Functional or Dysfunctional? A Refreshed Perspective on Functional Feeding Groups

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Abstract

Functional feeding groups (FFGs), introduced in the 1970s, provided a framework for understanding freshwater ecosystems by classifying macroinvertebrates according to feeding mode and diet. Since then, the FFG approach has been widely applied and has significantly advanced our knowledge of ecosystem processes and functions. However, the framework represents a simplified view of complex trophic interactions, ecological networks, and ecosystem functioning, and its misuse can lead to misleading conclusions. Addressing contemporary challenges in freshwater ecology requires updated approaches and methodologies. In this paper, we offer a renewed perspective on the FFG framework, outlining its limitations and providing guidance on contexts where its application is appropriate—and where it is not. Finally, we propose a framework that relaxes key assumptions of the original model and incorporates emerging technologies, enabling deeper insights into the dynamic trophic interactions of freshwater macroinvertebrates.

Keywords

Macroinvertebrates, foraging, diet, traits

Introduction

Despite most freshwater macroinvertebrates being opportunistic generalists (Hildrew and Giller (2023); Supplementary Material Figure S1), a consensus was reached that their diets are constrained by their mouthpart morphology (Cummins, 1973; Cummins, 1974; Cummins and Klug, 1979). This, in turn, informed a conventional wisdom that mouthpart morphology is indicative of the diet and foraging habits of freshwater invertebrates (Baptista et al., 2009). On this basis, functional feeding groups (FFGs) were proposed as a method to group freshwater macroinvertebrates based upon their feeding morphology and behaviour (Cummins, 1973), enabling greater insight into the functional roles of macroinvertebrates than taxonomy alone. Whilst the delineation of freshwater macroinvertebrates into FFGs allows for testing hypotheses surrounding the function and roles of organisms (Duffy and Hay, 1994), it also has significant limitations (Macneil et al., 1997). Now, over 50 years on from its proposal, it is timely to evaluate the drawbacks and opportunities of the FFG framework and its application to real world ecosystems. Here, we outline a refresh of assumptions made by the FFG framework and consider how these assumptions influence our conclusions about ecological systems.

Functional Ecology and Development of the FFG Framework

In his 1927 seminal book, *Animal Ecology,* Charles Elton laid foundational concepts of feeding guilds, grouping predators by their common prey through assimilation of taxonomic, dietary and body-size information (Elton, 1927; Thompson et al., 2020). Following this, similar functional insight into freshwater systems arose by the 1970s, beginning to associate structure and function within and across river system – contrasting with prior taxonomic-oriented approaches (Cummins, 1974; Minshall, 1978). Enquiry into ecosystem processes, such as energy and mineral cycling, led researchers to question the role of organisms in driving their dynamics (Cummins, 1973; Cummins and Klug, 1979). Food webs which detail functional processes (e.g., predation and competition), rather than simply taxonomic interactions, began arising more frequently (Larsson et al., 1978; Cren, 1976), accounting for the inter-dependent roles of detrivorous microbes, plant producers, microinvertebrates, macroinvertebrates, and vertebrates. Food webs, however, are costly to construct (Windsor, 2023). Thus, to conceptualise the role of macroinvertebrates in broader freshwater ecosystem function

without this additional burden, the FFG framework was devised (Cummins, 1973; Cummins and Klug, 1979).

FFGs are morpho-behavioural descriptors of freshwater macroinvertebrates, detailing feeding guilds to a higher resolution than coarse trophic-level descriptions. They have been devised through observations of mouthpart morphology and visual stomach content analysis, grouping on the basis of what and how macroinvertebrates eat, contrasting with previous solely taxonomic classification systems (see Table 1 for details of classification system).

