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DOI
10.1016/B978-0-443-23898-7.00020-8

Publication date
2024

Document Version
Final published version

Published in
Afrotropical Streams and Rivers

Citation (APA)
Masese, F. O., Wanderi, E. W., Dalu, T., Chari, L. D., & McClain, M. E. (2024). Food web dynamics. In T. Dalu, & F. O. Masese (Eds.), *Afrotropical Streams and Rivers: Structure, Ecological Processes and Management* (pp. 519-557). Elsevier. https://doi.org/10.1016/B978-0-443-23898-7.00020-8

Chapter 20

Food web dynamics

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Introduction and overview

An understanding of energy sources and flow in aquatic ecosystems is a major facet of ecosystem ecology. Food webs capture the energy resources and trace their flow in a network of feeding ("trophic") interactions among species that co-occur in given habitats. Studies on food webs seek to quantify and analyze direct and indirect interactions among diverse species and their sources of nourishment. Thus, food webs encompass whole communities, including bacteria, fungi, plants, invertebrates and vertebrates. At their base, food webs have a detrital component, autotrophic component or both. The autotrophic component constitutes organisms such as plants or chemoautotrophic bacteria, which produce complex organic compounds from an external energy source (e.g., light) and simple inorganic carbon molecules (e.g., carbon dioxide). The detrital component constitutes detritus (dead particulate organic matter) that derives from the tissues of plants and animals. The autotrophic and detrital resources at the bases of food webs—commonly known as basal resources—are transferred to other trophic levels through feeding in a series of food chains of varying lengths. The basal resources provide the energy, organic carbon and nutrients necessary to fuel the metabolism of all other organisms, referred to as heterotrophs.

The communities that constitute a food web are organized in trophic levels or groups through which energy in the form of biomass is transferred using different strategies such as detritivory, herbivory, predation, omnivory, cannibalism and parasitism. In streams and rivers, biodiversity within each trophic level is very diverse, contributing to food web stability, complexity and interecosystem connectivity. The trophic resources or groups also experience remarkable spatiotemporal heterogeneity caused by seasonality, changes in ecosystem size (e.g., stream order), location on the fluvial continuum (e.g., upstream and downstream changes in river connectivity) and human influences such as land use and land cover changes, flow alteration, the introduction of exotic species and pollution or habitat degradation (Masese and McClain, 2012; Abrantes et al., 2013; 2014, Masese et al., 2015, 2018, 2024b).

Many classical studies and reviews have investigated various components of food webs in streams and rivers, including the trophic basis of production (e.g., Woodward and Hildrew, 2002; Pingram et al., 2012), terrestrial-aquatic connectivity (e.g., Nakano et al., 1999; Baxter et al., 2005; Ballinger and Lake, 2006; Benjamin et al., 2024, Chapter 14), processing of organic matter and its contribution to food webs (Cummins and Klug, 1979; Roach, 2013), the relative importance of different sources of energy and how these change with scale, stream size or location on the longitudinal gradient (Finlay et al., 2002; Hoeinghaus et al., 2007; Lau et al., 2009a; Cross et al., 2013; Masese et al., 2022) and seasonality (Junk et al., 1989; Roach and Winemiller, 2015), the role of resource subsidies (Nakano and Murakami, 2001; Paetzold et al., 2008; Marcarelli et al., 2011), food web characteristics, including food chain length (Power et al., 1996; Power and Dietrich, 2002; Post, 2002; Woodward and Hildrew, 2002; Lau et al., 2009b), and rates of primary and secondary production (Rosi-Marshall and Wallace, 2002; Davies et al., 2008; Cross et al., 2013; Benke and Huryn, 2017). Similarly, many theories or concepts have been developed to explain and provide a general framework for the structure and function of streams and rivers, and the earliest of these are the river continuum concept (RCC; Vannote et al., 1980), the flood pulse concept (Junk

Afrotropical Streams and Rivers. https://doi.org/10.1016/B978-0-443-23898-7.00020-8

et al., 1989), and the riverine productivity model (RPM; Thorp and Delong, 1994, 2002). While most of the existing models of riverine ecosystem functioning were developed based on findings from temperate streams and large tropical rivers, studies on food webs in tropical streams continue to gain interest and focus, not only because of the accelerating human disturbances but also because of emerging evidence that they might be functionally different from their temperate counterparts (e.g., Boulton et al., 2008; Wantzen et al., 2008; Boyero et al., 2009; Dudgeon et al., 2010; Boyero et al., 2011a, 2011b; Masese et al., 2015, Masese et al., 2022; Masese and Dalu, 2024, Chapter 1). In the ongoing discussions, comparisons have been made between temperate and tropical streams and rivers regarding organic matter processing by detritivorous shredders, food web structure and the major energy sources fueling secondary production.

Because of differences between tropical and temperate streams and rivers, there is growing evidence that the models of riverine ecosystem functioning developed in temperate regions may not apply to tropical systems. For instance, many studies in tropical headwater streams support the importance of autotrophic production as a major source of energy for aquatic consumers (March and Pringle, 2003; Mantel et al., 2004; Brito et al., 2006; Lau et al., 2008, 2009a, 2009b; Li and Dudgeon, 2008; Masese et al., 2022), which is contrary to RCC prediction for small temperate forested streams. Low diversity and abundance of detritivorous shredders have also been reported in most streams outside the north-temperate zone, e.g., in New Guinea (Yule, 1996), New Zealand (Winterbourn et al., 1981), tropical Asia (Li and Dudgeon, 2008), East Africa (Tumwesigye et al., 2000; Dobson et al., 2002; Masese et al., 2023), and the Neotropics (Greathouse and Pringle, 2006). Shredders are macroinvertebrates that break down coarse particulate organic matter into fine particulate organic matter, making it available to other macroinvertebrates and increasing the surface area-to-volume ratio for microbes (Masese et al., 2014a, 2024a, Chapter 17; Masese et al., 2024c). A global assessment of the distribution of shredders in streams has reinforced the findings on the low abundance and diversity in the tropics (Boyero et al., 2011a, 2011b, 2021), although some studies present contrary findings (e.g., Cheshire et al., 2005; Yule et al., 2009; Masese et al., 2014b). Tropical riverine food webs have also been described as having short food chains, exhibiting high omnivory and dominance of macroconsumers (Douglas et al., 2005; Coat et al., 2009; Yang et al., 2020). However, within the tropics, even with these emerging shared characteristics, there is great heterogeneity in the structure and functioning of river ecosystems (Boulton et al., 2008; Boyero et al., 2015; Tiegs et al., 2019). While some streams and rivers display a highly variable flow regime characterized by periods of intermittence, especially those in semiarid savanna systems in the lowlands, others in mesic or montane regions are more stable (Poff et al., 2006; Kennard et al., 2010; McClain and Masese, 2024, Chapter 28; Onyari et al., 2024, Chapter 10).

