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Linking Taxonomic Diversity and Trophic Function: A Graph-Based Theoretical Approach

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Abstract: The purpose of this study is to develop a novel, visual method in analyzing complex functional trait data in freshwater ecology. We focus on macroinvertebrates in stream ecosystems under a gradient of habitat degradation and employ a combination of taxonomic and functional trait diversity analyses. Then we use graph theory to link changes in functional trait diversity to taxonomic richness and habitat degradation. We test the hypotheses that: 1) taxonomic diversity and trophic functional trait diversity both decrease with increased habitat degradation; 2) loss of taxa leads to a decrease in trophic function as visualized using a bipartite graph; and 3) loss of taxa will result in loss of redundancy. The first hypothesis was supported by the similarity of Shannon-Wiener diversity values for taxa and trophic function, correlated at $r = 81\%$. The bipartite graph theoretic approach we developed clearly was effective in showing the linkages between taxonomic diversity and trophic functional traits related to habitat condition. In the most impaired site, loss of taxa led to the complete loss of some trophic functions and significantly less overall redundancy, supporting the third hypothesis. The implications are that taxa loss directly affects trophic function and that loss of taxonomic diversity may affect ecosystem function.

Keywords: Graph theory, trophic function, biodiversity loss, ecosystem function, habitat degradation

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Introduction

Species richness and abundance indices are often used to characterize biodiversity (Whittaker 1972, Lande 1996, Purvis and Hector 2000). Common measures of biodiversity within ecosystems, such as the Shannon-Wiener diversity index, examine both species richness and evenness (Stevens et al 2003) and are used to link taxonomic diversity to ecosystem function in species-environment interactions (Cairns and Pratt 1993). Measures of biodiversity can be expanded to apply to functional traits of ecosystems (Noss 1990, Poff et al. 2006, de Bello et al 2010). Functional traits are features of an organism that define where it lives or how it responds to its environment (Lavorel and Grigulis 2012, Schmera et al 2017) and have long been used in plant ecology to link ecosystems to diversity via trait based ecology (Funk et al 2017).

Use of functional traits in aquatic ecology initially focused on trophic function (e.g. Cummins 1974), eventually expanding into a systematic approach of functional trait analysis utilized in Europe (e.g. Chevne, Dolédec, and Chessel 1994, Dolédec, Statzer, and Bournar, 1999) followed by applications of functional trait analysis in North America (Poff et al 2006, Schmera et al 2017). Functional trait diversity characterizes the functions that organisms perform in ecosystems and may be used to create a more detailed approach to the conservation of biodiversity

(Schleuter et al 2010). Functional traits have been used as biodiversity indicators (Vandewalle et al 2010) and possibly encompass more information than species diversity values can yield alone (Diaz and Cabido 2001, Petchey and Gaston 2006).

Despite its utility in conservation and biodiversity research, freshwater functional trait analysis has some limitations. For example, few autecological studies support functional trait assignments and many traits are actually based on surrogates, such as using mouth-part morphology to indicate trophic trait (Schemera et al 2017). Another limitation is that functional traits are complex and even a single species of aquatic macroinvertebrate may have a trait change across its geographic range and different stages of its life history. Thus, assigning functional traits for species can be difficult (Vandewalle et al 2010, Schleuter et al 2010), and these traits are often summarized or combined via methods such as fuzzy coding to facilitate analysis (Chevne, Dolédec, and Chessel 1994, Vandewalle et al 2010).

The purpose of this study is to develop a novel, visual method in analyzing complex functional trait data in freshwater ecology. We focus on macroinvertebrates in stream ecosystems under a gradient of habitat degradation and employ a combination of taxonomic and functional trait diversity analyses. Then we use graph theory

to link changes in functional trait diversity to taxonomic richness and habitat degradation. Freshwater functional trait diversity analyses employ many of the same analytical methods as taxonomic diversity analyses (Heino 2005, Mason et al 2005, Ricotta 2005, Petchey and Gaston 2006, Villéger, Mason, and Mouillot 2008), and studies are often designed to examine the response of functional trait diversity to environmental conditions (Schmera et al 2017). However, combining all traits into a single diversity estimate is confusing since traits may indicate different aspects of an organism. Traits may be categorized as effect traits, which are features of an organism that effect ecosystem function and response, or by the features of an organism that respond to its environment (Lavorel and Grigulis 2012, Schmera et al 2017). We focus on effect traits, particularly trophic functional traits, since these traits are complex and vary over geographic ranges of species and over their life stages (Merritt, Cummins, and Berg 2008) and these trophic traits have long been linked to ecosystem function (e.g. Vannote et al 1980). Trophic functional traits have been developed based on characteristics such as diet preferences and feeding methods (Bremner, Rogers, and Frid 2003, Stevens et al 2003, Petchey and Gaston 2006), based on specific functional traits measured for each species (Bremner, Rogers, and Frid 2003, Petchey and Gaston 2006), and based on morphology such as mouthparts (Merritt, Cummins, and Berg 2008), collectively forming a rich set of complex data for use in this study.