Since the assignments made by Cummins and colleagues during the 1970s, both the FFGs and the taxa they describe have been altered as new information has arisen about freshwater macroinvertebrate foraging behaviours and function (e.g., Macneil et al., 1997; Baptista et al., 2009). Whilst some trait databases have collapsed FFG types into coarser categories (Twardochleb et al., 2021; Phillips and Smith, 2018) others have further partitioned categories to provide more granular insight (i.e., filter feeders partitioned into active and passive; (Schmidt-Kloiber and Hering, 2015; Supplementary Material Table S1). Some databases also assign a single FFG to a taxon (Twardochleb et al., 2021), whilst others assign 'fuzzy-coded' traits (Chevenet et al., 2006) to exemplify the affinity of a taxon to a trait, such that a single taxon may exhibit variations in affinity towards multiple traits (Schmidt-Kloiber and Hering, 2015; Phillips and Smith, 2018). Assignment of multiple traits to a single species brings together different types of biological information (observational and experimental), informing a more refined description of ecosystem functions fulfilled by a species (Bremner et al., 2006).

Table 1. An overview of functional feeding group (FFG) classifications made by Cummins (1973) and Cummins and Klug (1979). Each of the FFGs may be further subdivided by the type of food that is consumed. Each FFG was assigned examples to family level between the two papers.

FFG	Sub-Class & Food Category	Examples
Shredders	Herbivorous Chewers & Miners	Lepidoptera Trichoptera (Phryganeidae, Leptoceridae) Coleoptera (Chrysomelidae) Diptera (Chironomidae)
	Detrivorous Chewers & Miners	Plecoptera (Filipalpia) Trichoptera (Limnephilidae, Lepidostomatidae) Diptera (Tipulidae, Chironomidae)
Collectors	Filter Feeders	Ephemeroptera (Siphlonuridae)

		Trichoptera (Philopotamidae, Psychomyiidae, Hydropsychidae, Brachycentridae) Lepidoptera Diptera (Simuliidae, Chironomidae, Culicidae)
	Sediment Feeders	Ephemeroptera (Caenidae, Ephemeridae, Leptophlebiidae, Baetidae, Ephemerellidae Heptageniidae) Hemiptera (Gerridae) Coleoptera (Hydrophilidae) Diptera (Chironomidae, Ceratopogonidae)
Scrapers	Mineral Scrapers	Ephemeroptera (Heptageniidae, Baetidae, Ephemerellidae) Trichoptera (Glossosomatidae, Helicopsychidae, Molannidae, Odontoceridae, Goeridae) Lepidoptera Coleoptera (Elmidae, Psephenidae) Diptera (Chironomidae, Tabanidae)
	Organic Scrapers	Ephemeroptera (Caenidae, Leptophlebiidae, Heptageniidae, Baetidae) Hemiptera (Corixidae) Trichoptera (Leptoceridae) Diptera (Chironomidae)
Predators	Swallowers/ Engulfers	Odonata Plecoptera (Setipalpia) Megaloptera Trichoptera (Rhyacophilidae, Polycentropodidae, Hydropsychidae) Coleoptera (Dytiscidae, Gyrinidae) Diptera (Chironomidae)
	Piercers	Hemiptera (Belastomatidae, Nepidae, Notonectidae, Naucoridae) Diptera (Rhagionidae)

FFGs have historically been applied to understand ecosystem-level consequences of macroinvertebrate community structure and function. Yet, more recently, they been extended as a tool to understand how these functions may shift as a result of environmental change and across biological scales (Tierno de Figueroa et al., 2019; Vimos-Lojano et al., 2020, Lima et al., 2022). Applications of the FFG framework in this way have identified the ecosystem functions which may be most threatened as a result of warming (Tomczyk et al., 2022; Charette and Harvey, 2025; Allen et al., 2024).

As challenges facing freshwater systems change over time, the applications of the FFG framework may have been extended beyond that which is appropriate. We propose that by

applying FFGs to investigate the effects of environmental change on freshwater community function, our conclusions become limited by the framework's assumption. This risks our predictions of how freshwater systems may respond to environmental change misaligning with observed responses, leading to potentially misguided efforts to conserve or restore the resilience of freshwater ecosystems. Below, we present the shortfalls, opportunities and future directions of the FFG framework. We present these ideas as a guide to applying the FFG framework – where it is useful, and where it may mislead conclusions.

