ORIGINAL RESEARCH

# The influence of nutrient enrichment on riverine food web function and stability

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## Abstract

Nutrient enrichment of rivers and lakes has been increasing rapidly over the past few decades, primarily because of agricultural intensification. Although nutrient enrichment is known to drive excessive algal and microbial growth, which can directly and indirectly change the ecological community composition, the resulting changes in food web emergent properties are poorly understood. We used ecological network analysis (ENA) to examine the emergent properties of 12 riverine food webs across a nutrient enrichment gradient in the Manawatu, New Zealand. We also derive Keystone Sensitivity Indices to explore whether nutrients change the trophic importance of species in a way that alters the resilience of the communities to further nutrient enrichment or floods. Nutrient enrichment resulted in communities composed of energy inefficient species with high community (excluding microbes) respiration. Community respiration was several times greater in enriched communities, and this may drive hypoxic conditions even without concomitant changes in microbial respiration. Enriched communities exhibited weaker trophic cascades, which may yield greater robustness to energy flow loss. Interestingly, enriched communities were also more structurally and functionally affected by species sensitive to flow disturbance making these communities more vulnerable to floods.

**KEYWORDS**
ecological network, energy flow, food web, indirect effects, mutualism, nutrients, productivity, respiration, river, stability

## 1 | INTRODUCTION

The eutrophication of rivers, lakes, and groundwater is increasing rapidly, and among the most influential drivers of the global decline in aquatic biodiversity (Dudgeon, 2014; Dudgeon et al., 2006; Vorosmarty et al., 2010). Many regions worldwide now having 10- to 15-fold greater nitrogen flux through their rivers than several decades ago, driven largely by intensive agriculture and wastewater

(Glibert, 2017; Howarth, 2008; Le Moal et al., 2019). Dissolved inorganic nitrogen (DIN) and dissolved reactive phosphorus (DRP) are the dominant culprits of eutrophication, both are limiting the growth of both autotrophs (usually algae and macrophytes) and heterotrophs (usually bacteria and invertebrates) (Camargo & Alonso, 2006; Conley et al., 2009; Ferreira et al., 2015; Smith & Schindler, 2009). At very high levels, they can be directly toxic to freshwater organisms (Camargo & Alonso, 2006; Camargo et al., 2005; Hickey &

Martin, 2009), but can result in hypoxic conditions if decomposition increases excessively. Nutrients promote the growth of microbes, which can rot dead organic matter, often nutrient-promoted excessive algae coincide and fuel this, with the microbial decomposition dramatically reducing ambient dissolved oxygen levels and changing pH, which in turn have adverse effects on instream invertebrates and fish (Dodds & Smith, 2016; Ferreira et al., 2015; Hilton et al., 2006; Smith et al., 2006). Furthermore, microbes can mine their environment for nutrients and condition nutrient-poor detritus, in turn, increasing the palatability for detritus-consuming invertebrates and relieving nutrient constrained growth (Evans-White & Halvorson, 2017; Ferreira et al., 2015; Guo et al., 2016; Hessen et al., 2013). Nutrient enrichment typically changes riverine invertebrate communities from being mayfly, stonefly, and caddisfly dominated to those dominated by worms, snails, and midges (Ballantine & Davies-Colley, 2014; Cullen et al., 2006; Tonkin et al., 2013). Surviving fish species may have poor condition as a result of stress and the dietary changes from the altered macroinvertebrate communities (Baker et al., 2013; Schreck & Tort, 2016; Sealey & Gatlin, 1999; Thera et al., 2020).

While riverine community composition changes with nutrient enrichment (Camargo & Alonso, 2006; Smith & Schindler, 2009), the influence of those changes on food web emergent properties/functioning is not well understood (Boersma et al., 2008; Dodds, 2007; Friberg et al., 2011; Price et al., 2019). Theoretical investigations have hypothesized that nutrient enrichment should yield increases in the relative importance of dietary specialists, increase the amount of energy flowing through the food web, drive longer food chains, alter nutrient stoichiometry, increase population variability, and reduce the amount of cycling (DeAngelis, 2012). Ecological network analysis (ENA) provides a toolbox of mathematical measures to quantify characteristics of weighted food webs, such as cycling and dietary specialists (Fath & Borrett, 2006; Fath & Patten, 1999; Latham Ii, 2006). Despite the potential application of ENA to inform how aquatic food web functioning differs with nutrient enrichment, the few empirical applications of ENA across enriched aquatic systems have yielded inconsistent results (Almunia et al., 1999; Baeta et al., 2011; Mukherjee et al., 2015; Patricio et al., 2006).

A difficult property of ecological communities to quantify is food web stability. Food web stability is the maintenance of food web structure and function over time, and it includes resilience, persistence, equilibrium, resistance, and robustness (Dunne et al., 2005; Mougi & Kondoh, 2016; Rooney & McCann, 2012; Saint-Béat et al., 2015). Current theory suggests that having many relatively weak indirect flows can stabilize webs by dampening the spread of destructive cascades (Canning & Death, 2017; Mougi & Kondoh, 2016; Rooney & McCann, 2012; Saint-Béat et al., 2015). When disturbances are species-specific, secondary extinctions are most likely to occur when species with the highest link weight (both direct and indirect effects) are perturbed (Zhang et al., 2016). Analysis of un-weighted food webs also suggested species connectivity had high influence on secondary species extinctions (Canning

& Death, 2018; Dunne et al., 2002; Montoya et al., 2006); however, connectivity has since been shown to be unimportant in weighted food webs (Zhang et al., 2016). Species with high influence on food web stability are often termed as being keystone (Mills et al., 1993). Therefore, if food webs change in a way that means the most sensitive species to disturbance are also keystone species, then the food web will likely have lower stability to the said disturbance.

Rivers often face multiple disturbances (both natural and anthropogenic), and some taxa may be resilient to one type of disturbance but sensitive to another. If all species within a community can be assigned a score of how keystone they are and how sensitive they are to a given disturbance, then the overall potential sensitivity of the food web to the given disturbance could be estimated by averaging the keystone scores of each species and weighting this by their respective disturbance sensitivity. High weighted averages would indicate a community with keystone species that are also sensitive to the given disturbance, which may mean that community is less stable to the disturbance than a community with a lower weighted-average.

New Zealand, like many developed countries, has experienced considerable decline in ecological health over the last 25 years—largely from eutrophication in lowland, agriculture-dominated catchments (Foote et al., 2015; Joy et al., 2019; Julian et al., 2017; Larned et al., 2016). Exacerbations of existing nutrient enrichment and natural floods are two of the most common disturbances facing rivers. Furthermore, for most New Zealand riverine macroinvertebrates there are well-established scores of their sensitivity to nutrient enrichment and well-established relationships between body traits and resilience to floods (Scarsbrook & Townsend, 1993; Stark & Maxted, 2007; Townsend et al., 2003). In this study, we assembled weighted food webs for twelve rivers across a nutrient gradient within the Manawatu, New Zealand. First, we used ENA to explore whether overall food web functioning differed across the nutrient gradient. Secondly, we scored the macroinvertebrate assemblages on their sensitivity to further nutrient enrichment and floods, and scored how keystone they are, to produce indices of the community sensitivity (termed here Keystone Sensitivity Indices) to further nutrient enrichment or floods. We then assessed whether these sensitivity indexes changed across the nutrient gradient.

## 2 | METHODS

### 2.1 | Study sites

Twelve sites in the Manawatu River catchment varying in nutrient enrichment were studied (Table 1). At each site, DIN and DRP concentrations were the average of 7 years (1999–2006) of monthly samples, collected as a part of state of environment monitoring, and processed in accordance with NZS/ISO/IEC 17025:1999 protocols (Death & Death, 2006). A 7-year monitoring period was chosen as single grab samples are highly variable and the observed ecological communities would have developed over multiple years; longer

**TABLE 1** The average dissolved inorganic nitrogen concentration (DIN, mg/L), dissolved reactive phosphorus (DRP, mg/L), species richness (N), connectance (C), total system throughflow (TST, J/m²/yr), and locations (WGS 84) of twelve river food webs sampled in 2007 in the Manawatu, NZ

| Site | Latitude | Longitude | DIN | DRP | N | C | TST |
|---|---|---|---|---|---|---|---|
| Mangatainoka River @ Putara Road | 40°40″49.9′S | 175°32″50.8′E | 0.02 | 0.003 | 33 | 0.11 | 8,749,303 |
| Pohangina River @ Piripiri Road | 40°03″04.9′S | 175°56″11.5′E | 0.05 | 0.005 | 62 | 0.09 | 16,377,036 |
| Pohangina River @ Raumai Reserve | 40°12″26.3′S | 175°47″21.5′E | 0.08 | 0.012 | 53 | 0.12 | 6,629,034 |
| Tokomaru River @ Horseshoe Bend Reserve | 40°29″14.3′S | 175°31″33.4′E | 0.08 | 0.005 | 67 | 0.12 | 19,844,310 |
| Raparapawai Stream @ Jacksons Road | 40°19″25.2′S | 175°59″45.8′E | 0.15 | 0.030 | 62 | 0.11 | 20,767,724 |
| Oroua River @ Nelson Street | 40°13″50.0′S | 175°34″55.1′E | 0.24 | 0.010 | 38 | 0.12 | 11,872,967 |
| Manawatu River @ SH2 | 40°23″60.7′S | 175°53″17.0′E | 0.40 | 0.009 | 64 | 0.12 | 34,246,823 |
| Mangatera Stream @ SH2 | 40°14″27.1′S | 176°05″55.6′E | 0.44 | 0.141 | 62 | 0.10 | 54,782,015 |
| Oroua River @ Awahuri Road | 40°16″32.4′S | 175°31″17.6′E | 0.53 | 0.101 | 37 | 0.09 | 34,819,550 |
| Mangatera Stream @ Timber Bay | 40°14″27.1′S | 176°05″55.6′E | 0.81 | 0.141 | 66 | 0.11 | 40,277,332 |
| Manawatu River @ Hopelands Road | 40°21″35.3′S | 175°57″42.1′E | 0.90 | 0.024 | 64 | 0.11 | 22,250,529 |
| Mangapapa Stream @ Troup Road | 40°20″31.0′S | 175°50″52.3′E | 0.90 | 0.024 | 67 | 0.12 | 40,237,153 |

