Uncovering food web structure using a novel trophic similarity measure

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ABSTRACT

Aggregation of species on the basis of their trophic relationships is a fundamental step for quantifying, visualizing and thereby uncovering the structure of food webs. Although the Additive Jaccard Similarity (AJS) has been widely used to measure trophic similarity between species, it has also been criticized for its limited ability to find species with equivalent trophic roles, especially when they do not share the same predators and prey. In this study, we proposed a new trophic similarity measure, the Extended Additive Jaccard Similarity (EAJS), which quantifies trophic similarity between species based not only on the similarity of their shared predators and prey at adjacent trophic levels but at all trophic levels throughout a food web. Average linkage clustering was then used to aggregate species in the mammalian food web for the Serengeti ecosystem in northern Tanzania and southern Kenya on the basis of both trophic similarity measures.

Compared to groups identified on the basis of AJS values, groups derived using EAJS had greater within-group similarity in terms of species' trophic relationships and greater discrimination vs. those in other groups. Groups based on EAJS values also better reflected ecological factors known to structure food webs, including producer-level habitat segregation and mammalian body mass. The advantage of EAJS lies in the fact that it is designed to consider species feeding relations in food webs that is not limited to adjacent trophic levels. Our approach provides a means for revealing the patterns of trophic relations among species in food webs and exploring known and unknown factors shaping food web structure.

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1. Introduction

Food webs have been and continue to be an important research focus in many areas of ecology because energy flows play a central role in structuring population dynamics and maintaining biodiversity and ecosystem integrity (De Ruiter et al., 2005; Allesina et al., 2015; Montoya et al., 2015). The search for order and simplicity within food webs has attracted the attention of researchers for over a century (Elton, 1927), including efforts to uncover their structural properties (e.g., Polis, 1991; Havens, 1992; Johnson et al., 2014), reveal the rules shaping their complexity (e.g., Williams and Martinez, 2000), and capture species roles and interactions within them (e.g., Luczkovich et al., 2003a, 2003b; Jordán, 2009; Baker et al., 2015; Gauzens et al., 2015). While the interactions among species that form the basis of food webs may be complex (Polis, 1991), food webs are non-random and highly patterned in nature (Pimm, 1982; Bascompte, 2009) and are often regulated by a limited number of biological processes. For example, Cohen et al. (1990) summarized five laws that shaped food web structures, while Williams and Martinez (2000) succeeded in predicting twelve properties of food webs using only two parameters: species number and connectance.

As with the taxonomic classification system used to order organisms, one efficient way of reducing the complexity of food webs to better understand them is to decompose them into groups of species according to certain criteria or definitions. Approaches from various disciplines have been adapted to aggregate species in food webs into groups in which species have similar traits or perform similar ecological functions.

Concepts and approaches typically employed to study individual roles and interactions in social networks have also been used to analyze species roles and feeding relations in food webs. For example, the concept of regular equivalence, in which two individuals with similar ties to analogous individuals are seen to play similar roles in a network (White and Reitz, 1983), has been adapted to partition food webs into isotrophic groups in which species have the same or similar trophic roles. This study provides useful information to determine trophic roles of species in food web models and to compare food webs over time and across geographic regions (Luczkovich et al., 2003a, 2003b).

Methods used to detect compartments have also been used to identify groups of species that have more feeding relations within the groups but fewer feeding relations across groups (Girvan and Newman, 2002; Krause et al., 2003). In social network analysis, compartments are equivalent to 'communities', defined in that context as groups of people having more 'within group' than 'between group' interactions (e.g., people in same villages or towns). From an ecological standpoint, compartmentalization is thought to contribute to food web stability (Melian and

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Bascompte, 2002). Krause et al. (2003), for example, investigated the response of a food web to two disturbance scenarios and found that compartmentalization could reduce the impact of disturbance on the other compartments by constraining its impact to a single compartment.

Statistical modeling provides another means for aggregating species to reveal patterns in food webs. Allesina and Pascual (2009) created a probabilistic model that simultaneously considered compartments and groups of species with similar patterns of interactions while Baskerville et al. (2011) used a Bayesian computational method to detect group structures in the plant–mammal food web from the Serengeti ecosystem. The latter study demonstrated the importance of habitat type on food web structure through its direct control on species patterns at the producer level and, more indirectly, on groups of associated herbivores and carnivores, suggesting the spatial coupling and energy channels related to different types of plant habitats in the Serengeti.

Another approach to defining trophic groups starts by quantifying pairwise trophic similarities for each species based on their feeding relationships with other species. A clustering method is then applied to the similarity matrix, yielding any desirable number of trophic groups. Trophic groups identified in this way have gained attention in ecological studies, because trophic interactions directly affect community dynamics and ecosystem functioning (Petchey and Gaston, 2006; Baiser et al., 2011; Gauzens et al., 2013).

One of the most influential and fundamental works involving the aggregation of species into trophic groups based on their observed trophic connections is provided by Yodzis and Winemiller (1999), who compared the performance of multiple criteria and clustering algorithms. They concluded that the use of the Additive Jaccard Similarity (AJS) index to capture species' roles as consumers and resources in food webs was superior to the use of multiplicative similarity and that average linkage and maximum linkage clustering methods produced the most consistent and ecologically-interpretable groups.