Common Assumptions of the Functional Feeding Group Framework

Several non-mutually exclusive assumptions are made by the functional feeding group framework. It supposes that functional feeding groups (a) are underpinned by evolutionarily fixed 'feeding traits'; (b) are non-plastic to changes in a species' biotic and abiotic environment, and (c) are not subject to ontogenic shifts. Here, we detail a series of limitations underlying these assumptions.

(a) FFGs are underpinned by evolutionarily fixed and optimised feeding traits

Predators are typically assigned by their mandibular musculature (Blanke et al., 2012), scrapers by their distal maxillae anatomy, and brushers by fine observation of setae morphology (Baptista et al., 2009). From these morphologies, the FFG framework posits that we can deduce how freshwater macroinvertebrates feed from these heritable traits, thus implying that they only exploit the single foraging method they are most effective at. These assignments however rely on the assumption that species behave optimally. For example, if macroinvertebrates possess a mouthpart morphology which is effective for scraping biofilms from substrates, their foraging mode is always scraping, irrespective of any other factors (e.g., competitive interactions for single resources or resource limitation due to changing abiotic conditions). Whilst it may be reasonable to conclude that under fixed, optimal environmental conditions, species will demonstrate a dominant feeding mode, we cannot conclude that suboptimal foraging strategies are not exploited – especially where resources are labile and switches in feeding strategy may be necessary for persistence. Macroinvertebrates which are prone to 'feast-or-famine' lifestyle in resource-variable environments generally feed proportionally to food present, switching between food as it comes and goes, across feeding guilds (Koslucher and Mishall, 1973; Hildrew and Giller, 2023).

Despite evolutionary insights informing of how organisms *should* behave (i.e., to optimise marginal returns of feeding), they do not provide certainty on how they *actually* behave. Where conditions are suboptimal from the perspective of a species (i.e., limiting high quality resource), they may instead switch feeding strategies to consume a relatively sub-optimal resource instead of ceasing to feed in the absence of their optimal resource.

To improve our perception of how freshwater macroinvertebrates feed, we suggest shifting framing away from 'feeding traits' and towards 'feeding strategies'. A trait may be defined as 'any morphological, physiological, or phenological heritable feature measurable at the level of the individual' (Garnier et al., 2015). Whilst the series of homologous structures comprising mouthparts may be described as 'traits' (Krenn, 2019), the feeding behaviours which they express may be more effectively conceptualised as strategies, of which multiple may be simultaneously exploited and switched between in response to environmental and community change. This distinction between heritable traits which enable feeding (i.e., mouthparts) and the behavioural strategies observed (e.g., shredding, gathering, predating, filtering) is essential for addressing the following two assumptions of plastic and ontogenic shifts in FFGs.

(b) FFGs are non-plastic to changes in a species' biotic and abiotic environment

It has been argued that as most freshwater macroinvertebrates are opportunistic generalists, any assignment to an FFG is arbitrary (Macneil et al., 1997). Yet, a core assumption of the FFG framework is that they may only be opportunistic generalists within the confines of their mouthpart morphology (Baptista et al., 2009). Whilst anatomy undoubtedly influences what may mechanistically be captured and consumed, assignment of set function and behaviour to morphology relies upon implicit assumptions that traits are evolutionarily fixed (see above) and non-plastic to changes in a species' biotic and abiotic environment (Tierno de Figueroa et al., 2019).