This chapter provides an overview of African riverine ecosystems regarding the structure, diversity, and intensity of trophic interactions and dynamics and how these differ spatially and temporarily. The chapter also explores the relative importance of major sources of energy and food web attributes in streams and rivers and how they have been impacted by human-mediated influences such as land use change. The specific questions being addressed include: (1) What are the major sources of energy supporting secondary production in streams and rivers? (2) What are the emergent characteristics of food webs in streams and rivers? (3) How do food webs in African streams and rivers differ or compare with those in other tropical and temperate systems? (4) What is the influence of human activities on these patterns? Though the information used to answer these questions is largely drawn from the literature on African streams and rivers, some studies have also been included on tropical streams and rivers in Asia, Australia, and South and Central America.

Trophic groups

Primary production

One of the fundamental processes occurring in riverine ecosystems is primary production, whereby plants (i.e., phytoplankton, macrophytes) and other autotrophs (e.g., certain bacteria) synthesize organic matter fix sunlight energy into organic matter or biomass through the process of photosynthesis (Dalu et al., 2024, Chapter 15; Fugère and Masese, 2024, Chapter 13; Mpopetsi et al., 2024a, Chapter 16). Primary production represents the foundation of food webs in terrestrial and aquatic ecosystems, providing energy essential for nourishing primary and secondary consumers. Primary productivity measures the rate at which photosynthetic organisms convert solar energy into organic matter (Pace et al., 2021). Quantification of productivity helps gauge the health and functionality of ecosystems and serves as an indicator of environmental changes.

Primary production in streams and rivers is controlled by light availability, nutrients, temperature, substrate type, hydrologic conditions or seasons, and the amount of suspended sediments, among other factors (Hill et al., 1995; Mulholland et al., 2001; Griffiths et al., 2013). These proximal factors are influenced by distal controls such as catchment land use, soil type or geology, vegetation and climate (Bernot et al., 2010). In temperate regions, primary productivity often follows a more pronounced seasonal pattern, with higher rates during spring and summer due to increased light availability and warmer temperatures (Dudgeon, 2011). In contrast, primary production in the tropics exhibits more consistent primary productivity throughout the year due to relatively stable high temperatures and higher solar radiation (Lévêque, 1995; Davies et al., 2008). Stream size or order and canopy cover strongly influence primary productivity at the local reach scale because they are linked to light availability and water temperature. Water clarity, depth, and vegetation cover determine the amount of light reaching the streambed. In clear and shallow waters with minimal shading, primary production is high due to light availability for photosynthesis. However, excessive turbidity or increased shading can reduce primary production by limiting light penetration. Under favorable light conditions, nutrients become the constraining factor for benthic periphyton accrual (Gagne-Maynard et al., 2017). However, primary production is predominantly light-limited in low-light areas, such as headwater streams and in deep and turbid large rivers.

Seasonality is another important determinant of primary production in streams and rivers because of its control on flow (discharge), water clarity and nutrient availability (Bernot et al., 2010; Griffiths et al., 2013; Masese et al., 2014b). Seasonal spates that actuate scour and sediment deposition in streams can reduce primary production during the rainy season (Griffiths et al., 2013). Similarly, higher turbidity levels during the rainy season can smother streambeds and limit the light availability for primary production. Conversely, primary production can be higher during the dry seasons because of the biomass accrual of primary producers in the benthos and increased water clarity. However, it can be limited by nutrients due to a lack of inputs from terrestrial sources.

The contribution of primary producers to river food webs largely depends on the amount of biomass accrued from primary production. Studies on primary production in African streams and rivers are very limited (Fugère and Masese, 2024, Chapter 13). Most studies focus on the composition and distribution of primary producers such as algae and macrophytes. Similarly, most of the studies that have investigated the contribution of primary producers to food webs in streams and rivers have used stomach contents to determine the food composition and feeding habits of consumers. Given the limitations of using stomach contents (discussed below) to determine the importance of different basal resources for food webs or consumers, some studies have used biomarkers such as fatty acids (e.g., Moyo and Richoux, 2018a; Dawson et al., 2020a) and stable isotopes analysis (e.g., Abrantes et al., 2013, 2014; Masese et al., 2015; Jackson et al., 2020; Soto et al., 2019; Bokhutlo et al., 2021; Masese et al., 2022; Benjamin et al., 2024, Chapter 14).

Detritivory and herbivory

Detritivory and herbivory by primary consumers play essential roles in nutrient cycling and food web stability. Detritivory is the frequent ingestion of detritus or decaying organic matter to meet consumers' nutritional and other requirements. Bacteria and plant or animal constituents can also meet a significant fraction of a detritivore's food requirements (Anderson, 1976). On the other hand, herbivory is feeding on living plant material. Herbivores may also consume algae or phytoplankton and appreciable detritus (Sanchez and Trexler, 2018). Unlike detritivory, meeting all the nutritional requirements from an exclusively herbivorous diet is difficult because the nutritional quality of food items varies and makes digestion and assimilation difficult because of structural and biochemical barriers (Newman, 1991; Choat and Clements, 1998; Sterner and Hessen, 1994; Mithöfer and Boland, 2012). Because herbivores are nutrient-limited, detrital inputs likely support their nutrition (Hall et al., 2001). Despite the prevalence of this view, there is increasing evidence suggesting that herbivory is common and is an important factor in vascular macrophytes and contributes significantly to both freshwater and marine food webs (Lodge et al., 1998; Valentine and Heck, 1999; Bakker et al., 2016). Moreover, because the nutritional requirements of freshwater herbivores and detritivores are difficult to distinguish, there are limited "true" herbivores in nature (White, 1985).

In streams, most plant biomass enters the food webs through the detrital pathway. Detritivores, such as certain species of fish, shredding insects and microorganisms, obtain the bulk of their energy from decaying plant matter and, in the process, help to break down complex organic materials and make them available for other organisms. Feeding on organic matter facilitates nutrient cycling, material decomposition, translocation, and primary production (Merritt and Cummins, 1996). The herbivory of phytoplankton by invertebrates and fish, as well as plant biomass by some invertebrates, birds, and mammals, is a significant energy source for primary consumers in streams and rivers. The most prominent herbivore in African rivers is the semiaquatic common hippopotamus (*Hippopotamus amphibius*), which feeds on vast amounts of terrestrial vegetation and deposits them in rivers through egestion and excretion. By doing so, hippos subsidize riverine food webs through increased primary production and direct consumption of hippo dung by invertebrates and fish (Masese et al., 2015, 2022; McCauley et al., 2015; Pringle, 2017; Voysey et al., 2023). Secondary production of primary consumers supports higher trophic levels, including predatory invertebrates, fishes, amphibians, reptiles, birds and mammals.