*Note:* Nutrient concentrations were based on 84 sampling occasions, sampled monthly between 1999 and 2006 inclusive

**TABLE 2** The confidence ratings of model parameters following Costanza et al. (1992)

| Group | Individual densities | Biomass conversion | Productivity | Respiration | Assimilation efficiency | Diet | Boundary flows |
|---|---|---|---|---|---|---|---|
| Periphyton | High | Medium | Medium | Medium | N/A | N/A | Low |
| Invertebrates | High | Medium | Medium | Medium | Medium | Medium | Low |
| Fish | High | Medium | Medium | Medium | Medium | Medium | Low |
| Detritus | Low | Low | N/A | N/A | N/A | N/A | Low |

than 7 years may run the risk of detecting change rather than state (ANZG, 2018).

## 2.2 | Food web construction

Food webs are ecological networks of who eats whom within an ecological community. At all twelve sites, the food webs were assembled to represent plausible Summer 2006/2007 configurations with currency being joules of energy. The main groups included in the food web models were fish, macroinvertebrates, periphyton, and detritus; all living compartments were resolved to the lowest taxonomic keys using the relevant keys available (see below for more details). Microbes were excluded because there was a lack of suitable data available, and the large energy flow through a single microbial compartment may result in uneven resolution and obscure network patterns (Abarca-Arenas & Ulanowicz, 2002; Baird et al., 2009; Fath et al., 2013). Omitting microbes will, however, underestimate total system throughflow and total system cycling, so

readers should keep this in mind when comparing against webs assembled with microbes. The food webs were assembled in WAND (Allesina & Bondavalli, 2004) format. For consumers, rates of consumption were assumed equal to productivity + respiration + unassimilated food. Where consumption exceeded that estimated to be produced locally, it was assumed that invertebrate and detritus drift into the local community accounted for the shortfall to ensure the webs were energetically balanced. Where species were predicted to grow faster than they are consumed, then outputs set equal to any net gains in a species biomass (i.e., drift downstream, death, and microbial processing).

To depict the quality of model parameters, following the data quality rating framework proposed by Costanza et al. (1992), qualitative confidence levels were assigned to model parameters for each group (Table 2). High indicates direct measurement of field data, medium indicates indirect measurements, calculated data, or handbook estimates, while low indicates educated guesses, very indirect approximations, and "rule of thumb" estimates (Costanza et al., 1992).

## 2.2.1 | Basal compartments

Periphyton biomass was approximated from the average chlorophyll a (mg/m$^2$) measured between January and March 2007. At each site, chlorophyll a density was estimated from five unglazed tiles (0.25 m × 0.25 m) and from five randomly collected stones. Stone surface area was estimated following Graham et al. (1988) with periphyton assumed to be covering half of the total surface area. Pigments were collected separately for each tile or stone in known volumes of 90% acetone at 5°C in the dark for 24 hr. Pigment densities were converted from absorbances determined using a Varian Cary 50 Conc UV-visible Spectrophotometer, following Steinman et al. (1996). Algal species composition was also determined from stone scrapings following Steinman et al. (1996). The approximate biomass of each species was determined by rationing the total periphyton biomass (from chlorophyll a–biomass relationships) by relative species abundance (Banse, 1977; Brey et al., 2010; Keenan & Morar, 2015). Periphyton annual production/biomass (P/B) was estimated to be 35 by extrapolating the hourly rate determined in Elwood and Nelson (1972). The annual respiration/biomass (R/B) rate was approximated to be 10.95 following an approximate daily R/B of 0.03 (0.03 over 365 days is 10.95) calculated by McIntire and Phinney (1965).

## 2.2.2 | Invertebrate compartments

At each site, macroinvertebrates were sampled using five randomly positioned Surber samplers (0.1-m$^2$ and 250-μm mesh) between January and March 2007. Invertebrates within the 0.1-m$^2$ quadrat were scrubbed off all cobbles and fine sediment stirred down to a depth of approximately 10 cm for 1 min. Samples were preserved in 10% formalin, sorted, and enumerated to the lowest practicable taxonomic level (Winterbourn et al., 1989).

Mean individual lengths and biomasses for each species were determined from the literature and length-biomass regressions (Moore, 1998; Stoffels et al., 2003; Towers et al., 1994; Winterbourn et al., 1989). Invertebrate biomass (dry weight) was converted to Joules following Brey et al. (2010). The annual production and respiration were estimated using empirical models for aquatic invertebrates with a typical annual median temperature of 14°C (Brey, 2010, 2012; Death & Death, 2006). The estimated production rates were similar to those derived for the same or similar taxa throughout other parts of New Zealand (Collier et al., 2004; Hopkins, 1971; Huryn, 1996, 1998; Tank & Winterbourn, 1996). Rates of consumption were assumed equal to productivity + respiration + unassimilated food.

The presence of dietary links between species was estimated from their functional feeding group, and predator diets were established from the literature (Collier et al., 2004; Cowley, 1978; Devonport & Winterbourn, 1976; Hollows et al., 2002; Jaarsma et al., 1998; McFarlane, 1976; Polegatto & Froehlich, 2003; Rounick & Hicks, 1985; Thompson & Townsend, 2004; Towns & Peters, 1996; Winterbourn, 1978, 1982, 1996, 2000; Winterbourn et al., 1984,

1989). Dietary proportions of each resource were assumed proportional to the productivity of prey/basal taxa unless literature indicated there was strong dietary preference. The assimilation efficiency (assimilation/ingestion) of dietary components was the same as those used in Benke et al. (2001).

## 2.2.3 | Fish compartments

Fish density and approximate lengths were determined from electric fishing surveys collected during the 2006/2007 Summer period (same period as the macroinvertebrate surveys) and recorded in the New Zealand Freshwater Fish Database (Richardson, 1989).

Fish biomass was estimated from approximate lengths following the length–mass equations in Jellyman et al. (2013). Fish productivity rates were assumed to be the same as those determined in neighboring streams (Hopkins, 1971). Clarke and Johnston (1999) was used to estimate respiration rates assuming typical median temperature is 14°C (Death & Death, 2006).

Fish diet was determined from previous dietary studies, and flows were proportional to the abundance of prey biomass unless literature indicated a high dietary preference (Cadwallader, 1975; Glova & Sagar, 1989, 1991; Jellyman, 1996; Kusabs & Swales, 1991; Main & Winterbourn, 1987; Montori et al., 2006; Sagar & Glova, 1995).

## 2.2.4 | Detrital compartments

Two detrital compartments were used to represent fine particulate organic matter (FPOM) and course particulate organic matter (CPOM). All organisms that died from causes other than consumption entered the CPOM pool. Detritus compartment storages were all set to a nominal figure of 100 J/m$^2$ and steady state maintained by assuming imports (i.e., upstream vegetation and detritus flowing into the reach) equaled the outputs from invertebrate consumption. The assumption of steady state is likely unrealistic; however, the network analyses used in this study rely on networks being balanced at equilibrium (i.e., at steady state) and should be interpreted as snapshot assessments. The nominal detritus storage value is relatively small and will have a consistent, but small, effect on the total system storage that readers should be aware of. The nominal detritus storage value will have no effect on flow-based metrics.