Graph theoretical analyses have been used in freshwater ecology. Most notably neural networks are used to study geomorphology of streams (Mathon et al 2013), and more recently graph theory has been used to study patterns in biodiversity (Perkin et al 2015, Rocha et al 2017), but to our knowledge graph theoretical methods have not been used to link taxonomic richness and functional trait richness in freshwater ecology. Our main question is whether graph theory is useful in retaining the complexity of functional trait data. We use bipartite graphs to link taxonomic diversity to trophic functional traits along a habitat gradient. Bipartite graphs are graphs that have two specific columns of vertices that connect only to the opposite column via edges (lines). A bipartite graph was formed in which taxa and trophic functional traits served as vertices, and the edges of the graphs linked the taxa and function vertices present for each site. The number of edges incident to a vertex is the degree of that vertex and, in this analysis, the degree for each trophic functional vertex represents the redundancy of taxa for each trophic functional trait.

We combine the graph theory analysis with other diversity analyses as the linkage of diversity to ecosystem to test the hypotheses that: 1) taxonomic diversity and trophic

functional trait diversity both decrease with increased habitat degradation; 2) loss of taxa leads to a decrease in trophic function as visualized using a bipartite graph; and 3) loss of taxa will result in loss of redundancy. Finally, this study is placed in the context of linking taxonomic and trophic functional trait diversity related to habitat degradation because habitat diversity is important in explaining species diversity patterns (Lengyel, Déri, and Magura 2016).

Methods and Materials

Data from streams across Iowa, Nebraska, and Kansas were obtained with permission from Central Plains Center for Bio-assessment. Previous research had ranked sites based on a habitat diversity index (HDI) (Donley, Ferrington, and Huggins 1998). A total of 32 sites were studied, comprising 16 streams with two sites per stream. Non-insect macroinvertebrates whose trophic functional traits had not been determined were excluded based on the database. The remaining taxa were assigned trophic functional traits from Merritt, Cummins, and Berg (2008) and the EPA searchable Freshwater Biological Traits Database (EPA 2016). Most macroinvertebrates have more than one trophic functional trait documented in the above sources. We designated the first trait listed as the primary trait, second trait as secondary, and so on. Our decision to rank the traits thusly is supported in many cases by additional information in the source materials providing details on the relative primacy of the traits. Insects without an assigned trophic function were removed from analyses. Our resulting database included 79 total taxa. Two streams were selected to examine effects of habitat degradation on taxonomic and trophic functional diversity, one being of high-quality and one of low-quality based on the HDI. Taxa not present across the two streams were excluded from analyses.

To determine the overall relationship between taxonomic and trophic functional trait diversity, a Pearson product correlation was performed on Shannon-Wiener diversity for both taxonomic and functional diversity based on all sites. Taxonomic Shannon-Wiener values were calculated using the equation

$$H' = -\sum p_i \ln p_i$$

with p_i representing the proportion of individuals present for each taxon. Trophic functional trait Shannon-Wiener was calculated using the same equation such that p_i is the proportion of functional traits.

Based on the HDI developed by Donley, Ferrington, and Huggins (1998), sites with the least habitat degradation (French Creek, Nemaha County, Kansas) and sites with the most habitat degradation (Walnut-Jasper Creek,

Jasper County, Iowa) were compared using a bipartite graph. Graph theory is the study of the relationships and interactions (represented by edges) between entities (represented as vertices). For the bipartite graphs, described above, edges were weighted by primary, secondary, and tertiary affinities between taxa and trophic function and these affinities were denoted by edge color. Assignment of primary, secondary, and tertiary affinity was based on the order the trait appeared in Merritt, Cummins, and Berg (2008) or predominance in the EPA searchable Freshwater Biological Traits Database (EPA 2016).