One implicit limitation in using AJS to define trophic similarity is that it is based solely on first order feeding links while the feeding relations in second or more distant neighbors are not considered. This may limit the ability of AJS-based approaches to find species with equivalent trophic roles, if they do not share the same predators or prey (Luczkovich et al., 2003a, 2003b). We therefore propose a novel trophic similarity measure, Extended Additive Jaccard Similarity (EAJS), which extends AJS to consider all orders of trophic relationships in a food web. Specifically, we aggregated plant and mammal species in the Serengeti ecosystem food web into groups based on pairwise species similarity values calculated using AJS and EAJS. We then evaluated the aggregations of species based on AJS and EAJS using a cluster validity index and explored the biological and ecological factors which may account for the clustering of species.

2. Study area and dataset

We chose to examine the food web for the Serengeti, which covers an area of plains and open woodlands in northern Tanzania and southern Kenya. Famous for its biodiversity, including the largest herds of grazing mammals in the world (Sinclair and Norton-Griffiths, 1984), the Serengeti has been the site of several seminal studies in grassland and savanna ecology, including research examining environmental factors contributing to community organization (McNaughton, 1978) and patterns of predation (Sinclair et al., 2003). The feeding linkages used to define the food web were developed by Baskerville et al. (2011) based on published information (Casebeer and Koss, 1970; McNaughton, 1978; Cooper et al., 1999; Sinclair et al., 2003) and personal observation from the authors of Baskerville et al. (2011). The resulting food web was composed of 592 feeding links among 161 species, which included 129 plants, 23 herbivores, and 9 carnivores and omnivores. While these linkages were undoubtedly incomplete, they represent one of the best documented food webs available.

Feeding relationships were analyzed as binary linkages and thus were not proportional to feeding pressure (e.g., the degree to which a certain predator preys on various species). Although food webs that incorporate more detailed fluxes of energy and materials are available in some studies (e.g., Cross et al., 2011) and are recognized as the new generation of food webs (Thompson et al., 2012), those with binary linkages are dominant in food web studies because it is much easier to observe the existence of feeding relationships than to quantify the fluxes of energy among specific species.

3. Methods

3.1. Calculating pairwise species similarity values

To aggregate species into groups and reveal food web structure, we first defined the similarity between each pair of species based on predator–prey relationships. We did so using two measures of species similarity: the Additive Jaccard Similarity (AJS) coefficient used by Yodzis and Winemiller (1999) and others, and a new trophic similarity measure, Extended Additive Jaccard Similarity (EAJS, described below). For two species i and j, AJS is defined as:

$$AJS(i, j) = \frac{a}{a + b + c} \tag{1}$$

where a is the total number of predator or prey species shared by species i and species j; b is the number of predator or prey species for species i but not species j, and c is the number of predator or prey for species j but not species i. Values equal 1.0 when two species share the same predators and prey, and decrease when species have few predator or prey species in common.

EAJS differs in that it incorporates not only the similarity of shared predators and prey at adjacent trophic levels but at all the trophic levels associated with both species (Fig. 1). EAJS is calculated by iteratively searching for all predators and prey in bottom-up (species preyed upon by a prey species) and top-down (predators of a predator species) directions until no additional linkages are found. If a species appears on two or more levels (e.g., the species is the predator of species i and the predator's predator of species i), only the feeding relationship on the closer level is considered. In doing so, the predators and prey of species i and j at all trophic levels are identified. The AJS of species i and j is then determined at each equivalent level (e.g., the prey of species i and j, the
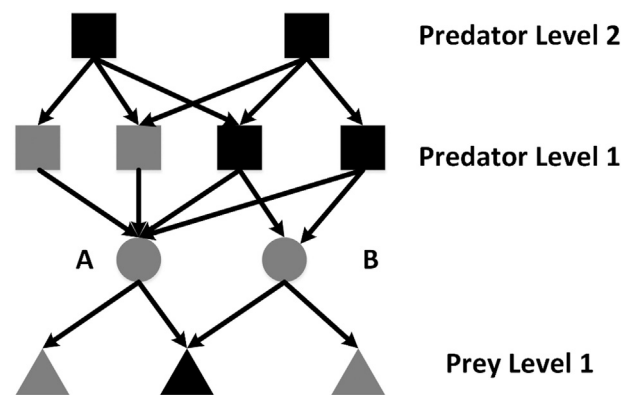

Fig. 1. Comparison of Additive Jaccard Similarity (AJS) and Extended Additive Jaccard Similarity (EAJS) for species A and B. AJS is calculated based on prey and predators only at adjacent trophic levels (predator level 1 and prey level 1), while EAJS is based on prey and predators at all the trophic levels (predator level 1, predator level 2 and prey level 1). Arrows represent the feeding relationship with the end pointing to the prey. Triangles indicate prey of species A or B and squares represent predators of species A or B at all trophic levels. Species in dark color are those prey or predators shared by both species A and B at each trophic level.