## 2.3 | Food web analysis

For each web (e.g., Figure 1.), network metrics were calculated using the functions from the enaR package (Borrett & Lau, 2014) and implemented within R 3.3.1 (R Core Team, 2016). Initially, any remaining small imbalances were balanced using the AVG2 method described by Allesina and Bondavalli (2003) prior to calculating the following metrics: total system throughflow, sum of loss to respiration, sum of loss to exports, total system storage,
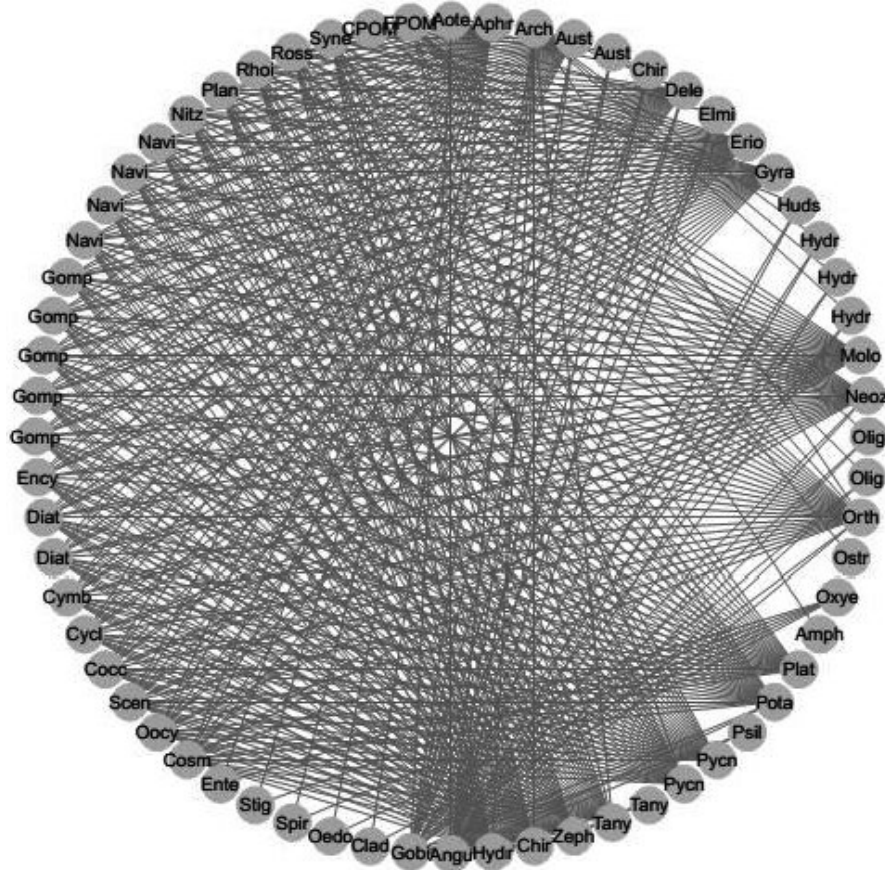
**FIGURE 1** The linkages within food web assessed at the Manawatu River at Hopelands Road in Summer 2007. Letters are the first four characters of each taxon name

network aggradation, indirect flow intensity, homogenization (inputs), relative ascendency, flow-based network synergism, and the flow-based network mutualism (Borrett et al., 2006; Fath, 2007; Fath & Patten, 1999; Finn, 1976; Ulanowicz, 1997a). The AVG2 balancing algorithm was used to balance networks to steady state, an assumption required for computing the network metrics, as this methods typically generate the least distortion of network traits (Allesina & Bondavalli, 2003). Metric interpretations are included in Table 3.

Regression analysis using R 3.3.1 (R Core Team, 2016) was used to test the relationship between each network metric calculated (the network metrics in Table 3 all comprised as independent variables) and the respective DIN concentration (dependent variable) for all twelve webs. Given that DIN concentration was significantly correlated with DRP (log–log-transformed, $r^2 = 0.56$, $F_{1,10} = 12.51$, $p = .005$), we only regressed metrics with DIN. Here, we use DIN as the indicator of nutrient enrichment and do not necessarily consider it the only limiting factor.

## 2.4 | Keystone macroinvertebrate sensitivity

Two common disturbances in New Zealand rivers are increasing nutrient enrichment and floods. If keystone food web invertebrates are sensitive to high nutrients, then the web will be sensitive to increasing nutrient enrichment. Likewise, if keystone species have only one

terrestrial life stage, are crawlers, have cylindrical body forms, exposed gills, and low dissemination potential, then the communities may be more sensitive to flow disturbance than those with keystone taxa that have multiple terrestrial life stages, are burrowers, have streamlined body forms, plastron respiration, and high dissemination potential (McIntosh et al., 1994; Scarsbrook & Townsend, 1993; Townsend et al., 2003).

To investigate whether nutrient enrichment changed the web-wide influence of disturbance-sensitive macroinvertebrates, we calculated five keystone sensitivity indexes (KSI) for each web. Each of the five KSIs was based on five species trait categories known to be influenced by enrichment or flow disturbance, being: body form, locomotion, means of respiration, dispersal potential, and organic enrichment sensitivity. The KSIs for each web and each trait were calculated following Equation 1.

$$KSI = \frac{\sum_m \text{Sensitivity score} \times \text{Average environ centrality}}{\sum_m \text{Average environ centrality}} \quad (1)$$

where $m$ is each of the macroinvertebrate species within a given food web.

The average environ centrality (AEC) is an indicator of the web-wide influence a species has and measures a species web-wide direct and indirect effect (Fann & Borrett, 2012) and was calculated for each species in each web using enaR (Borrett & Lau, 2014). The AEC values represent the relative contribution of a species, as a proportion, to the

**TABLE 3** The regression statistics of ten network metrics, and their definition, across twelve rivers (Manawatu, New Zealand) along a dissolved inorganic nitrogen (DIN) gradient

| Network metric | Abbreviation | Metric interpretation | Relationship | $R^2$ | F-statistic | p-value |
|---|---|---|---|---|---|---|
| Total system throughflow | TST | Sum of energy flows entering or exiting all taxa. It is an indicator of the size of the food web | Log–log | 0.58 | 13.50 | .004 |
| Respiration flows | Resp. | Sum of all energy lost from respiration | Log–log | 0.54 | 11.90 | .006 |
| Export flows | Exports. | Sum of all energy leaving the system, this could be via death (transfer to microbes), emigration, or drift from floods | Log–log | 0.05 | 0.48 | .50 |
| Network aggradation | Net. Agg. | The average food chain length based on weighted energy flows | Linear | 0.03 | 0.03 | .58 |
| Indirect flow intensity | IFI | Proportion of all energy flows that has arisen from indirect flows. Indirect flows are energy that has been transferred from one species to another via an intermediate species, such as through trophic cascades | Log-linear | 0.53 | 10.02 | .01 |
| Homogenization (input, flow) | Hmg (input) | A maximally homogeneous network is one in which species receive an equal amount of energy from each of the other species in the community and distributes an equal amount to all the other species (either directly or indirectly) | Linear | 0.05 | 0.51 | .49 |
| Relative ascendency | Rel. Asc. | Indicates both the size and the complexity of a web. A low relative ascendency indicates a web with low energy flow and/or many generalists. A high relative ascendency indicates a web with high energy flow and/or many specialists | Quadratic | 0.64 | 6.97 | .02 |
| Total system storage | TSS | Sum of energy stored in all taxa. It is an indicator of the size of the community | Linear | 0.05 | 0.52 | .49 |
| Mutualism (flow) | Mut. (flow) | Measure of the obligatory positive feedback flows | Linear | 0.11 | 1.21 | .30 |
| Synergism (flow) | Syn. (flow) | Measure of the nonobligatory positive feedback flows | Linear | 0.73 | 24.6 | <.001 |

*Note:* DF = 10.

total energy-matter exchange within a system, with all species summing to one—permitting comparison between webs.

Species traits were sourced from the Freshwater Biodata Information System (National Institute for Water & Atmospheric Research, 2004), and trait-specific sensitivity scores were assigned as follows (higher values being more sensitive):

1. **Body form**: Cylindrical (3), flattened (2), and streamlined (1).
2. **Locomotion**: Crawler (3), swimmer (2), and burrower/sessile (1).
3. **Respiration/gas exchange mechanism**: Gills/aerial (3), tegument (2), and plastron (1).
4. **Dispersal ability**: Low (3), moderate (2), and high (1)
5. **Organic enrichment sensitivity**: Individual species sensitivity scores adopted from the MCI (Clapcott et al., 2017; Stark & Maxted, 2007).

Using regression analysis in R 3.3.1 (R Core Team, 2016), the relationships between each of five trait-specific KSIs (each as a

dependent variable) and DIN concentration (independent variable) were examined (Table 3). Linear regressions were used with Box-Cox transformations (Osborne, 2010) applied to DIN (where necessary) using the MASS package (Ripley et al., 2013).

## 3 | RESULTS

Across all twelve food webs, the mean dissolved inorganic nitrogen (DIN) concentration ranged from 0.05 to 0.90 mg/L, taxonomic richness ranged from 33 to 67, and total system throughflow from 6,629,034 to 54,782,015 $J/m^2/year$ (Table 1).

As DIN concentration increased, total system throughflow, total respiration, and the indirect flow intensity all increased up to a point, after which values remained similar despite increasing DIN. Synergism declined slightly with increasing DIN also until a threshold was met, after which values remained similar with increasing DIN. There was no relationship between DIN and exports,

homogenization, total system storage, and mutualism. Relative ascendency increased with increasing DIN until a threshold, after which relative ascendency reduced with increasing DIN (Figure 2, Table 3).

Of the disturbance sensitivity indices, only the body form sensitivity index increased with DIN concentration, while the remainder were not correlated with DIN (Figure 3, Table 4).