The assumption of limited-to-no plasticity appears to be regularly violated in real-world ecosystems. For example, *Gammarus* spp. (Amphipoda) have been rigidly assigned as shredders, harvesting allochonthous particulate organic matter (Cummins and Klug, 1979). However gut content analysis has indicated both consumption of algae and zooplankton (Gladyshev et al., 2000) and experimental studies have indicated their predation of *Baetis*

rhodani (Ephemeroptera) nymphs both with and without leaf presence (Kelly et al., 2002). Interestingly, Kelly et al. (2002) found that relative shredding and predation was contingent both upon the type of prey and the quality of the leaf material. In combination, this suggests that *Gammarus* spp. are not obligate shredders and instead alternate efforts between shredding and predation as a function of resource abundance and quality, in contravention with the original assignment made by Cummins and Klug (1979). This finding suggests that the feeding strategy exploited is dependent on the environmental and community conditions, instead of being entirely constraint to a single strategy as imposed by mouthpart morphology. Importantly, these two strategies may not be exhaustive of those exploited by *Gammarus* spp*.,* only the strategies we hold evidence for. In fact, Allan and Malmqvist (1989) demonstrated that *Gammarus* spp. will consume Danish cheese, implying their capacity to switch towards a collector-gatherer strategy where suitable resources are available. Similarly, the Baetidae (Ephemeroptera) for example are frequently (although not entirely) assigned as collector-gatherers based on their labial palp morphology, appearing specialised for manipulating food (Baptista et al., 2009). Whilst solely based upon morphological observations, Baetidae would be assigned as collector-gatherers, experimental evidence reported by Moulton et al. (2004) indicates abundance of tightly substrate-bound periphyton to be negatively correlated with Baetidae abundance, suggesting their role as a scraper in foraging periphyton. Whilst we cannot determine whether this strategy is universal of Baetidae, in this instance we can conclude that the mouthpart morphology is not entirely indicative of feeding strategy. As a final example, Baptista et al. (2009) also suggested that collecting information about the substrate a sample is collected from is important for making similar descriptions. Mouthpart observations of *Leptohyphes* spp., *Tricorythodes* spp., and *Trichorythopsis* spp. were all assigned by Baptista et al. (2009) as scrapers, on the basis that their fine setae are unsuitable for brushing or filtering strategies. Whilst from the observations made by Baptista et al. (2009) it may be reasonable to ascribe scraping as the dominant strategy, we cannot determine that brushing or filtering doesn't occur at all without consideration of behavioural evidence.

It appears that upon inspection, many different organisms exhibit plasticity or variability in foraging and diet. Certainly, it may be the case that all invertebrate taxa are able to feed on a diverse range of resources, and that variation is not just a result of accidental ingestion (Tercel

et al., 2021). This emphasises the importance on the earlier proposition made by McShaffrey and McCafferty (1988) that descriptions of macroinvertebrate feeding roles requires both morphological, behavioural observations and analysis of gut contents to effectively understand their feeding mechanisms and behaviours.

(c) FFGs are not subject to ontogenic shift

It is well understood that niches occupied by species shift over their lifetime (Werner and Gilliam, 1984; Macneil et al., 1997) – a phenomenon historically associated with changes in body size throughout a lifecycle (Werner and Gilliam, 1984). However, these shifts in niche are rarely accounted for in food webs, which typically aggregate life stages into single taxon-representing nodes (e.g., inter-specific networks). Construction of food webs in this way makes the implicit assumption that interspecific interactions are fixed throughout a species' lifecycle, which may have substantial implications for our estimations of their structure, dynamics and resilience (Preston et al., 2014). For taxa with complex lifecycles, aggregation of these life stages heavily simplifies their diverse functional roles and misrepresents trophic positioning in food webs (Preston et al., 2014).

