Estuary (dry season)
igraphdata	Food Web	Mang wet	Food web of Mangrove Estuary (wet season)
igraphdata	Biological	Immuno	Immunoglobin interaction network
igraphdata	Biological	Yeast	Yeast protein interaction network
igraphdata	Biological	Brain	Visuotactile brain areas and connections
networkdata	Biological	Ants_1	Ant colony
networkdata	Biological	Ants_2	Ant colony
networkdata	Biological	Protein	Protein interactions
networkdata	Biological	Meta_Areans	Metabolic network of the roundworm Caenorhabditis elegans
networkdata	Infrastructure	Euro	Europe road network
networkdata	Infrastructure	USFlights	US Flights networks (2010)
networkdata	Infrastructure	Chicago	Chicago road transportation network
igraphdata	Infrastructure	USAirports	US Airport network (2010)
networkdata	Infrastructure	bktecc	Interactions in a technical research group at a West Virgina University
networkdata	Infrastructure	Covert_16	Network of hyperlinks between domestic terrorist group websites

networkdata	Infrastructure	powergrid	Network of the USA western states power grid
networkdata	Infrastructure	Usa_borders	Network of USA bordering states
igraphdata	Social	Hosp	Records of contacts among patients and various types of health care workers
networkdata	Social	Czech	Czech corruption
igraphdata	Social	EnEmail	Enron email network
igraphdata	Social	UKFaculty	Friendship network of UK university faculty
Swedish National Data Service	Social	MPNetKVA	Kristianstad vattenrik " Biosphere programme
Swedish National Data Service	Social	MPNetFABN	"Frontenac Arch" Biosphere programme
Swedish National Data Service	Social	MPNetGBBR	"Georgian Bay" Biosphere programme
Swedish National Data Service	Social	MPNetOV	"Östra Vätternbranterna" Biosphere programme
Swedish National Data Service	Social	MPNetAHVVF	Hjalmaren water council actors
Swedish National Data Service	Social	MPNetAMVVF	Malaren water council actors
networkdata	Social	FT	Fishermen Ties
networkdata	Social	WR1	Wildfire responders
networkdata	Social	Bott	Interactions of preschool children
networkdata	Social	Arenas_email	Email communication network at the University Rovira I Virgili
networkdata	Social	Highschool_boys	Friendships among high School boys
networkdata	Social	Dnc_corecipients	A network of people who received the same email leak.
networkdata	Social	ffe_friends	Friendships between the French financial elite
networkdata	Social	Law-cowork	Network of corporate law partnerships
networkdata	Social	sufersb	California windsurfer interactions