## 4 | DISCUSSION

Total energy flow increased (measured using TST) with increasing nutrient enrichment until a DIN concentration of approximately 0.5 mg/L after which total energy flow remained constant. The initial increase in throughflow is consistent with bottom-up control theory whereby an increase in algal and microbial productivity (in this case from greater nutrient enrichment) results in increasing

productivity of consumers (Bumpers et al., 2017; Cross et al., 2007; Ferreira et al., 2015). The total food web biomass was unaffected by nutrient enrichment, rather the per-capita throughflow of energy increased instead. Thereby indicating that either: (a) production increased and organisms moved across the system boundary (organisms drifted or swam out of the area or died) thereby maintaining total system biomass and increasing throughflow; or (b) the webs are composed of more energetically demanding/more inefficient species that require greater energy consumption resulting in increased throughflow. Interestingly, while exports (nonrespiratory boundary flows out of the system) remained unchanged, total community respiration increased markedly with increasing nutrient enrichment. This supports the latter hypothesis that the communities became composed of energetically inefficient species with increasing enrichment. Hypoxia is often associated with the microbial decomposition of algal blooms and detritus (Hilton et al., 2006; de Jonge et al., 2002; Smith et al., 2006); however, our results show that
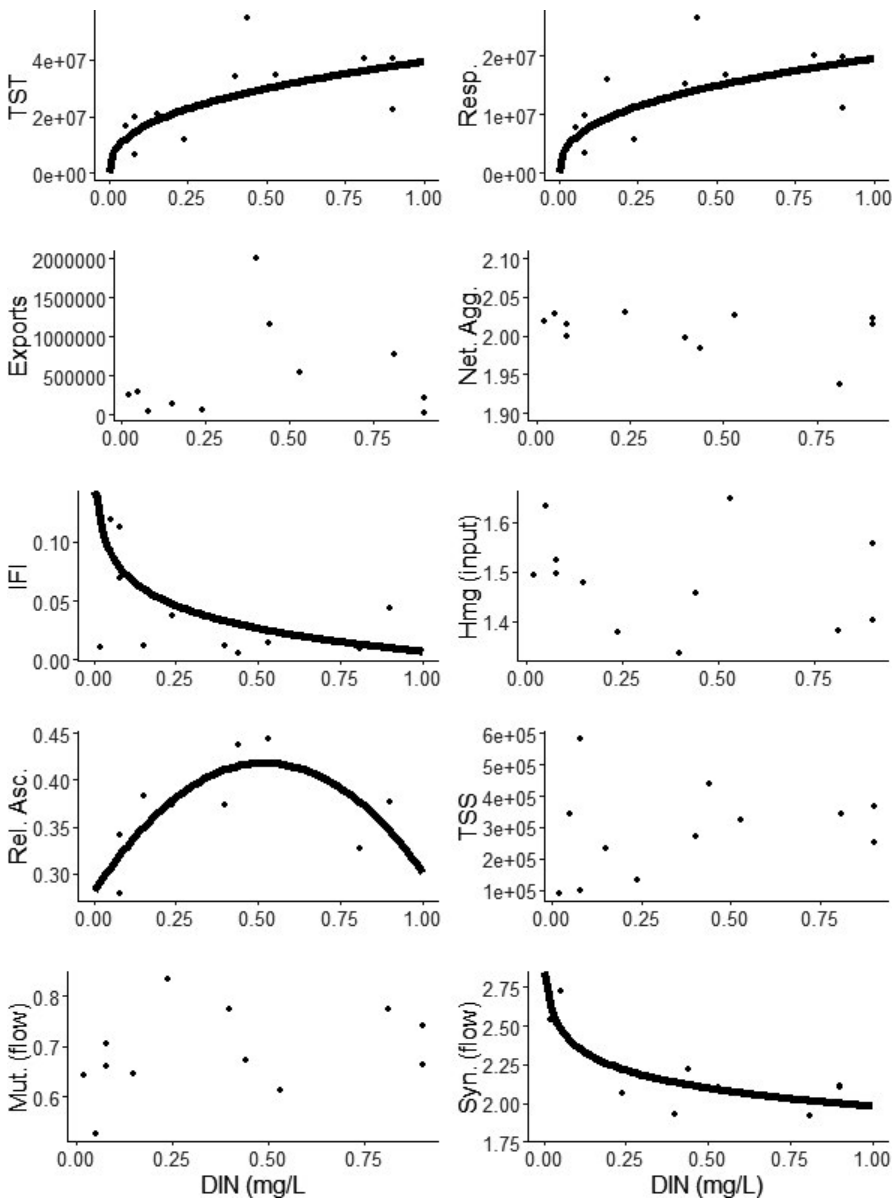


**FIGURE 2** Ten network metrics from riverine food webs across a dissolved organic nitrogen (DIN, mg/L) gradient throughout the Manawatu, NZ. Lines represent statistically significant regressions ($p < .05$, Table 3)
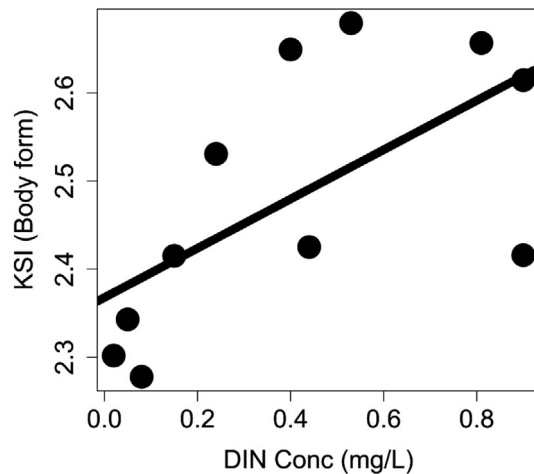
**FIGURE 3** The Keystone Sensitivity Index (body form) across riverine food webs along a dissolved organic nitrogen (DIN, mg/L) gradient throughout the Manawatu, NZ. Linear regression line is statistically significant ($F_{1,10} = 6.02$, $p = .04$)

**TABLE 4** The regression statistics for five Keystone Sensitivity Indices (KSI) across twelve rivers (Manawatu, NZ) along a dissolved inorganic nitrogen (DIN) gradient

| Keystone Sensitivity Index trait | $R^2$ | F-statistic | p-value (>|F|) |
|---|---|---|---|
| Body form | 0.40 | 6.0 | .04 |
| Locomotion | 0.003 | 0.03 | .86 |
| Respiratory mechanism | 0.001 | 0.01 | .92 |
| Dispersal potential | 0.03 | 0.35 | .57 |
| Organic enrichment sensitivity | 0.001 | 0.01 | .92 |

Note: DF = 10.

at DIN concentrations greater than approximately 0.35 mg/L that respiratory energy demand, and consequently oxygen demand, for the entire community excluding microbes can be three to four times greater than in oligotrophic conditions. The change in invertebrate community composition could therefore also be having a considerable influence on the frequency and intensity of hypoxic conditions without the need to invoke any microbial processes.

Nutrient enrichment may have resulted in an increase in the composition of inefficient species by increasing the frequency and/or intensity of both hypoxic and substrate movement disturbances. Highly disturbed communities tend to be composed of smaller bodied species as they are typically fast growing and can recover more easily (Dinh & Death, 2018; Dolédec et al., 2006; Townsend et al., 2003). While a small-bodied invertebrate on its own will likely have low respiration demand, when biomass differences are accounted for smaller bodied invertebrates tend to have greater respiration rates than larger invertebrates (Brey, 2010; Gillooly et al., 2001; Robinson et al., 1983); thus, making communities with smaller invertebrates less energy efficient than larger invertebrates assuming total biomass is the same. Eutrophic streams in general have more prolific

periphyton growth. Prolific periphyton can disturb communities by increasing the frequency and intensity of hypoxic events (Dodds & Smith, 2016; Glibert, 2017; Le Moal et al., 2019). Also, if periphyton dominates the base of the food web, then substrate movement (which scours periphyton from rocks) will also be disturbing for the invertebrates that rely on periphyton (Canning et al., 2017, 2019; Lake, 2000; Marks et al., 2000). Therefore, if hypoxic events and periphyton scouring disturb the community, then the increased frequency and/or intensity of stream disturbances may drive more enriched communities to be composed of small-bodied, energetically inefficient species (Hilton et al., 2006; Townsend & Hildrew, 1994).

Similarly to total energy flow, the confinement of energy flows (measured by relative ascendency) also increased with enrichment until an approximate DIN concentration of 0.50–0.55 mg/L, after which energy flow confinement relaxed slightly. Mageau et al. (1998) suggested that relative ascendency would increase with nutrient enrichment; however, they did not account for the potential effects of a dominant competitor collapsing which would revert the network to a state with relatively unconstrained energy flows (the large, specialized flows of dominant competitor are lost). In river systems, nutrient enrichment may increase algal growth and drive more energy through the algal consumers, thereby increasing relative ascendency (Almunia et al., 1999; Ulanowicz, 1986, 1997a; Zorach & Ulanowicz, 2003). Relative ascendency may also increase if algal composition changes in way where some species are preferable for invertebrates than others, and the food web becomes skewed toward preferable or more rewarding species (Guo et al., 2016; Guo, Kainz, Valdez, et al., 2016). As explained above, prolific periphyton growth may increase disturbance frequency and/or intensity (Hilton et al., 2006). Disturbance often returns communities to earlier successional stages that have more uniform energy flow distributions (i.e., relative ascendency drops) (Genoni & Pahl-Wostl, 1991; Mageau et al., 1998; Ulanowicz, 1997b). It is plausible that when DIN concentrations exceed 0.55 mg/L that hypoxic events occur and disturb the system sufficiently to drop relative ascendency. Ulanowicz (1997b) found that most weighted food webs have very similar relative ascendency values, which has been suggested to represent a common trade-off between adaptable yet inefficient communities and efficient yet brittle communities—termed the window of vitality (Canning & Death, 2018; Ulanowicz, 2009; Ulanowicz et al., 2009). Interestingly, all the webs we assessed were within the window of vitality, with the webs of highest relative ascendency occurring approximately at the upper boundary of the established window.