Seasonal dietary shifts have been investigated broadly across the animal kingdom, including fishes (Thompson et al., 2020; Nolan and Britton, 2025), snakes (Hampton, 2018; Patterson et al., 2022) and birds (Davies et al., 2022). Whilst some describe these as ontogenic shifts in diet (Hampton, 2018, Thompson et al., 2020), few effectively disentangle true ontogenic shifts in diet with seasonal density dependence (although Davies et al. (2022) achieves this more effectively by capturing Dipteran population dynamics alongside dietary analysis). Looking towards taxa with highly complex lifestyles such as parasites, these shifts are yet more profound (Preston et al., 2014). *Schistocephalus* spp. (Cestoda), for example, successively parasitise copepods, three-spined sticklebacks, and piscivorous birds over the course of their lifecycle (Nguyen and Gokhale, 2025). Aggregation of these interactions into an inter-specific food web, or singular FFG, would grossly misrepresent the trophic position of *Schistocephalus* spp. and its influence over food web dynamics (see Figure 1). Whilst there is little literature surrounding ontogenic shifts in diet of freshwater macroinvertebrates, perhaps one of the most understood lifecycles is that of *Aedes* spp. mosquitos (Diptera: Culicidae) due to their role in *Plasmodium* spp. malaria transmission and implications for global health. The holometabolous *Aedes* spp. undergo stark morphological transition throughout their

lifecycles, transitioning between eggs, pupae, larvae and adults. Each stage of the lifecycle is also associated with distinct habitats, foraging traits, and diets, where the diet of a former life stage has influence over functional trait development of later life stages (Carvajal-Lago et al., 2021). These ontogenic changes in diet are seen broadly among the freshwater macroinvertebrates. For example, Tanypodinae (Diptera: Chironomidae) shift between herbivory/detrivory to predation over the course of their lifecycle, whilst the *Isoperla* (Plecoptera: Perlodidae) transition between herbivory and carnivory through their development (Hildrew and Giller, 2023).

Studies investigating the implications of ontogenic shifts in feeding in food web analyses (Preston et al., 2014; Clegg et al., 2018) find them to have significant effects on food webs structural characteristics. Clegg et al. (2018) analysed five aquatic food webs and demonstrated unique effects of life-stage inclusion independent of diversity and complexity effects, with inclusion of life stages reducing network linkage (relative to that expected by the power law), altering proportions of basal to intermediate nodes, and increasing potential for indirect effects within the network. Whilst highly resolved data which record feeding at different life stages are limited, those described above do indicate feeding to be non-fixed during a species' lifecycle (although the extent varies between species).

The above examples discussing both the ontogenic shifts in feeding at the species-level, and their implications for food web structure and dynamics, highlight that ascribing a single FFG to a species irrespective of life stage may lead to erroneous conclusions implicating perceived dynamics of freshwater communities. Importantly, failing to account for such may mislead conclusions about species' extinction risks under changing conditions (such as the scenario described by Figure 1).

Is there a future for the FFG framework?

The extent to which the above assumptions limit conclusions are highly dependent upon the context (whether at individual- or ecosystem-levels) and the specific phenomena being studied (nutrient cycling or community/individual response to global change). Whilst FFGs may effectively describe the feeding behaviours freshwater macroinvertebrates *can* demonstrate, conclusions become limiting where we look to better understand responses of these feeding behaviours to changing conditions or over the course of a lifecycle. Faced with

changing climate, for example, several outcomes are possible for freshwater macroinvertebrates: adapt, move or die (Parmesan, 2006). A similar process could occur under changing resource availability. Species may either adapt to a new resource, plastically switch towards a sub-optimal resource, move to a location where resources are more abundant, or become extirpated. By consistently following the logic of the FFG framework, we risk failing to capture the full range of possible responses seen among macroinvertebrates to changing resource availability, and underestimate their resilience. Yet by acknowledging the assumptions outlined here, we can be better informed of the specific scenarios in which it is beneficial to utilise the FFG framework, and those in which its applications may misguide conclusions (for an example overview, see Table 2).