Taxa vertices were weighted by abundance of individuals (e.g. 363 individuals of *Baetis* present at French Creek sites); trophic function vertices were weighted by degree, or the number of taxa they contained (e.g. 28 taxa perform the function of collector-gatherer at the French Creek sites). To aid interpretation, taxa from the same order of aquatic insects were given the same color. Functional traits were given similar colors for similar functions within food webs. For example, the various herbivore assignments were denoted in shades of green. We hypothesized that loss of taxa would not only result in loss of trophic functional traits, but would also result in loss of degree or redundancy. This is due to many taxa having more than one trophic functional trait assignment (Figure 1). Our null hypothesis is that due to redundancy in taxa representing trophic functional traits (Merritt, Cummins, and Berg 2008) a loss of taxa will not result in a loss of functional traits (Figure 1).

We performed a second test of the hypothesis that that loss of taxa would result in loss of redundancy visualized as the degree within each vertex. Redundancy is the number of taxa that possess the same trait, thus is a measure of the taxonomic diversity within a trait. Redundancy is visualized as the numbers weighting each trait vertex in the bipartite graph. We created arbitrary weights of the primary ($=1.0$), secondary ($=0.5$), and tertiary ($=0.25$) edges, then summed them for the four most common trophic functional traits in French Creek and Walnut-Jasper Creek. We ran an analysis of variance to test whether redundancy varied significantly between the two sites. Variables met assumptions of normality. The ANOVA was performed using Number Crunching Statistical Software with significance set at $P \leq 0.05$.

Results

The 79 taxa (mostly genera) in this study comprise eight orders related to 12 trophic functional traits. Taxonomic diversity and trophic functional trait diversity were highly correlated across the study sites ($r = 0.81$, $p \leq 0.05$), also indicating that 19% of the relationship between taxonomic and trophic functional diversity is not explained.

Figure 1: Graphical representation of the (A) hypothesis and (B) null hypothesis. Blue circles represent taxon vertices and orange circles represent trophic function vertices and lines connected vertices are edges.

A clear loss of important EPT (Ephemeroptera, Plecoptera, and Trichoptera) indicator taxa represented by a loss of taxa vertices as well as a loss of edges connecting taxa vertices to trophic function vertices is observed when comparing the high HDI site with the low HDI site (Figure 2). The three most abundant orders at the high HDI site, French Creek, are Diptera (true flies), Coleoptera (beetles), and Ephemeroptera (mayflies). At the low HDI site, Walnut-Jasper Creek, three orders are lost: Plecoptera (stoneflies), Odonata (dragonflies and damselflies), and Megaloptera (alderflies), which is visually indicated by a disappearance of all the genera vertices within those orders (Figure 2). The relative degree or redundancy in predators declined slightly between the high HDI site and low HDI site while the redundancy in decomposer/decomposer and herbivore trophic functional traits increased (Figure 2).

Figure 2: Graph theory visualization of linkages between taxa and trophic functional traits at (A) a high-quality habitat site and at (B) a low-quality habitat site. Numbers in each taxon vertex indicate the number of individual collected in that taxon and the numbers in each trophic functional trait represent the number of edges that connect that trait to taxon vertices. edges were weighted by primary, secondary, and tertiary affinities between taxa and trophic function and these affinities were denoted by edge color. Assignment of primary, secondary, and tertiary affinity was based on the order the trait appeared in Merritt, Cummins, and Berg (2008) or predominance in the EPA searchable Freshwater Biological Traits Database (EPA 2016).

The bipartite graph shows a loss of taxa vertices, trophic functional trait vertices, and edges, and overall complexity in the low HDI site relative to the high HDI site, indicating that the null hypothesis may be rejected (Figure 1, 2). Twelve taxa are shared between the two sites. The 68 taxa shown using vertices were present in the high HDI site while 14 were present in the low HDI site (Figure 2). Due to a clear decrease in biodiversity, a loss of redundancy occurs as expressed by the compression of taxa within trophic functions (i.e. a decrease in the number of taxa exhibiting a function) exhibited by a loss of edges connecting taxa and function vertices. The Walnut-Jasper stream site lost 8 trophic functional traits relative to the French Creek stream site (Figure 2), indicating that Walnut-Jasper Creek showed considerable compression of taxa within trophic functions (Figure 2). This may be because the loss of certain taxa vertices will subsequently result in the loss of multiple trophic functional edges. Relationships between taxonomic diversity and trophic functions are more complex in the high HDI site and are comparatively simple in the low HDI site (French Creek, Figure 2). Thus, the use of a graph theoretic model allowed this analysis to retain the dimensionality of the relationship between taxa and trophic function while also showing a loss of complexity along a habitat gradient. This loss of complexity is evidenced by loss of vertices and edges representing taxa and trophic function (Figure 2). The results of the graph theoretic analysis may help to explain the remaining 19% of variability between taxonomic and functional diversity, as not explained by the correlation analysis.