The indirect flow intensity (measures the dominance of trophic cascades) decreased sharply with increasing nutrient enrichment until an inflection at DIN concentrations of approximately 0.3–0.4 mg/L, after which indirect flows remained consistently at very low levels of total system flow. Weak indirect effects have been shown to increase food web robustness as they dampen the spread of disruptive cascades induced by disturbance. On the contrary, strong indirect effects have been associated with greater biocomplexity by supporting species coexistence through increased heterogeneity in space and time. Therefore, increasing enrichment

may stabilize webs yet reduce their biocomplexity by reducing the proportion of indirect flows.

Synergistic effects, being nonobligatory positive feedback relationships (Fath & Patten, 1998), also reduced slightly with increasing enrichment between DIN concentrations of approximately 0.10–0.20 mg/L, after which synergism remained unaffected by increasing DIN. Despite differences in synergism, mutualistic effects, being obligatory positive feedback relationships (Fath, 2007), were unaffected by increasing DIN. Synergistic energy flows allow for the simultaneous growth of multiple species. Since species in synergistic relationships are not reliant on each other for survival but complimented, then if one species in a synergistic loop is perturbed then the others will support the recovery of the perturbed species, thereby supporting food web resilience (the ability of a food web to recover following disturbance) (Okuyama & Holland, 2008; Saint-Béat et al., 2015). The reduction in synergism with nutrient enrichment may, therefore, reduce resilience.

While our analysis used nutrient samples that averaged over a 7-year period, the biological communities were a single snapshot at the end of that period. This decision may have resulted in a mismatch between measured nutrient concentrations and measured biological communities, particularly for periphyton biomass, which can also be variable. However, we consider that long-term and regular nutrient samples are required to establish the nutrient enrichment status of a stream as singular grab samples are highly variable. Large nutrient variability can arise from nutrient discharge practices, rainfall patterns, and the biological exchange of nutrients. Biological communities develop over long periods and are exposed to a wide variety of nutrient concentrations over that period. If our analysis was to only use a single nutrient grab sample at the time of biological community collection, then the assessed nutrient enrichment status may not be representative of that exposed to the biological community over the long term. Therefore, the latter approach may have resulted in different relationships to that observed in this analysis.

If nutrient enrichment shifts disturbance-sensitive species from positions of low influence to positions of high influence, then their loss during the next disturbance would likely be more pervasive than when they were less influential (Zhao et al., 2016). We found that as nutrient enrichment increased, the community structure changed in a way that meant species whose body forms were sensitive to flood disturbances became more influential (greater environ centrality; Figure 3). Therefore, in our webs, floods are more likely to cause disruptive cascades and destabilize webs that are highly enriched as species with body forms that are more easily disturbed by flood disturbances are shifted to more influential positions.

In conclusion, as nutrient enrichment increased, the communities became energy inefficient as community (excluding microbes) respiration increased. Increased community oxygen demand may drive or exacerbate hypoxic events. Furthermore, the strength of trophic cascades reduced with increasing enrichment, this may reduce the effects of disruptive cascades. Interestingly, enriched communities were also structured in a way that resulted in flood-sensitive species (based on body form) being more influential than in pristine communities; therefore, the communities may be more sensitive to collapse from flow disturbance.

## CONFLICTS OF INTEREST

None declared.

## AUTHOR CONTRIBUTIONS

**Adam D. Canning:** Conceptualization (lead); data curation (supporting); formal analysis (lead); funding acquisition (equal); investigation (lead); methodology (lead); project administration (lead). **Russell G. Death:** Conceptualization (equal); data curation (lead); methodology (equal); supervision (lead); writing–original draft (supporting); writing–review and editing (equal).

## DATA AVAILABILITY STATEMENT

Compiled food webs available at: https://doi.org/10.5061/dryad.fqz612jrh.

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## REFERENCES

Abarca-Arenas, L., & Ulanowicz, R. (2002). The effects of taxonomic aggregation on network analysis. *Ecological Modelling*, *149*(3), 285–296. https://doi.org/10.1016/S0304-3800(01)00474-4

Allesina, S., & Bondavalli, C. (2003). Steady state of ecosystem flow networks: A comparison between balancing procedures. *Ecological Modelling*, *165*(2–3), 221–229. https://doi.org/10.1016/S0304-3800(03)00075-9

Allesina, S., & Bondavalli, C. (2004). WAND: An ecological network analysis user-friendly tool. *Environmental Modelling & Software*, *19*(4), 337–340. https://doi.org/10.1016/j.envsoft.2003.10.002

Almunia, J., Basterretxea, G., Arístegui, J., & Ulanowicz, R. E. (1999). Benthic-pelagic switching in a coastal subtropical lagoon. *Estuarine, Coastal and Shelf Science*, *49*(3), 363–384. https://doi.org/10.1006/ecss.1999.0503

ANZG (2018). *Australian and New Zealand Guidelines for Fresh and Marine Water Quality*. Retrieved from www.waterquality.gov.au/anz-guidelines

Baeta, A., Niquil, N., Marques, J., & Patrício, J. (2011). Modelling the effects of eutrophication, mitigation measures and an extreme flood event on estuarine benthic food webs. *Ecological Modelling*, *222*(6), 1209–1221. https://doi.org/10.1016/j.ecolmodel.2010.12.010

Baird, D., Fath, B., Ulanowicz, R., Asmus, H., & Asmus, R. (2009). On the consequences of aggregation and balancing of networks on system properties derived from ecological network analysis. *Ecological Modelling*, *220*(23), 3465–3471. https://doi.org/10.1016/j.ecolmodel.2009.09.008

Baker, M., Gobush, K., & Vynne, C. (2013). Review of factors influencing stress hormones in fish and wildlife. *Journal for Nature Conservation*, *21*(5), 309–318. https://doi.org/10.1016/j.jnc.2013.03.003

Ballantine, D., & Davies-Colley, R. (2014). Water quality trends in New Zealand rivers: 1989–2009. *Environmental Monitoring and Assessment*, *186*(3), 1939–1950. https://doi.org/10.1007/s10661-013-3508-5

Banse, K. (1977). Determining the carbon-to-chlorophyll ratio of natural phytoplankton. *Marine Biology*, *41*(3), 199–212. https://doi.org/10.1007/bf00394907

Benke, A., Wallace, J., Harrison, J., & Koebel, J. (2001). Food web quantification using secondary production analysis: Predaceous invertebrates of the snag habitat in a

subtropical river. *Freshwater Biology*, 46(3), 329–346. https://doi.org/10.1046/j.1365-2427.2001.00680.x

Boersma, M., Aberle, N., Hantzsche, F., Schoo, K., Wiltshire, K., & Malzahn, A. (2008). Nutritional limitation travels up the food chain. *International Review of Hydrobiology*, 93(4–5), 479–488. https://doi.org/10.1002/iroh.200811066

Borrett, S., & Lau, M. (2014). enaR: An r package for ecosystem network analysis. *Methods in Ecology and Evolution*, 5(11), 1206–1213. https://doi.org/10.1111/2041-210x.12282

Borrett, S., Whipple, S., Patten, B., & Christian, R. (2006). Indirect effects and distributed control in ecosystems: Temporal variation of indirect effects in a seven-compartment model of nitrogen flow in the Neuse River Estuary, USA—Time series analysis. *Ecological Modelling*, 194(1–3), 178–188. https://doi.org/10.1016/j.ecolmodel.2005.10.011

Brey, T. (2010). An empirical model for estimating aquatic invertebrate respiration. *Methods in Ecology and Evolution*, 1(1), 92–101. https://doi.org/10.1111/j.2041-210X.2009.00008.x

Brey, T. (2012). A multi-parameter artificial neural network model to estimate macrobenthic invertebrate productivity and production. *Limnology and Oceanography: Methods*, 10, 581–589.

Brey, T., Müller-Wiegmann, C., Zittier, Z., & Hagen, W. (2010). Body composition in aquatic organisms—A global data bank of relationships between mass, elemental composition and energy. *Journal of Sea Research*, 64(3), 334–340.

Bumpers, P., Rosemond, A., Maerz, J., & Benstead, J. (2017). Experimental nutrient enrichment of forest streams increases energy flow to predators along greener food-web pathways. *Freshwater Biology*, 62(10), 1794–1805. https://doi.org/10.1111/fwb.12992

Cadwallader, P. (1975). Feeding relationships of galaxiids, bullies, eels and trout in a New Zealand river. *Marine and Freshwater Research*, 26(3), 299–316. https://doi.org/10.1071/MF9750299

Camargo, J., & Alonso, Á. (2006). Ecological and toxicological effects of inorganic nitrogen pollution in aquatic ecosystems: A global assessment. *Environment International*, 32(6), 831–849. https://doi.org/10.1016/j.envint.2006.05.002

Camargo, J., Alonso, A., & Salamanca, A. (2005). Nitrate toxicity to aquatic animals: A review with new data for freshwater invertebrates. *Chemosphere*, 58(9), 1255–1267. https://doi.org/10.1016/j.chemosphere.2004.10.044

Canning, A., & Death, R. (2017). Trophic cascade direction and flow determine network flow stability. *Ecological Modelling*, 355, 18–23. https://doi.org/10.1016/j.ecolmodel.2017.03.020

Canning, A., & Death, R. (2018). Relative ascendency predicts food web robustness. *Ecological Research*, 33(5), 873–878. https://doi.org/10.1007/s11284-018-1585-1

Canning, A., Death, R., & Gardner, E. (2017). The effect of forest canopy and flood disturbance on New Zealand stream food web structure and robustness. *Austral Ecology*, 43(3), 352–358. https://doi.org/10.1111/aec.12573

Canning, A., Death, R., & Gardner, E. (2019). Forest canopy affects stream macroinvertebrate assemblage structure but not trophic stability. *Freshwater Science*, 38(1), 40–52. https://doi.org/10.1086/701378

Clapcott, J., Wagenhoff, A., Neale, M., Storey, R., Smith, B., Death, R., Harding, J., Matthaei, C., Quinn, J., Collier, K., Atalah, J., Goodwin, E., Rabel, H., Mackman, J., & Young, R. (2017). *Macroinvertebrate metrics for the National Policy Statement for Freshwater Management*.