Table 2. **Possible research questions/scenarios, and the suitability of applying the FFG framework in their study.**

Question / Scenario	**Opportunities / Drawbacks of Applying the FFG Framework**	**Alternative approaches, if applicable.**
Studying the effects of riparian restoration on allochthonous energy inputs into rivers.	The FFG framework is advantageous here. It allows us to understand which invertebrates are well adapted to processing allochthonous material.	
Studying the effect of warming on freshwater ecosystem function.	The FFG framework is more limited here, as its assumption that feeding strategies are evolutionary fixed and non-plastic to changes in biotic and abiotic conditions implicate conclusions.	*In vitro o*bservational studies and DNA dietary metabarcoding of populations to capture changing feeding habits under warming conditions.
Studying temporal shifts in freshwater ecosystems functioning.	The FFG framework is more limited here, as its assumption that feeding behaviours, and their contribution to ecosystem function, are be fixed over the course of a species' lifecycle.	Field sampling and DNA dietary metabarcoding of macroinvertebrates at seasonal intervals to capture shifts in feeding and relative allochthonous/autochthonous energy processing.

Whilst perspectives introduced in this paper shed light on the shortfalls of the FFG framework, its applications in instances have, and will continue, to remain useful. We suggest that in community-level studies investigating the species' functional role in nutrient cycling, the FFG framework remains a central tool. Yet, since the formalisation of the FFG framework, we have begun to address different questions about natural systems. In addition to understanding processes and functions of freshwater systems, we now also look to understanding how they will be implicated by anthropogenic global change. When relying on the assumptions of the FFG framework to study food web structure and dynamics under scenarios of global change, its assumptions become troublesome and heighten risk in drawing erroneous conclusions unrepresentative of the natural system being studied.

Historically, we have had limited options to study aquatic invertebrate feeding and have had to rely on FFGs despite the framework's drawbacks. However, as use of tools and techniques to study freshwater invertebrates in their living systems expand, the utility of the FFG framework may lessen. As high resolution and throughput technologies for investigating natural systems develop, it is vital we consistently readdress their opportunities to improve biological insight – to relax assumption previously imposed by methodology, and improve the accuracy of information we capture about nature.

Cummins (2016) justified continued application of the FFG framework on the basis that visual gut content analysis reveals little insight into actual consumption by freshwater macroinvertebrates. Since however, advancements in dietary metabarcoding (Pompanon et al., 2012) technologies have alleviated this challenge, affording improved understanding of macroinvertebrate feeding without reliance on observational gut content examination. As these methodologies have been developed, a wealth of guidance on the applications of dietary metabarcoding to studying feeding interactions has been generated (for example: Tercel et al., 2021; Cuff et al., 2023; Cuff et al., 2022; Deagle et al., 2019; Pinol et al., 2015). These techniques enable direct determination of freshwater macroinvertebrates feeding habits, without a requirement to rely upon mouthpart morphology as its proxy. Our ability to now independently contrast *what* species each from *how* they eat represents an important milestone in understanding the feeding, foraging mechanisms, and behaviours underpinning freshwater macroinvertebrates' diet. Our framework to study freshwater macroinvertebrate feeding is summarised in Figure 2.

Conclusions

Following its proposal, the FFG framework has proven a useful tool to study the functional diversity of freshwater macroinvertebrates in their ecosystems. The applications of the framework have laid the groundworks for a large portion of our contemporary understanding of freshwater systems – bridging functional and freshwater ecology. Whilst useful for understanding ecosystem-level energy flows, we suggest that the FFG framework is insufficient for addressing questions requiring mechanistic insight into feeding; where feeding plasticity may implicate organismal and ecosystem functional response to environmental change, and in the construction of food webs.

At a time where greater understanding of biological responses to global change is vital for ensuring ecological resilience, we propose novel high-throughput approaches to enable deeper understanding of feeding and foraging strategies than attainable through the FFG approach – conducive with the more refined understanding we require to address pressing questions of species' responses to global change. Alongside this, we recommend that (a) greater emphasis should be placed on the distinction between *what* species eat and *how* they eat; (b) the effects of both plastic and ontogenic intraspecific variation in feeding should be of central consideration when constructing food webs, and (c) we should shift our framing of functional feeding groups away from 'traits' and towards 'strategies'.