Results of the ANOVA based on redundancy, or degrees within each trophic functional trait, support the outcome of the bipartite graph (Figure 3, Figure 2). Redundancy was significantly lower in the Walnut-Jasper, the low HDI site ($df = 14$, $p \leq 0.005$) indicating that the loss of taxa also affected the diversity of taxa filling a trophic functional role in the stream.

Discussion

The graph theoretic approach clearly was effective in showing the linkages between taxonomic diversity and trophic function across a degradation gradient (Figure 2). The unique approach of representing the data and relationships through bipartite graphs was used to retain the dimensionality and complexity of these interactions. Assigning functional traits to taxa is difficult (Vandewalle et al 2010, Schleuter et al 2011) due to variation of traits across space and within life cycles for individual taxa (Merritt, Cummins, and Berg 2008). Use of the bipartite graph allowed examination of all traits rather than using a summative or synthesizing approach with functional

Figure 3: Mean redundancy and standard error bars represent variation in redundancy between a high-quality and a low-quality habitat site. Redundancy is the degree or number of taxa that fill a trophic functional trait in the sites.

traits (e.g. Chevne, Doléadec, and Chessel 1994). Trait assignments are based on decades of research going back to Cummins (1974) but our weighting is tentative. Any affinity or weighting methods must be considered tentative until more research is done on the autecology of most species across space and time (as per arguments in Schmera et al. 2017). However, the bipartite graph shows how weighting may be used once more is known about trophic function for individual species. Finally, this visual approach may have use in communicating the impact of loss of species on functionality of ecosystems to policy makers.

Typically, rare taxa decline with loss of habitat (Valiente-Banuet et al 2015). However, in Walnut-Jasper (Figure 2), the more common and originally more abundant order of Odonata is lost, perhaps indicating an overall loss of predators. Functional traits indicate ecosystem function (e.g. Poff 1997, Vaughn 2010), but there is still a lack of understanding regarding many aspects of what links a loss of biodiversity to the decline of ecosystem function (Hooper et al 2005), especially in freshwater ecosystems (Covich et al 2004, Giller et al 2004, Dudgeon et al 2006, Vaughn 2010). In this study, the loss of a large, predatory group such as Odonata may affect community structure (Wallace and Webster 1996), possibly resulting in an increase in the redundancy in decomposer/detritivore and herbivore trophic functional traits from the high HDI site to the low HDI site (Figure 2). Overall, redundancy declined, visualized as a loss of degree in the expression of trophic functional traits (Figure 2) and further supported by the results of the ANOVA (Figure 3). Redundancy may be used to show how the loss of species richness may affect functional traits and hence ecosystem function. Greater redundancy may buffer communities

from loss of functionality under changing environments (Gallagher, Hughes, and Leishman 2013, Feld, Bello, and Dolédec 2014) unless a system already has low redundancy (e.g. Suárez et al 2017). In this case compression of degree resulting in the loss of redundancy, as seen in this study (Figure 2, 3), will quickly change the trophic functional traits and thus function of the stream.

The results showed that a loss of biodiversity leads to a loss of diversity of trophic functions across the geographic range of sites. The goal of the original study from which we obtained these data was based on the concept of empirically designating reference conditions for stream comparisons (Donley, Ferrington, and Huggins 1998). Reference sites are the best available environmental conditions found today (Gibson et al 1996) theoretically reflecting pre-impairment conditions that may have existed in the past. Thus, the reference condition approach in this study, employing sites with high and low HDI, may reflect loss of taxa, complexity, and a compression of redundancy through time, but we use caution in making this interpretation. Regardless, these results may seed further conservation, restoration, and biomonitoring research to stem further change in biodiversity over time or monitor improvements in streams under restoration similar to applications in terrestrial ecology (e.g. Kaiser-Bunbury et al 2017).

Application of mathematical graph theory provides a powerful tool in ecosystem analysis because it allows for retention of the complexity and multidimensionality of a system. To extrapolate, there is much potential for the use of graph theory in future research linking taxonomic diversity to functional traits due to its ability to quantify, clarify, and express complex ecological relationships. Biodiversity is directly linked to ecosystem function (via functional trait diversity); therefore, a loss of biodiversity causes a loss of ecosystem function. When combining research on both taxonomic and functional diversity these methods are useful as an early warning system of ecosystem collapse. The graph theoretic tools could be further used to determine where a threshold for loss of ecosystem function lies along a degradation gradient.

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