Clarke, A., & Johnston, N. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, 68(5), 893–905. https://doi.org/10.1046/j.1365-2656.1999.00337.x

Collier, K., Wright-Stow, A., & Smith, B. (2004). Trophic basis of production for a mayfly in a North Island, New Zealand, forest stream: Contributions of benthic versus hyporheic habitats and implications for restoration. *New Zealand Journal of Marine and Freshwater Research*, 38(2), 301–314. https://doi.org/10.1080/00288330.2004.9517239

Conley, D., Paerl, H., Howarth, R., Boesch, D., Seitzinger, S., Havens, K., Lancelot, C., & Likens, G. (2009). Controlling eutrophication: Nitrogen and phosphorus. *Science*, 323(5917), 1014–1015.

Costanza, R., Funtowicz, S., & Ravetz, J. (1992). Assessing and communicating data quality in policy-relevant research. *Environmental Management*, 16(1), 121–131. https://doi.org/10.1007/bf02393914

Cowley, D. R. (1978). Studies on the larvae of New Zealand Trichoptera. *New Zealand Journal of Zoology*, 5(4), 639–750. https://doi.org/10.1080/03014223.1978.10423816

Cross, W., Wallace, J., & Rosemond, A. (2007). Nutrient enrichment reduces constrains on material flows in a detritus-based food web. *Ecology*, 88(10), 2563–2575. https://doi.org/10.1890/06-1348.1

Cullen, R., Hughey, K., & Kerr, G. (2006). New Zealand freshwater management and agricultural impacts. *Australian Journal of Agricultural and Resource Economics*, 50(3), 327–346. https://doi.org/10.1111/j.1467-8489.2006.00338.x

de Jonge, V., Elliott, M., & Orive, E. (2002). Causes, historical development, effects and future challenges of a common environmental problem: Eutrophication. *Hydrobiologia*, 475(1), 1–19. https://doi.org/10.1023/a:1020366418295

DeAngelis, D. (2012). *Dynamics of nutrient cycling and food webs* (Vol. 9). Springer Science & Business Media.

Death, F., & Death, R. (2006). *River health of the Manawatu-Wanganui Region. State of the Environmental Report 2006 – Invertebrate and Periphyton Communities*. Massey University.

Devonport, B., & Winterbourn, M. (1976). The feeding relationships of two invertebrate predators in a New Zealand river. *Freshwater Biology*, 6(2), 167–176. https://doi.org/10.1111/j.1365-2427.1976.tb01601.x

Dinh, Y. T. H., & Death, R. G. (2018). Do disturbance and periphyton productivity affect stream invertebrate traits? *Freshwater Science*, 37(2), 367–379. https://doi.org/10.1086/697924

Dodds, W. (2007). Trophic state, eutrophication and nutrient criteria in streams. *Trends in Ecology & Evolution*, 22(12), 669–676. https://doi.org/10.1016/j.tree.2007.07.010

Dodds, W., & Smith, V. (2016). Nitrogen, phosphorus, and eutrophication in streams. *Inland Waters*, 6(2), 155–164. https://doi.org/10.5268/IW-6.2.909

Dolédec, S., Phillips, N., Scarsbrook, M., Riley, R. H., & Townsend, C. R. (2006). Comparison of structural and functional approaches to determining landuse effects on grassland stream invertebrate communities. *Journal of the North American Benthological Society*, 25(1), 44–60. 10.1899/0887-3593(2006)25[44:COSAFA]2.0.CO;2

Dudgeon, D. (2014). Threats to freshwater biodiversity in a changing world. In B. Freedman (Ed.), *Global Environmental Change* (pp. 243–253). Springer. https://doi.org/10.1007/978-94-007-5784-4_108

Dudgeon, D., Arthington, A., Gessner, M., Kawabata, Z., Knowler, D., Lévêque, C., Naiman, R., Prieur-Richard, A., Soto, D., Stiassny, M., & Sullivan, C. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, 81(2), 163–182. https://doi.org/10.1017/S1464793105006950

Dunne, J., Brose, U., Williams, R., & Martinez, N. (2005). Modeling food-web dynamics: Complexity-stability implications. In A. Belgrano, U. Scharler, J. Dunne & R. Ulanowicz (Eds.), *Aquatic Food Webs: An Ecosystem Approach* (pp. 117–129). Oxford, UK: Oxford University. https://doi.org/10.1093/acprof:oso/9780198564836.001.0001

Dunne, J., Williams, R., & Martinez, N. (2002). Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecology Letters*, 5(4), 558–567. https://doi.org/10.1046/j.1461-0248.2002.00354.x

Elwood, J., & Nelson, D. (1972). Periphyton production and grazing rates in a stream measured with a 32P material balance method. *Oikos*, 23(3), 295–303. https://doi.org/10.2307/3543167

Evans-White, M. A., & Halvorson, H. M. (2017). Comparing the ecological stoichiometry in green and brown food webs – A review and

meta-analysis of freshwater food webs. *Frontiers in Microbiology*, 8(1184), 1–14. https://doi.org/10.3389/fmicb.2017.01184

Fann, S. L., & Borrett, S. R. (2012). Environ centrality reveals the tendency of indirect effects to homogenize the functional importance of species in ecosystems. *Journal of Theoretical Biology*, 294, 74–86. https://doi.org/10.1016/j.jtbi.2011.10.030

Fath, B. D. (2007). Network mutualism: Positive community-level relations in ecosystems. *Ecological Modelling*, 208(1), 56–67. https://doi.org/10.1016/j.ecolmodel.2007.04.021

Fath, B. D., & Borrett, S. R. (2006). A MATLAB® function for network environ analysis. *Environmental Modelling & Software*, 21(3), 375–405. https://doi.org/10.1016/j.envsoft.2004.11.007

Fath, B. D., & Patten, B. C. (1998). Network synergism: Emergence of positive relations in ecological systems. *Ecological Modelling*, 107(2–3), 127–143. https://doi.org/10.1016/S0304-3800(97)00213-5

Fath, B. D., & Patten, B. C. (1999). Review of the foundations of Network Environ Analysis. *Ecosystems*, 2(2), 167–179. https://doi.org/10.1007/s100219900067

Fath, B. D., Scharler, U. M., & Baird, D. (2013). Dependence of network metrics on model aggregation and throughflow calculations: Demonstration using the Sylt-Rømø Bight Ecosystem. *Ecological Modelling*, 252, 214–219. https://doi.org/10.1016/j.ecolmodel.2012.06.010

Ferreira, V., Castagneyrol, B., Koricheva, J., Gulis, V., Chauvet, E., & Graça, M. A. S. (2015a). A meta-analysis of the effects of nutrient enrichment on litter decomposition in streams. *Biological Reviews*, 90(3), 669–688. https://doi.org/10.1111/brv.12125

Finn, J. T. (1976). Measures of ecosystem structure and function derived from analysis of flows. *Journal of Theoretical Biology*, 56(2), 363–380. https://doi.org/10.1016/S0022-5193(76)80080-X

Foote, K. J., Joy, M. K., & Death, R. G. (2015). New Zealand dairy farming: Milking our environment for all it's worth. *Environmental Management*, 56(3), 709–720. https://doi.org/10.1007/s00267-015-0517-x

Friberg, N., Bonada, N., Bradley, D. C., Dunbar, M. J., Edwards, F. K., Grey, J., Hayes, R. B., Hildrew, A. G., Lamouroux, N., & Trimmer, M. (2011). Biomonitoring of human impacts in freshwater ecosystems: The good, the bad and the ugly. *Advances in Ecological Research*, 44, 1–68.

Genoni, G. P., & Pahl-Wostl, C. (1991). Measurement of scope for change in ascendency for short-term assessment of community stress. *Canadian Journal of Fisheries and Aquatic Sciences*, 48(6), 968–974. https://doi.org/10.1139/f91-113

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science*, 293(5538), 2248–2251. https://doi.org/10.1126/science.1061967

Glibert, P. M. (2017). Eutrophication, harmful algae and biodiversity — Challenging paradigms in a world of complex nutrient changes. *Marine Pollution Bulletin*, 124(2), 591–606. https://doi.org/10.1016/j.marpolbul.2017.04.027

Glova, G. J., & Sagar, P. M. (1989). Feeding in a nocturnally active fish, Galaxias brevipinnis, in a New Zealand stream. *Marine and Freshwater Research*, 40(3), 231–240. https://doi.org/10.1071/MF9890231

Glova, G. J., & Sagar, P. M. (1991). Dietary and spatial overlap between stream populations of a native and two introduced fish species in New Zealand. *Marine and Freshwater Research*, 42(4), 423–433. https://doi.org/10.1071/MF9910423

Graham, A. A., McCaughan, D. J., & McKee, F. S. (1988). Measurement of surface area of stones. *Hydrobiologia*, 157(1), 85–87. https://doi.org/10.1007/bf00008813

Guo, F., Kainz, M. J., Sheldon, F., & Bunn, S. E. (2016). Effects of light and nutrients on periphyton and the fatty acid composition and somatic growth of invertebrate grazers in subtropical streams. *Oecologia*, 181(2), 449–462. https://doi.org/10.1007/s00442-016-3573-x

Guo, F., Kainz, M. J., Valdez, D., Sheldon, F., & Bunn, S. E. (2016). High-quality algae attached to leaf litter boost invertebrate

shredder growth. *Freshwater Science*, 35(4), 1213–1221. https://doi.org/10.1086/688667

Hessen, D. O., Elser, J. J., Sterner, R. W., & Urabe, J. (2013). Ecological stoichiometry: An elementary approach using basic principles. *Limnology and Oceanography*, 58(6), 2219–2236. https://doi.org/10.4319/lo.2013.58.6.2219

Hickey, C. W., & Martin, M. L. (2009). *A review of nitrate toxicity to freshwater aquatic species*. Environment Canterbury.