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Author Contribution Statement

Conceptualisation: FR, FW. Developing methods: FR, FW. Data Analysis: FR. Preparation of figures and tables: FR. Conducting the research, data interpretation, writing: FR, FW.

Data Availability Statement

No new data were created during this research. Secondary datasets referenced throughout.

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Figures

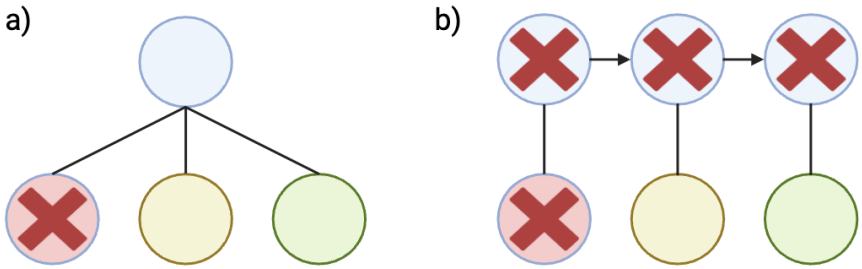

Figure 1. Predator-prey bipartite food webs. (a) represents a taxon food web, where a single predator consumes three different prey items. (b) represents a life-stage food web, where a single predator has three life stages, which each consume a single prey item. In (a), the extinction of a single resource (represented by the red cross) does not necessitate the extinction of the predator, as switching between prey items may occur. In (b), the extinction of the resource in the first life stage renders the predator extinct for all successive life stages, irrespective of prey item presence during later life stages.

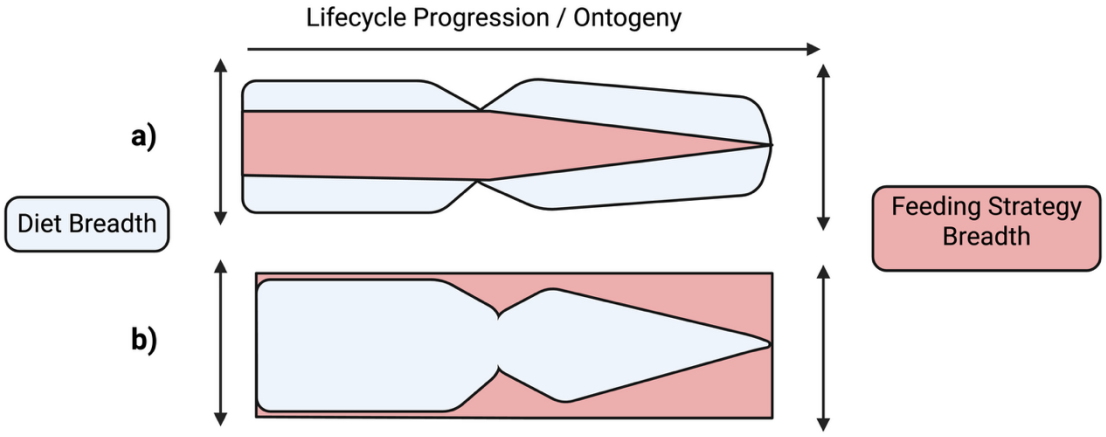

Figure 2. A schematic illustrating shifts in diet breadth (blue bar width) and feeding strategy breadth (red bar width) across a hypothetical species' lifecycle. Over the course of species' (a) lifecycle, a relatively constant breadth of feeding strategies is employed with reductions in strategy breadth towards the end of the lifecycle; diet breadth is maintained broadly constant with narrowing in breadth at the midstage of the lifecycle. Over the course of species' (b) lifecycle, a constant broad feeding strategy breadth is maintained, whilst the diet breadth undergoes fluctuations throughout the lifecycle. Diet breadth may be determined through dietary DNA metabarcoding, feeding strategies through field or laboratory observational studies and details of ontogenic dietary shift through longitudinal field or laboratory studies to capture diets of all life stages of the study species.