Secondary and tertiary consumers

In African streams and rivers, the dynamics of food webs are intricately woven with the presence of secondary and tertiary consumers, which play critical roles in maintaining ecological balance and biodiversity. These consumers are pivotal in transferring energy across different trophic levels, controlling the population sizes of other species, and shaping the structure of their ecosystems. Secondary consumers in these aquatic environments primarily include various fish species and amphibians that feed on invertebrates and smaller fish. For example, many cyprinids, such as *Barbus* (*Enteromius*) and *Labeobarbus* spp., are insectivores that prey on insects and aquatic larvae, acting as a natural control mechanism for these populations. Similarly, certain amphibians consume vast amounts of insects, helping regulate their populations and preventing overpopulation.

Tertiary consumers are typically apex predators in these ecosystems and include larger fish species such as tigerfish (*Hydrocynus vittatus*), Goliath tigerfish (*Hydrocynus goliath*), Nile perch (*Lates niloticus*), Electric catfish (*Malapterurus electricus*), and African pike (*Hepsetus odoe*), Nile crocodile (*Crocodylus niloticus*), and some birds such as the African Fish-Eagle (see O'Brien et al., 2024, Chapter 18; Keates and Reid, 2024, Chapter 19). These consumers are at the top of the food chain and have a profound effect on the population dynamics of secondary consumers. For instance, the Nile crocodile, one of Africa's renowned river predators, feeds on various fish, amphibians, and occasionally large mammals, including humans, that venture too close to the water's edge.

Models and approaches used to quantify trophic interactions

Functional trait, diversity and responses

Community ecology has increasingly incorporated the functional trait, diversity and response framework to provide a mechanistic understanding of the structure of communities, ecosystem processes and general patterns shaping communities, making it a useful tool for exploring the adaptability and vulnerability of communities to environmental stressors (Villéger et al., 2017). In comparison to purely taxonomic studies, a functional trait-based approach allows data to be compared without the constraints of geography, climate or highly divergent taxa (Bower and Winemiller, 2019a, 2019b), can support understanding of processes governing regional community assembly (Pease et al., 2015) and guide regionally specific management and conservation of aquatic systems (Sternberg and Kennard, 2013). The functional trait approach has been used to understand community assemblages in tropical regions at different spatial scales, including environmental filtering and limiting, aquatic—terrestrial linkages and environmental gradients (Walsh et al., 2022). Thus, functional responses are mostly used to understand how an organism's feeding rate changes in response to the density of its prey, and this is important for understanding the dynamics of predator—prey interactions and food webs. For instance, they make us (i) understand how changes in prey density might affect vertebrate and invertebrate feeding rates, and this information would help us in developing aquatic management plans in the world of alien species invasions, (ii) assess and understand the impact of alien invasive species on native vertebrate and invertebrate communities, since these alien invasive species tend to compete with native organisms for food resources and habitat. Thus, functional responses can predict how this competition will affect native species' growth and survival, and (iii) functional responses aim to understand the role of predators in controlling prey populations, as this would make us understand how predators could help control and keep prey populations in check. Furthermore, using trait-based approaches, broadly describing communities' functional diversity, presents a more relevant and better description of community patterns because these approaches consider both species functional traits and their role in an ecosystem (Mpopetsi and Kadye, 2023). Some studies have unravelled discrepancies regarding important traits in facilitating the establishment success of non-native fishes, and the impacts of species invasions on local functional diversity appear to be context-dependent (Qin et al., 2020). Therefore, identifying context-specific functional traits conferring potential advantages for species in disturbed environments can better inform the conservation and management of these ecosystems (Mpopetsi and Kadye, 2023).

Within the African river ecosystems, the use of functional traits, diversity, and responses is limited compared with other regions of the world. Afrotropical river systems support diverse ecological communities, including many taxonomically undescribed species, yet few studies have been undertaken in this region, and they remain poorly understood (Walsh et al., 2022). Functional diversity and environment patterns documented show unique patterns of functional richness that may assist in improving understanding of responses, vulnerabilities, and conservation needs in Afrotropical systems (Walsh et al., 2022). For example, working in a South African river system on the banded tilapia *Tilapia sparrmanii*, Mbedzi et al. (2020) found that the fish consumed microplastic even when they were relatively rare in their environment. Consumption rates were negatively related to concentrations supplied and conducive to a saturating Type II (i.e., inversely-density-dependent) functional response. In another study, Alexander et al. (2014), when testing functional responses of an invasive largemouth bass (*Micropterus salmoides*), with a native Cape kurper *Sandelia capensis*, and an emerging invader, the sharptooth catfish *Clarias gariepinus*, with the native river goby *Glossogobius callidus* in South Africa using tadpoles *Hyperolius marmoratus* as prey found that the invaders consumed significantly more than natives. Attack rates at low prey densities within invader/native comparisons reflected similarities in predatory strategies; however, both invasive species displayed significantly higher Type II functional responses than the native comparators driven by significantly low prey handling times by invaders, resulting in significantly high maximum feeding rates. Alexander et al. (2014) then highlighted that the high functional responses of these invaders are thus congruent with, and can predict, their impacts on native communities.

Hocutt and Johnson (2001), working on a first seasonal survey of fishes of the Kavango River along the Angola and Namibia border, reported that the data indicated a pronounced structural and functional response of the fish community in relation to the alternating flood and drought conditions in the river. Thus, the catch per unit effort and diversity were high during peak flooding (i.e., May and June), and low during the month of least flow (i.e., November). The piscivorous cichlid and tigerfish fish species reproductive strategies showed *k*−*k*-selection during peak flooding, and many cyprinids and other invertivore fish (i.e., *r*-selected taxa) were in relative synchrony with flooding and the stimulation of littoral zone plant growth. Herbivores had low relative abundances during peak flooding, which could potentially be related to the swamping of the system with young-of-the-year *r*-selected invertivores (Hocutt and Johnson, 2001).