Hilton, J., O'Hare, M., Bowes, M. J., & Jones, J. I. (2006). How green is my river? A new paradigm of eutrophication in rivers. *Science of the Total Environment*, 365(1), 66–83. https://doi.org/10.1016/j.scitotenv.2006.02.055

Hollows, J. W., Townsend, C. R., & Collier, K. J. (2002). Diet of the crayfish Paranephrops zealandicus in bush and pasture streams: Insights from stable isotopes and stomach analysis. *New Zealand Journal of Marine and Freshwater Research*, 36(1), 129–142.

Hopkins, C. L. (1971). Production of fish in two small streams in the North Island of New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 5(2), 280–290. https://doi.org/10.1080/00288330.1971.9515381

Howarth, R. W. (2008). Coastal nitrogen pollution: A review of sources and trends globally and regionally. *Harmful Algae*, 8(1), 14–20. https://doi.org/10.1016/j.hal.2008.08.015

Huryn, A. D. (1996). An appraisal of the Allen paradox in a New Zealand trout stream. *Limnology and Oceanography*, 41(2), 243–252. https://doi.org/10.4319/lo.1996.41.2.0243

Huryn, A. D. (1998). Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream system. *Oecologia*, 115(1–2), 173–183. https://doi.org/10.1007/s004420050505

Jaarsma, N. G., De Boer, S. M., Townsend, C. R., Thompson, R. M., & Edwards, E. D. (1998). Characterising food-webs in two New Zealand streams. *New Zealand Journal of Marine and Freshwater Research*, 32(2), 271–286. https://doi.org/10.1080/00288330.1998.9516825

Jellyman, D. J. (1996). Diet of longfinned eels, Anguilla dieffenbachii, in Lake Rotoiti, Nelson Lakes, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 30(3), 365–369.

Jellyman, P. G., Booker, D. J., Crow, S. K., Bonnett, M. L., & Jellyman, D. J. (2013). Does one size fit all? An evaluation of length–weight relationships for New Zealand's freshwater fish species. *New Zealand Journal of Marine and Freshwater Research*, 47(4), 450–468. https://doi.org/10.1080/00288330.2013.781510

Joy, M. K., Foote, K. J., McNie, P., & Piria, M. (2019). Decline in New Zealand's freshwater fish fauna: Effect of land use. *Marine and Freshwater Research*, 70(1), 114–124. https://doi.org/10.1071/MF18028

Julian, J. P., de Beurs, K. M., Owsley, B., Davies-Colley, R. J., & Ausseil, A.-G.-E. (2017). River water quality changes in New Zealand over 26 years: Response to land use intensity. *Hydrology and Earth System Sciences*, 21(2), 1149–1171. https://doi.org/10.5194/hess-21-1149-2017

Keenan, L., & Morar, S. (2015). *Rivers State of the Environment Monitoring Programme Annual data report 2014/15*. Greater Wellington Regional Council.

Kusabs, I. A., & Swales, S. (1991). Diet and food resource partitioning in koaro, Galaxias brevipinnis (Günther), and juvenile rainbow trout, Oncorhynchus mykiss (Richardson), in two Taupo streams, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 25(3), 317–325.

Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*, 19(4), 573–592. https://doi.org/10.2307/1468118

Larned, S. T., Snelder, T., Unwin, M. J., & McBride, G. B. (2016). Water quality in New Zealand rivers: Current state and trends. *New Zealand Journal of Marine and Freshwater Research*, 50(3), 389–417. https://doi.org/10.1080/00288330.2016.1150309

Latham Ii, L. G. (2006). Network flow analysis algorithms. *Ecological Modelling*, *192*(3–4), 586–600. https://doi.org/10.1016/j.ecolmodel.2005.07.029

Le Moal, M., Gascuel-Odoux, C., Ménesguen, A., Souchon, Y., Étrillard, C., Levain, A., Moatar, F., Pannard, A., Souchu, P., Lefebvre, A., & Pinay, G. (2019). Eutrophication: A new wine in an old bottle? *Science of the Total Environment*, *651*, 1–11. https://doi.org/10.1016/j.scitotenv.2018.09.139

Mageau, M. T., Costanza, R., & Ulanowicz, R. E. (1998). Quantifying the trends expected in developing ecosystems. *Ecological Modelling*, *112*(1), 1–22. https://doi.org/10.1016/S0304-3800(98)00092-1

Main, M., & Winterbourn, M. (1987). Diet and feeding of koaro (Galaxias brevipinnis) in forested, South Westland streams. *Mauri Ora*, *14*, 77–86.

Marks, J. C., Power, M. E., & Parker, M. S. (2000). Flood disturbance, algal productivity, and interannual variation in food chain length. *Oikos*, *90*(1), 20–27. https://doi.org/10.1034/j.1600-0706.2000.900103.x

McFarlane, A. G. (1976). A generic revision of New Zealand hydropsychinae (trichoptera). *Journal of the Royal Society of New Zealand*, *6*(1), 23–35. https://doi.org/10.1080/03036758.1976.10421463

McIntire, C. D., & Phinney, H. K. (1965). Laboratory studies of periphyton production and community metabolism in lotic environments. *Ecological Monographs*, *35*(3), 238–258. https://doi.org/10.2307/1942138

McIntosh, A. R., Crowl, T. A., & Townsend, C. R. (1994). Size-related impacts of introduced brown trout on the distribution of native common river galaxias. *New Zealand Journal of Marine and Freshwater Research*, *28*(2), 135–144. https://doi.org/10.1080/00288330.1994.9516602

Mills, L. S., Soulé, M. E., & Doak, D. F. (1993). The keystone-species concept in ecology and conservation. *BioScience*, 219–224. https://doi.org/10.2307/1312122

Montori, A., Tierno De Figueroa, J. M., & Santos, X. (2006). The diet of the brown trout *Salmo trutta* (L.) during the reproductive period: size-related and sexual effects. *International Review of Hydrobiology*, *91*(5), 438–450.

Montoya, J. M., Pimm, S. L., & Solé, R. V. (2006). Ecological networks and their fragility. *Nature*, *442*(7100), 259–264.

Moore, S. C. (1998). *A Photographic Guide to Freshwater Invertebrates of Taranaki's Rivers and Streams*. Taranaki Regional Council.

Mougi, A., & Kondoh, M. (2016). Food-web complexity, meta-community complexity and community stability. *Scientific Reports*, *6*, 24478. https://doi.org/10.1038/srep24478

Mukherjee, J., Scharler, U. M., Fath, B. D., & Ray, S. (2015). Measuring sensitivity of robustness and network indices for an estuarine food web model under perturbations. *Ecological Modelling*, *306*, 160–173. https://doi.org/10.1016/j.ecolmodel.2014.10.027

National Institute for Water and Atmospheric Research. (2004). *Freshwater Biodata Information System (FBIS)* (2004th ed.). National Institute for Water and Atmospheric Research.

Okuyama, T., & Holland, J. N. (2008). Network structural properties mediate the stability of mutualistic communities. *Ecology Letters*, *11*(3), 208–216. https://doi.org/10.1111/j.1461-0248.2007.01137.x

Osborne, J. (2010). Improving your data transformations: Applying the Box-Cox transformation. *Practical Assessment, Research, and Evaluation*, *15*(1), 12.

Patricio, J., Ulanowicz, R., Pardal, M. A., & Marques, J. C. (2006). In K. Martens, H. Queiroga, M. R. Cunha, A. Cunha, M. H. Moreira, V. Quintino, A. M. Rodrigues, J. Seroôdio, & R. M. Warwick (Eds.), *Ascendency as ecological indicator for environmental quality assessment at the ecosystem level: A case study BT - Marine Biodiversity: Patterns and Processes, Assessment, Threats, Management and Conservation* (pp. 19–30). Springer. https://doi.org/10.1007/1-4020-4697-9_2

Polegatto, C. M., & Froehlich, C. G. (2003). Feeding strategies in Atalophlebiinae (Ephemeroptera: Leptophlebiidae), with considerations on scraping and filtering. *Research Update on Ephemeroptera and Plecoptera. Perugia, University of Perugia, 488p*, 55–61.

Price, E. L., Sertić Perić, M., Romero, G. Q., & Kratina, P. (2019). Land use alters trophic redundancy and resource flow through stream food webs. *Journal of Animal Ecology*, *88*(5), 677–689. https://doi.org/10.1111/1365-2656.12955

R Core Team (2016). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Richardson, J. (1989). The all-new freshwater fish database. *Freshwater Catch*, *41*, 20–21.