Supplementary Materials for

Functional or Dysfunctional? A Refreshed Perspective on Functional Feeding Groups

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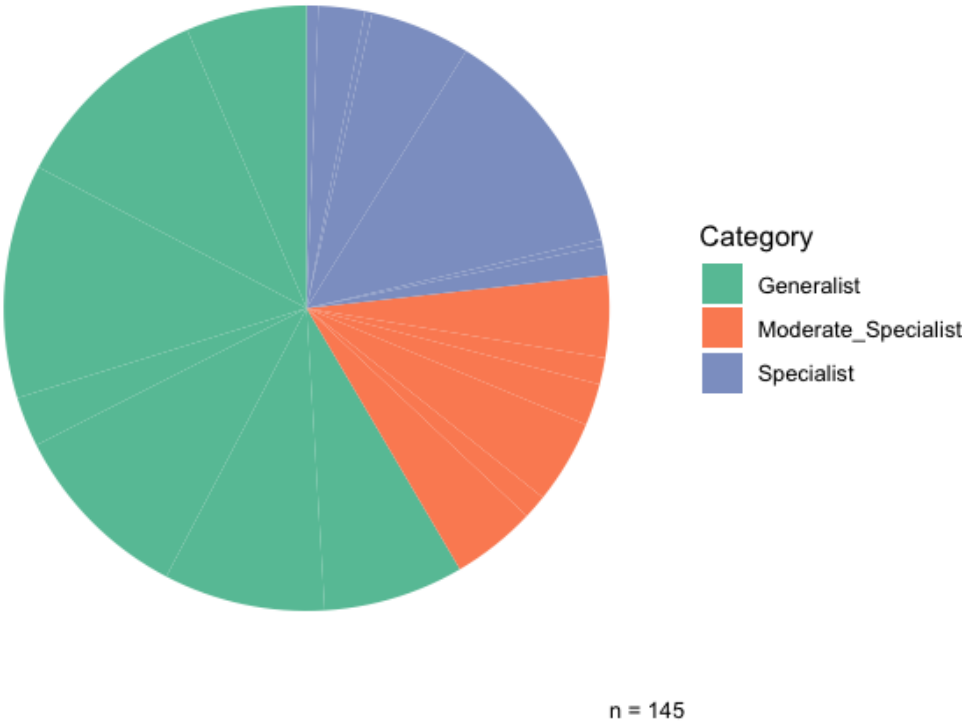

Figure S1. Proportions of Ephemeroptera, Plecoptera, Trichoptera, Odonata, Coleoptera, Diptera, Hemiptera and Megaloptera held in the NIWA database. Taxa are assigned 'generalist', 'moderate specialist' and 'specialist' levels of nutritional specialisation. Data obtained through the NIWA database (see Phillips and Smith (2018)) and presented using R (R-Core-Team (2024); version 4.4.1) package ggplot2 (Wickham (2016); version 4.4.0).

Table S1. Functional feeding group categories across different databases. CONUS (United States; Twardochleb et al., 2021), Freshwater Ecology excluding contributions made by Tachet et al. (2010) (Europe; Schmidt-Kloiber and Hering, 2015), Tachet (Europe; Tachet et al., 2010) and NIWA (New Zealand; Phillips and Smith, 2018) databases. With exception of CONUS, all databases fuzzy code group assignment (see Chevenet et al. (2006) for details of fuzzy coding).

	CONUS Database	**Freshwater Ecology Database (exc. Tachet Groupings)**	**Tachet's Assignments**	**NIWA Database**
Fuzzy Coded?	N	Y	Y	Y
Functional feeding groups	Predator Shredder Collector-gatherer Collector-filterer Herbivore Parasite	Active filter-feeders Gatherers/collectors Grazers/scrapers Miners Passive filter feeders Xylophagous taxa Other feeding types	Absorbers Deposit feeders Filter-feeders Parasites Piercers (plant/animal) Predators (carvers/ engulfers swallowers) Scrapers Shredders	Shredders Scrapers Deposit-feeders Filter-feeders Predators Algal piercers

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