Walsh et al. (2022), using functional trait-based approaches to describe the functional traits and diversity of fish assemblages in the Republic of Congo, found moderate to weak community nestedness and various traits associated with resistance and feeding, which were significantly correlated with habitat variables in the upper and lower basins, respectively. Environmental filtering was an important process of community assembly at the basin scale, with nonrandom processes being evident in the upper basin and high turnover being noted in the lower basin. High functional turnover between headwaters and lower reaches suggested different functional strategies in fish assemblages between localities along the fluvial river gradient. In contrast to expectations derived from temperate lotic systems, functional richness was comparable across both basins, suggesting that the region's headwater zones harbor substantial functional diversity, especially when considering upstream catchment sizes (Walsh et al., 2022). Lastly, Mpopetsi and Kadye (2023), using the Great Fish River system in South Africa, employed functional trait-based approaches to explore patterns associated with the co-occurrence of multiple non-native fish species, and they determined 19 functional traits that defined two broad ecological attributes (i.e., habitat use and feeding) for 13 fish species (i.e., eight natives, five non-natives). From a functional diversity perspective, there were no significant differences in most functional diversity indices between native and non-native species. Despite the interspecific variation in body morphology-related traits, Mpopetsi and Kadye (2023) found no clear separation between native and non-native species based on the ordination analysis of the functional traits. The weak species-trait-environment relationship observed in this study suggests that environmental filtering was likely a poor determinant of functional trait structure within the Great Fish River, with flow modification having likely weakened the relationship between species traits and environment as has been shown in other systems (Mpopetsi and Kadye, 2023).

Gut contents analysis

The earliest studies on energy sources and flow in African riverine food webs mostly focused on dietary food composition and feeding habits of fishes determined by analysis of stomach contents. Corbet's (1961) study on the non-cichlid fishes of Lake Victoria and influent rivers and Jackson's (1961) study on *Hydrocynus vittatus* in the Zambezi River are some of the pioneering works on the feeding habits of riverine fishes in Africa. Other studies are those of Groenewald (1964a, 1964b), who described the feeding of *Clarias gariepinus* and *Eutropius clepressirosrris* in the Transvaal region in South Africa. These and other works have shown that the feeding regime of fishes is extremely variable depending on the locality, age or size and the presence of other fishes in the same habitat. Corbet (1961) indicated that the diet may also vary depending on the season and availability of food. In nature, fish display different feeding habits, including those that feed on plankton, insect larvae, detritus, molluscs, organic matter and other fish. Fishes are also opportunistic and feed on what is available at the time. Hulot's (1950) study was one of the earliest to describe the feeding habits of many African fishes and classified them as herbivores, planktivores, predators or omnivores. In terms of dietary food composition, studies on stomach contents have shown that filamentous algae, diatoms, organic matter and insects (larvae and nymphs) are the most important food items for fishes in African streams and rivers (Corbet, 1961; Balirwa, 1979; Eccles, 1985; Kraiem, 1996; Nakangu et al., 2023). In a study of six *Barbus* (*Enteromius*) species in the Lake Victoria basin, Balirwa (1979) indicated that these species are omnivorous, and their food includes organic matter (debris), diatoms, algae, insects and molluscs. During a survey of the diet of *Barbus aeneus* in a South African dam, Eccles (1985) observed that detritus formed about 50% of the diet. This, however, changed to copepods, cladocerans and arachnids when the waters became clear, and prey could be located visually. While describing the diet of *Barbus callensis* in streams and a reservoir in Northern Tunisia, Kraiem (1996) noted that the main diet mainly consisted of insect larvae and plant fragments, but large fishes also fed on smaller fish. Although most fishes are secondary consumers, some are primary consumers and feed on primary producers (algae and macrophytes), such as the herbivorous cichlids.

Like fishes, several studies have investigated the food composition and feeding habits of benthic macroinvertebrates in African streams and rivers. In a study in a second-order stream in the Western Cape, South Africa, King et al. (1987) noted that fine particulate organic matter (FPOM) was the predominating food item in the gut contents of macroinvertebrates. In another South African study in the middle and lower reaches of the Buffalo River, Eastern Cape, Palmer et al. (1993) analyzed the foregut contents of macroinvertebrates and similarly noted that the food contents of 12 species were dominated by fine amorphous detritus. In the Kenyan central highlands and the headwaters of the Mara River basin, Dobson et al. (2002) and Masese et al. (2014a), respectively, also reported that FPOM dominated food items in the guts of macroinvertebrates. The predominance of FPOM or fine detritus in the guts of stream macroinvertebrates is not unique to the Afrotropics. In Australia, a study of stonefly larvae reported that 13 out of 19 species had gut contents consisting of between 69% and 100% detritus (Sephton and Hynes, 1983). Fine detritus was similarly important in the diets of Australian oligoneuriid and siphlonurid mayflies (Campbell, 1985), and in the diets of 127 macroinvertebrate taxa from two Victorian rivers (Chessman, 1986). Studies from the Neotropics have also reported FPOM as being the most consumed food item by stream macroinvertebrates (Tomanova et al., 2006; Ceneviva-Bastos and Casatti, 2014; Silveira-Manzotti et al., 2016; Rosas et al., 2020). Despite the importance of FPOM to macroinvertebrate diets reported in these studies, there are often significant variations in gut contents caused by seasonality, sites (locations) and macroinvertebrate size. In addition to FPOM, macroinvertebrates also feed on a wide selection of food items that include filamentous algae, diatoms, cyanobacteria, leaf fragments, and animal remains (Palmer et al., 1993; Masese et al., 2014b). These food items may be consumed in smaller amounts than FPOM, but their level of assimilation and incorporation into the biomass of consumers is higher because of their superior quality (low C:N ratio) and palatability.

While gut content analysis is considered standard practice for identifying food sources for consumers and can provide direct evidence of an organism's potential food resources (Hyslop, 1980; Foley et al., 2017), they are not very effective in determining the number of different food items assimilated and incorporated into biomass. Gut contents also provide a snapshot of food items consumed during sampling. Yet, consumers' feeding habits can change spatially and seasonally depending on several factors, including seasonality in flow and environmental conditions (Corbet, 1961; Nakangu et al., 2023). For this reason, biomarkers such as fatty acids (Iverson, 2009; Kelly and Scheibling, 2012) and stable isotopes (Peterson and Fry, 1987; Fry and Sherr, 1989; McCutchan et al., 2003) are used to provide time-integrated information on the long-term assimilation of dietary food sources and trophic interactions (Thompson et al., 2012; Wood et al., 2016).

Use of biomarkers in food webs

Biomarker techniques such as fatty acid analysis, stable isotope analysis or DNA barcoding are powerful tools for unravelling trophic interactions within riverine food webs (e.g., Kato et al., 2004; Kautza and Sullivan, 2016). These techniques offer valuable insights into various aspects of ecosystem dynamics, including dietary preferences, trophic position, energy transfer, dietary specialization, and the influence of environmental factors (Richoux et al., 2018). Compared with traditional methods such as gut content analysis or natural history observations, biomarker techniques provide a higher resolution and more precise understanding of the complex relationships within riverine food webs.