Ripley, B., Venables, B., Bates, D. M., Hornik, K., Gebhardt, A., Firth, D., & Ripley, M. B. (2013). Package 'MASS'. *Cran R*, *538*, 170. https://cran.r-project.org/web/packages/MASS/MASS.pdf

Robinson, W. R., Peters, R. H., & Zimmermann, J. (1983). The effects of body size and temperature on metabolic rate of organisms. *Canadian Journal of Zoology*, *61*(2), 281–288. https://doi.org/10.1139/z83-037

Rooney, N., & McCann, K. S. (2012). Integrating food web diversity, structure and stability. *Trends in Ecology & Evolution*, *27*(1), 40–46. https://doi.org/10.1016/j.tree.2011.09.001

Rounick, J. S., & Hicks, B. J. (1985). The stable carbon isotope ratios of fish and their invertebrate prey in four New Zealand rivers. *Freshwater Biology*, *15*(2), 207–214. https://doi.org/10.1111/j.1365-2427.1985.tb00193.x

Sagar, P. M., & Glova, G. J. (1995). Prey availability and diet of juvenile brown trout (*Salmo trutta*) in relation to riparian willows (Salix-spp.) in three New Zealand streams. *New Zealand Journal of Marine and Freshwater Research*, *29*(4), 527–537.

Saint-Béat, B., Baird, D., Asmus, H., Asmus, R., Bacher, C., Pacella, S. R., Johnson, G. A., David, V., Vézina, A. F., & Niquil, N. (2015). Trophic networks: How do theories link ecosystem structure and functioning to stability properties? A review. *Ecological Indicators*, *52*, 458–471. https://doi.org/10.1016/j.ecolind.2014.12.017

Scarsbrook, M. R., & Townsend, C. R. (1993). Stream community structure in relation to spatial and temporal variation: A habitat templet study of two contrasting New Zealand streams. *Freshwater Biology*, *29*(3), 395–410. https://doi.org/10.1111/j.1365-2427.1993.tb00774.x

Schreck, C. B., & Tort, L. (2016). 1 - The Concept of Stress in Fish. In C. B. Schreck, L. Tort, A. P. Farrell, & C.- J.- B.- T.-F.- P. Brauner (Eds.), *Biology of Stress in Fish* (Vol. 35, pp. 1–34). Academic Press. https://doi.org/10.1016/B978-0-12-802728-8.00001-1

Sealey, W. M., & Gatlin, D. M. (1999). Overview of nutritional strategies affecting health of marine fish. *Journal of Applied Aquaculture*, *9*(2), 11–26. https://doi.org/10.1300/J028v09n02_02

Smith, V. H., Joye, S. B., & Howarth, R. W. (2006). Eutrophication of freshwater and marine ecosystems. *Limnology and Oceanography*, *51*(1part2), 351–355. https://doi.org/10.4319/lo.2006.51.1_part_2.0351

Smith, V. H., & Schindler, D. W. (2009). Eutrophication science: Where do we go from here? *Trends in Ecology & Evolution*, *24*(4), 201–207. https://doi.org/10.1016/j.tree.2008.11.009

Stark, J. D., & Maxted, J. R. (2007). A user guide for the Macroinvertebrate Community Index, Cawthron Report. Nelson, New Zealand. Retrieved from https://www.mfe.govt.nz/sites/default/files/mci-user-guide-may07.pdf

Steinman, A. D., Lamberti, G. A., & Leavitt, P. R. (1996). Biomass and pigments of benthic algae. In F. G. Hauer, & G. A. Lamberti (Eds.), *Methods in stream ecology* (pp. 295–313). Academic Press.

Stoffels, R. J., Karbe, S., & Paterson, R. A. (2003). Length-mass models for some common New Zealand littoral-benthic macroinvertebrates, with a note on within-taxon variability in parameter values among published models. *New Zealand Journal of Marine and Freshwater Research*, *37*(2), 449–460. https://doi.org/10.1080/00288330.2003.9517179

Tank, J., & Winterbourn, M. (1996). Microbial activity and invertebrate colonisation of wood in a New Zealand forest stream. *New Zealand*

*Journal of Marine and Freshwater Research*, *30*(2), 271–280. https://doi.org/10.1080/00288330.1996.9516714

Thera, J. C., Kidd, K. A., & Bertolo, R. F. (2020). Amino acids in freshwater food webs: Assessing their variability among taxa, trophic levels, and systems. *Freshwater Biology*, *65*(6), 1101–1113. https://doi.org/10.1111/fwb.13495

Thompson, R. M., & Townsend, C. R. (2004). Land-use influences on New Zealand stream communities: Effects on species composition, functional organisation, and food-web structure. *New Zealand Journal of Marine and Freshwater Research*, *38*(4), 595–608. https://doi.org/10.1080/00288330.2004.9517265

Tonkin, J. D., Death, R. G., & Barquín, J. (2013). Productivity–diversity relationships for stream invertebrates differ geographically. *Aquatic Ecology*, *47*(1), 109–121. https://doi.org/10.1007/s10452-013-9429-0

Towers, D. J., Henderson, I. M., & Veltman, C. J. (1994). Predicting dry weight of New Zealand aquatic macroinvertebrates from linear dimensions. *New Zealand Journal of Marine and Freshwater Research*, *28*(2), 159–166. https://doi.org/10.1080/00288330.1994.9516604

Towns, D. R., & Peters, W. L. (1996). *Leptophlebiidae (Insecta: Ephemeroptera)*. Manaaki Whenua Press Lincoln.

Townsend, C., DolÉDec, S., & Scarsbrook, M. (2003). Species traits in relation to temporal and spatial heterogeneity in streams: A test of habitat templet theory. *Freshwater Biology*, *37*(2), 367–387. https://doi.org/10.1046/j.1365-2427.1997.00166.x

Townsend, C., & Hildrew, A. (1994). Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, *31*(3), 265–275. https://doi.org/10.1111/j.1365-2427.1994.tb01740.x

Ulanowicz, R. (1986). A phenomenological perspective of ecological development. *Aquatic Toxicology and Environmental Fate*, *9*, 73–81.

Ulanowicz, R. (1997a). *Ecology, the ascendent perspective*. Columbia University Press.

Ulanowicz, R. (1997b). Limitations on the connectivity of ecosystem flow networks. In A. Rinaldo & A. Marani (Eds.), *Biological Models* (pp. 125–143). Venice, Italy: Istituto Veneto de Scienze.

Ulanowicz, R. (2009). The dual nature of ecosystem dynamics. *Ecological Modelling*, *220*(16), 1886–1892. https://doi.org/10.1016/j.ecolmodel.2009.04.015

Ulanowicz, R., Goerner, S., Lietaer, B., & Gomez, R. (2009). Quantifying sustainability: Resilience, efficiency and the return of information theory. *Ecological Complexity*, *6*(1), 27–36. https://doi.org/10.1016/j.ecocom.2008.10.005

Vorosmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S. E., Sullivan, C. A., Liermann, C. R., &

Davies, P. M. (2010). Global threats to human water security and river biodiversity. *Nature*, *467*(7315), 555–561. https://doi.org/10.1038/nature09440

Winterbourn, M. (1978). The food and occurrence of larval Rhyacophilidae and Polycentropodidae in two New Zealand rivers. In *Proceedings of the 2nd International Symposium on Trichoptera* (pp. 55–66).

Winterbourn, M. (1982). The invertebrate fauna of a forest stream and its association with fine particulate matter. *New Zealand Journal of Marine and Freshwater Research*, *16*(3–4), 271–281. https://doi.org/10.1080/00288330.1982.9515970

Winterbourn, M. (1996). Life history, production and food of Aphrophila neozelandica (Diptera: Tipulidae) in a New Zealand stream. *Aquatic Insects*, *18*(1), 45–53.

Winterbourn, M. (2000). Feeding ecology. In K. Collier, & M. Winterbourn (Eds.), *New Zealand stream invertebrates: Ecology and implications for management* (pp. 100–124). The New Zealand Limnological Society.

Winterbourn, M., Cowie, B., & Rounick, J. S. (1984). Food resources and ingestion patterns of insects along a west coast, South Island, river system. *New Zealand Journal of Marine and Freshwater Research*, *18*(3), 379–388. https://doi.org/10.1080/00288330.1984.9516058

Winterbourn, M., Gregson, K., & Dolphin, C. (1989). *Guide to the Aquatic Insects of New Zealand* (Vol. *9*). Entomological Society of New Zealand Auckland.

Zhang, H., Zhao, L., Tian, W., & Huang, H. (2016). Stability of food webs to biodiversity loss: Comparing the roles of biomass and node degree. *Ecological Indicators*, *67*, 723–729. https://doi.org/10.1016/j.ecolind.2016.03.045

Zhao, L., Zhang, H., O'Gorman, E. J., Tian, W., Ma, A., Moore, J. C., Borrett, S. R., & Woodward, G. (2016). Weighting and indirect effects identify keystone species in food webs. *Ecology Letters*, *19*(9), 1032–1040. https://doi.org/10.1111/ele.12638

Zorach, A. C., & Ulanowicz, R. E. (2003). Quantifying the complexity of flow networks: How many roles are there? *Complexity*, *8*(3), 68–76. https://doi.org/10.1002/cplx.10075