Use of fatty acids

The use of fatty acids in trophic studies has seen a notable increase over the past few decades, largely due to their higher resolution and sensitivity compared with other methods. Fatty acids are fundamental building blocks of biological organisms, playing pivotal roles in various cellular processes such as energy storage, membrane structure, and signalling pathways. The use of fatty acids as tracers in food webs is made possible by the fact that primary producers synthesize certain fatty acids, especially polyunsaturated fatty acids (PUFAs), that are usually transferred predictably to primary consumers and higher trophic levels (Dalsgaard et al., 2003; Budge et al., 2006). Their heterogeneous nature and high diversity enable them to be incorporated into different tissues and organisms, reflecting the intricacies of dietary sources and dynamics (Iverson et al., 2004; Torres-Ruiz et al., 2007). The diverse composition and distinct origins of fatty acids make them valuable tools for assessing consumer diets (Iverson et al., 2004). Consequently, fatty acid analysis offers insights into consumers' dietary preferences and trophic interactions within ecosystems. However, much of the research in this field has been conducted in developed countries due to the high costs and level of expertise required. Nevertheless, a growing number of studies in African countries, particularly in South Africa, have begun to incorporate this tool to investigate trophic dynamics in rivers.

Fatty acid analysis has been employed for various purposes in ecological research in Africa, providing insights into trophic dynamics and ecosystem functioning of rivers. For instance, studies conducted in the Kowie River, South Africa, have utilized fatty acid analyses to investigate reciprocal trophic subsidies between streams and riparian areas (Dalu and Froneman, 2014; Richoux et al., 2015; Dalu et al., 2016; Moyo, 2016; Moyo et al., 2017; Chari et al., 2020). A common finding is the enrichment of rivers with essential highly unsaturated fatty acids (Moyo and Richoux, 2018a), which are lacking in terrestrial ecosystems, while adjacent riparian landscapes also supply essential fatty acids to aquatic ecosystems through infalling arthropods and plants (Moyo et al., 2017). Riparian predators such as flying insects (Chari et al., 2018a, 2018b), spiders (Chari et al., 2020), and frogs (Sikutshwa, 2015) have been shown to have high concentrations of these highly unsaturated essential fatty acids, suggesting their suitability as natural sampling devices for monitoring nutrient transference from rivers to adjacent terrestrial uplands.

Furthermore, Moyo et al. (2017) revealed that seasonal and spatial fluctuations in biomass exchange between riverine and terrestrial ecosystems are decoupled from the quality of the subsidies, as the quantity of physiologically key essential fatty acids is highly variable. This highlights the importance of considering both the quantity and quality of trophic subsidies. Additionally, fatty acid analyses have shed light on the dynamic width of riverine trophic subsidy zones, demonstrating the diffusion of aquatically derived subsidies into riparian habitats (Chari et al., 2020). By analyzing fatty acid markers, researchers have identified the influence of river proximity on the dietary contributions of aquatic insect prey to riparian spiders, offering valuable insights into cross-ecosystem trophic linkages (Chari et al., 2020).

Moreover, investigations into the dietary niches of odonates in South African river systems have utilized fatty acid to infer feeding patterns (Chari et al., 2018a, 2018b). These studies revealed niche separation among species, foraging guilds, and size classes, highlighting the role of body size, foraging behavior, and environmental conditions in shaping dietary preferences (Chari et al., 2018a, 2018b). Apart from studies on invertebrates, fatty acid analysis has also been instrumental in examining the impact of hippo defecation on aquatic ecosystems, revealing alterations in basal resource pools and shifts in trophic dynamics (Dawson et al., 2020a). Additionally, studies on the freshwater mullet across river-estuary interfaces have utilized fatty acid analysis to explore ontogenetic and seasonal variations in diet, emphasizing the dietary flexibility of this species and the importance of invertebrate-derived prey (Carassou et al., 2017).

These studies collectively demonstrate the versatility and utility of fatty acid analysis in ecological research, providing valuable insights into trophic interactions, nutrient fluxes, and ecosystem dynamics in diverse aquatic environments, as evidenced by the multispecies study done in the Kowie River, South Africa (Richoux et al., 2015). From a management perspective, trophic studies such as these have the potential to show how differences in land use can influence the quality and quantity of subsidies to and from riverine ecosystems. For example, research in the Lake Victoria catchment revealed distinct fatty acid profiles associated with different land use activities in the upstream catchment, reflecting variations in the source and quality of organic matter discharged by rivers (Ngugi et al., 2017).

Despite significant progress in using fatty acid biomarkers in trophic studies in Africa, more baseline data across a wider climatic range are needed to improve the reliability of results. Currently, most biomarkers have been identified from studies in the developed world and often in marine studies. For instance, some taxa of microalgae collected from the Northern Hemisphere are known to synthesize large amounts of highly unsaturated fatty acids such as eicosapentaenoic acid (EPA; 20:5ω3) and docosahexaenoic acid (DHA; 22:6ω3) (Gladyshev, 2019), of which most terrestrial plants contain only trace amounts (Hixson et al., 2015; Taipale et al., 2015). Studies in Kowie River confirmed that 20:5ω3 was indeed highly abundant in freshwater ecosystems, but the same could not be said for 22:6ω3, which was not very abundant (or was undetected in many consumers) and hence not a good biomarker for African freshwater studies (e.g., Moyo et al., 2017). Furthermore, interpreting variations in fatty acid profiles in African aquatic ecosystems requires accounting for the diverse array of species and environmental conditions present. Integrating fatty acid analysis with other biomarker techniques, such as stable isotope analysis or DNA metabarcoding, can enhance the accuracy and reliability of dietary assessments (e.g., Moyo, 2016; Chari et al., 2018a, 2018b), but adaptation to African ecosystems is necessary. Long-term monitoring programs and experimental studies in African aquatic ecosystems are needed to provide valuable insights into the temporal dynamics of fatty acid profiles and their responses to environmental change. Replicated studies using multiple species across different macro-habitats will further help us understand how fatty acid biomarkers vary in the environmental context.

Use of stable isotopes

Developments in using natural abundances of stable isotopes (particularly of nitrogen and carbon) in ecological studies have profoundly influenced how ecologists study energy flow and trophic structure (Michener and Lajtha, 2008). They are considered steady, time-integrated tools for considering the effective assimilation of dietary items in organisms (Post, 2002). Isotopic signatures in tissues of slow-growing or long-lived organisms may require several weeks to months to turn over, thereby describing long-term trophic relationships (Vander Zanden and Rasmussen, 1999; Hadwen et al., 2010a).

Stable isotope analyses (SIA) of carbon (^{13}C:^{12}C), nitrogen (^{15}N:^{14}N), sulphur (^{34}S:^{32}S), hydrogen (^{2}H:^{1}H), and oxygen (^{18}O:^{16}O) represent useful tools in food web studies and complements stomach content analysis when investigating trophic dynamics in aquatic ecosystems (Davis et al., 2012; Mofu et al., 2023). SIA has been used widely to characterize consumer feeding habits and the relative importance of terrestrial versus aquatic energy sources (Peterson and Fry, 1987; Michener and Kaufman, 2007). SIA can uncover many important feeding links between consumers and their primary food sources (Jepsen and Winemiller, 2002; Phillips and Eldridge, 2006) as well as effectively describing the ecological niche an organism occupies (Bearhop et al., 2004). SIA has also been used in streams and rivers to study local watershed influences on energy sources (Ojwang et al., 2007; Winemiller et al., 2011). Ratios of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes have also been used to examine for variations in food web structure across longitudinal fluvial gradients (e.g., Hoeinghaus et al., 2007; Saito et al., 2007; Hadwen et al., 2010b) as well as in relation to anthropogenic allochthonous inputs from the watershed (e.g., Saito et al., 2008). The $\delta^{15}N$ signature has been used as a tracer of biomagnifying persistent pollutants such as PCB and methylmercury in aquatic pelagic food webs (e.g., Cabana and Rasmussen, 1994).

Stable C isotope has proved effective in the study of aquatic food webs where there are marked differences in the isotope signatures of the major primary sources (Hadwen et al., 2010a); whether the major source of organic matter to a stream or river are the $C_{3,}$ C_4 or CAM plants (Marshall et al., 2007). These characteristics are important when the stable isotope approach is compared with analyses of gut contents, which only provide a snapshot of the feeding habits of an organism (Lau et al., 2009a, 2009b). With the realization that autochthonous algal production might be the primary energy source in streams of many tropical biomes, identifying its $\delta^{13}C$ signature presents some challenges. Variation in algal $\delta^{13}C$ largely determines the overlap between allochthonous and autochthonous sources in freshwaters (Finlay and Kendall, 2007). Algal $\delta^{13}C$ can have a range that exceeds 15‰ within a site because of variations in water flow (Trudeau and Rasmussen, 2003; Singer et al., 2005), biomass (Hill and Middleton, 2006), dissolved CO_2 concentrations and $\delta^{13}C$ of dissolved inorganic carbon (Finlay, 2004). Seasonal variation in source signatures has also been reported in riverine ecosystems where environmental conditions are highly dynamic (Hadwen et al., 2010a).

Many studies have used fatty acids and stable isotope analysis to study different aspects of food webs in African streams and rivers (Table 20.1). These include identifying the major sources of energy (autochthonous vs. allochthonous) fuelling metazoan production (Bokhutlo et al., 2021; Masese et al., 2015, 2022), the dietary patterns of consumers, including ontogenetic shifts (Gerber et al., 2023), the influence of human activities, including land use change, on trophic resources and food web structure (Masese et al., 2014b), and reciprocal flows of energy transfer between terrestrial and riverine ecosystems (Moyo and Richoux, 2018a, 2018b, 2022; Chari et al., 2020).

Use of DNA-based methods

Traditionally, species' diets have been identified through direct observation of predation or by analyzing stomach, gut, or fecal contents (Caryl et al., 2012; Reñones et al., 2002), along with stable isotopes and fatty acids. These methods have limitations: morphological analysis is time-consuming and requires taxonomic knowledge, as prey items can be difficult to identify due to digestion (Sheppard & Harwood, 2005), while stable isotopes and fatty acids are invasive and not prey-specific (Bradshaw et al., 2003; Iverson et al., 2004). DNA-based approaches, like metabarcoding, have emerged to address these challenges, improving species identification, including of rare and cryptic species and linking different life stages (Packer et al., 2009). Unlike morphological methods or stable isotopes, DNA barcoding provides species-level taxonomic resolution, giving a clearer picture of prey diversity (Granquist et al., 2018; Jeanniard-du-Dot, et al., 2017). Metabarcoding, which is the most common method, uses high-throughput sequencing (HTS) and universal primers to target multiple prey species (Ruppert et al., 2019; Wu et al., 2023). HTS processes hundreds of samples simultaneously, each distinguished by unique barcodes, with sequences matched to reference databases (GenBank, Barcode of Life Data System, Greengenes) using a 95% similarity threshold (Ruppert et al., 2019; Traugott et al., 2021; Wu et al., 2023).

Despite the promise offered by the use of DNA-based approaches in ecological studies, they face some challenges when applied to study the diet of aquatic organisms (de Sousa et al. 2019): (a) the difficulty to use noninvasive methods, such as collecting feces or pellets; (b) the rarity of an opportunistic encounter of a recently deceased animal to access its gut content; and (c) the less likelihood of a direct observation of feeding interactions than in the terrestrial environment. Nevertheless, several metabarcoding studies have been done on aquatic taxa and the number continue to rise (reviewed by de Sousa et al., 2019). However, we have not be able to find a study that has used barcoding techniques to study the diets of consumers in African aquatic systems.

Influence of river typology on trophic dynamics

Understanding the major sources of energy fuelling ecosystems has long remained a foundational and fundamental question in ecology. Since Linderman's classical work (Lindeman, 1942) and his coinage of the concept of trophic dynamics, there has been enormous interest in understanding energy sources and transfer in ecosystems. Trophic dynamics in

TABLE 20.1 Examples of studies in African streams, rivers and estuaries that have used fatty acids and stable isotope analysis in food web studies.

Biomarkers	Study aim or objective	Examples of studies
Stable isotopes	- Dietary patterns of African tigerfish (*Hydrocynus vittatus*)	Gerber et al. (2023)
	- Determining the relative importance of terrestrial subsidies mediated by large mammalian herbivores (wildlife and livestock) for riverine food webs	McCauley et al., (2015), Masese et al. (2015, 2022)
	- Estimation of proportions of autochthonous and allochthonous food resources assimilated by consumers	Benstead and Pringle (2004), Soto et al. (2019), Bokhutlo et al. (2021), Masese et al. (2022)
	- Effect of land use on the relative importance of different sources of energy for riverine consumers	Masese et al. (2015)
	- Determine the spatial and temporal changes in trophic/food web structure	Abrantes et al. (2014)
	Determine the influence of land use and other stressors (e.g., climate) on trophic structure	Masese et al. (2014b), Jackson et al. (2020)
Fatty acids	- Consumer diets and relative assimilation of autochthonous versus allochthonous food resources	Moyo and Richoux (2018a,2018b)
	-Nutritional quality of basal resources	Richoux et al. (2018)
	- Cross-boundary aquatic-terrestrial energy fluxes and linkages	Chari et al. (2020), Moyo and Richoux (2022)
	- Sources of particulate and sedimentary organic matter and its input into the food web	Shilla and Routh (2017)
	- Spatial and temporal differentiation of diets of consumers	Richoux et al. (2014)
	- Determining the relative importance of terrestrial subsidies mediated by hippos for riverine food webs	Dawson et al. (2020a,2020b)

Afrotropical rivers are highly heterogeneous, determined by highly diverse biological communities and complex trophic webs with a high degree of interaction.

The earliest studies on energy sources and flow in African aquatic ecosystems focused on the largest and ecologically significant Great Lakes. This includes the study on Lake Victoria, conducted nearly a century ago (Graham, 1929), which noted the diverse fish communities, their niches, and resource partitioning. The research attention devoted to the ecology of these lakes is understandable, given the interest they have generated over the years in the speciation and evolution of major fish species, groups such as the cichlids. Early research into the lakes' ecology also considered the influent rivers, and these were some of the earliest studies on the feeding habits and food composition of fishes in African rivers (e.g., Corbet, 1961). Similar to the African Great Lakes, large African rivers that are important for fisheries, such as the Niger, Nile, Zaire and Zambezi, have received more research attention than headwater streams and medium-sized rivers.

Headwater streams

Data on food web structure and trophic dynamics of low-order headwater African streams are limited. Yet, these streams are increasingly influenced by anthropogenic activities and are being modified before we fully understand their functioning. Thus, understanding the food web structure and the major energy sources fuelling metazoan production in these systems is of great ecological and conservation importance.

Food webs in low-order (first-third order) headwater streams are postulated to be more reliant on allochthonous energy sources because shading by riparian vegetation limits instream primary production (Vannote et al., 1980). Despite this prediction, many studies in tropical streams have highlighted the importance of autotrophic production for consumers (March and Pringle, 2003; Mantel et al., 2004; Lau et al., 2009a, 2009b; Neres-Lima et al., 2016; Cortés-Guzmán et al., 2022). Similarly, although limited, studies have shown that autochthonous resources are more or equally important in supporting food webs in Afrotropical headwater forested streams. In the upper Mara River basin, analysis of stable C and N isotopes determined that periphyton, including diatoms and cyanobacteria, contribute nearly 50%, on average, of energy for macroinvertebrates in forested streams (Masese et al., 2022). In a study in Ranomafana National Park and adjoining areas in Madagascar, Benstead and Pringle (2004) were unable to determine the relative importance of allochthonous and autochthonous carbon for macroinvertebrates because of the ambiguous $\delta^{13}C$ signature of epilithic biofilms and CPOM in forested streams. However, they reported increased use of biofilm as a food resource for macroinvertebrates in agriculture streams. Apart from shading by riparian vegetation, the limited contribution of allochthonous resources to food webs in low-order tropical streams has also been linked to the low diversity of shredders that are responsible for the breakdown of coarse organic matter into fine detritus, making it available to other consumers (Masese et al., 2024c, Chapter 12; Boulton et al., 2008; Boyero et al., 2011a, 2011b; Boyero et al., 2015). Many studies in African streams have reported a paucity of shredders (e.g., Tumwesigye et al., 2000; Dobson et al., 2002; Abdallah et al., 2004; Masese et al., 2023), but other studies have reported a high diversity and abundance of shredders (Masese et al., 2014a) that are playing important roles in organic matter processing (Masese et al., 2024c, Chapter 12).

Large rivers

The relative importance of different energy sources fuelling large river food webs has been an active topic of discussion for nearly half a century. In large rivers worldwide, it is estimated that autochthonous production is the major carbon source supporting their food webs, except in systems with high turbidity (Roach, 2013). Tropical rivers export high amounts of allochthonous carbon as suspended sediments to the oceans with limited contributions from autochthonous production (Coynel et al., 2005). Similarly, fishes in these systems feed on large quantities of detritus (Bowen, 1983), and detritivorous fish and associated food webs are generally thought to be filled mainly by allochthonous energy resources. However, a growing body of evidence has demonstrated that the importance of algae and other autochthonous food sources, either directly or indirectly, are more important than traditionally thought, even in systems with large inputs of terrestrial organic matter (Thorp and Delong, 2002; Masese et al., 2015; Brett et al., 2017).

As already indicated above, many studies aiming to determine the degree to which aquatic (autochthonous) and terrestrial (allochthonous) primary production fuel consumers in Afrotropical rivers have often used the stomach contents of fishes. Most of these studies show that fishes ingest large amounts of detritus (Corbet, 1961; Ochumba and Manyala, 1992), but the fraction of this resource that is assimilated and incorporated into animal biomass cannot be inferred from conventional stomach content analysis. As a result, many recent studies have used stable isotope ratios of C, N, H and O to assess trophic linkages and determine the trophic basis of secondary production.

Soto and others (2019) used C, N and H stable isotopes to determine the relative importance of allochthonous versus autochthonous food resources in the Congo River. They determined that terrestrial C3 plants (allochthonous sources) contributed approximately 74% and 52% to fish and invertebrates in the river, respectively. The contribution of C3 plants to the food webs was either indirectly through ingesting aquatic invertebrates and other fishes or directly through consuming terrestrial animals and plants (Soto et al., 2019). The limited contribution of autochthonous food resources to invertebrates (~7%) and fishes (~20%) was attributed to high turbidity and low primary production reported during the dry season (Descy et al., 2017).

Dryland rivers

It has been estimated that over 40% of the world's land mass is semiarid, and another 25% is arid or hyper-arid (Davies et al., 1994; Middleton and Thomas, 1997). These drylands are drained by many intermittent streams and ephemeral rivers (IRES). The sparse vegetation of IRES catchments and riparian zones certainly influences the quantity and quality of terrestrial inputs to rivers, as will the unpredictable and highly variable nature of their flow regimes (Puckridge et al., 1998; Young and Kingsford, 2006). The characteristic flow extremes of IRES are also considered the major drivers of "boom or bust" productivity cycles, especially in systems with extensive floodplains and associated wetland systems (Walker et al., 1995; Kingsford et al., 1999). The high turbidity of some IRES systems also has a marked influence on the distribution and productivity of algae and other aquatic plants (Bunn et al., 2003).

In Africa, IRES systems drain 66% of the continent (Middleton and Thomas, 1997), and most occur in southern and northern Africa. Despite their vast expanse, many African IRES are unexplored, and their structure and functioning are poorly understood because of limited data. Primary production in dryland rivers is mainly limited by nutrient availability and high turbidity (Grimm et al., 1981; Bunn et al., 2006). IRES systems are also prone to flooding from episodic rain events. Like humid rivers with expansive floodplains, the duration of inundation of dryland river floodplains affects decomposition, nutrient cycling and the biomass and productivity of plants and animals (Davies et al., 1994; Boulton et al., 2006). Floods in Namibian rivers carry vast quantities of organic matter, which are deposited in the lower reaches and greatly contribute to the productivity of floodplain soils (Jacobson et al., 1995, 2000a, 2000b). Inundated floodplain areas of dryland rivers can also be areas of increased primary production stimulated by shallow, warm and nutrient-rich waters. For instance, in the Central Delta of the Niger River, abundant phytoplankton blooms dominated by the diatom *Melosira* are known to occur (Welcomme, 1986a).

Because of water availability, riparian vegetation of dryland rivers is often markedly distinct from the surrounding catchment. In dryland rivers of western Namibia, this strand of vegetation is called ‘linear oases’ (Jacobson et al., 2000a). In these systems, riparian inputs (leaves and invertebrates) represent a potentially important source of organic carbon for river food webs, though annual rates are considerably less than those in more temperate or tropical systems (Bunn et al., 2006). Although dryland rivers can have substantial amounts of large wood (Jacobson et al., 1999), many desert rivers in southern Africa lack wood and debris dams (Davies et al., 1995). Massive episodic floods in these systems can demolish whole reaches of riparian forests, which, in turn, can influence terrestrial inputs (leaves and invertebrates) and the supply of wood to the channel (Jacobson et al., 1995).

Although data on the relative importance of autochthonous versus allochthonous food resources in dryland rivers in Africa are limited, there is ample evidence to suggest that autochthonous inputs may not be such an important source of carbon for consumers (e.g., Jones et al., 1997; Vidal-Abarca et al., 2001; Bunn et al., 2003). First, the limited extent of riparian vegetation in many dryland rivers implies limited input of terrestrial organic matter for riverine food webs (e.g., Velasco et al., 2003). Secondly, extreme flooding can significantly reduce the storage of leaf litter and its availability to consumers (Vidal-Abarca et al., 2001). Thirdly, riparian vegetation in dryland areas often produces litter of low nutritional quality (Francis and Sheldon, 2002) and may make the leaves unpalatable to invertebrates. Shredder densities in arid and semiarid stream systems are typically low (Davies et al., 1994), and leaching, microbial respiration and physical breakdown are likely to be the most important processing agents of coarse organic matter.

Fish species in African dryland rivers of Africa such as the Orange, Niger and the Nile are depauperate compared with those of mesic rivers such as the Congo and Zambezi. Studies on the feeding habits of fish in these rivers show a lack of specialized feeding niches. Fish of the Orange River display a wide spectrum of feeding habits, and most would be considered omnivorous (Skelton, 1986). In the Niger River, the feeding habits of fish are strongly influenced by flooding and feeding is either reduced or suspended during the dry season (Welcomme, 1986b). Exceptions are zooplanktivorous fish, which feed during slack water when their food is concentrated. There is a stepped growth of some fish in the Centre Delta of the Niger associated with annual flooding, and interannual variations in growth are associated with flood intensity and duration (Welcomme, 1986b).

Studies have used stable isotope analysis to infer the relative importance of different basal resources for food webs in African dryland rivers. In the Lower Okavango Delta, in the Boro and Boteti rivers, Bokhutlo et al. (2021) found that seston—which was FPOM consisting of algae, cyanobacteria, and macrophyte tissues—and C4 grasses were the major source of energy supporting most fish species. During the dry, when flows were minimal and access to the floodplain restricted, shrinkage in aquatic habitats resulted in greater reliance of fishes on local sources of production (seston), a pattern observed in other tropical dryland rivers (Taylor et al., 2006; Jardine et al., 2012). Below we present a case study on longitudinal trends in the relative importance of different energy sources for riverine consumers assessed using stable C and N isotopes in the Mara River, Kenya (Inbox 20.1).

Influence of seasonality

Streams and rivers in large portions of the African continent experience seasonal flow regimes in response to irregular occurrence and distribution of rainfall (McClain and Masese, 2024, Chapter 29; Herrmann and Mohr, 2011). While most areas experience a single wet season, some parts of Eastern Africa and some pockets in Southern Africa experience two wet seasons. Furthermore, some areas with single wet seasons also experience bimodal or trimodal peaks (Herrmann and Mohr, 2011). Depending on prevailing flow or discharge conditions, trophic energy sources are equally dynamic in space and time. Changes in flow levels and hydroperiod drive contrasting patterns of habitat size, organic matter flux, light and nutrient availability for primary production and overall ecosystem productivity (Lowe-McConnell, 1985; Junk et al., 1989; Jardine et al., 2012; Humphries et al., 2014; Garcia et al., 2017; Venarsky et al., 2020). Subsidy pathways can also change seasonally because of changes in connectivity, flow paths and transport vectors (Masese et al., 2024b,c, Chapters 10 and 12).

In African streams and rivers, seasonal changes in river connectivity and habitat size are major drivers of changes in basal resource availability and the predominant energy pathways supporting secondary production (Inbox 20.2). During the dry season, terrestrial animals visit watering points more frequently, and many herbivores, including large wildlife and

INBOX 20.1 Longitudinal trends in different sources of energy for riverine consumers.

Not many studies have explored the relative importance of different energy sources in Afrotropical rivers in response to changes in stream size, i.e., longitudinal or upstream-downstream changes in trophic dynamics as rivers become larger. Moreover, because of widespread human activities, such as land use and land cover changes, that have a strong influence on trophic dynamics, these relationships are often confounded as most rivers drain catchments with mixed land uses. In order to eliminate confoundment by human activities and inputs of organic matter and nutrients by large mammalian herbivores, the influence of stream size on the relative importance of different sources of carbon (C3 vegetation or trees, C4 grasses and periphyton or algae) to macroinvertebrate functional feeding groups (FFGs) was evaluated in forested streams in the Mara River basin. In this study, the river distance from the source (RDS) was used as a measure of stream size, which is calculated as the square root of the catchment area in km^2 (Rasmussen et al., 2009).

Remarkably, no effect (linear regression) of stream size was noted on the relative importance of the three sources for all macroinvertebrate functional feeding groups (FFGs) in the forested streams (Fig. 20.1). Regarding the relative importance of different energy sources, C4 carbon was the least important source, while the importance of C3 vegetation and periphyton

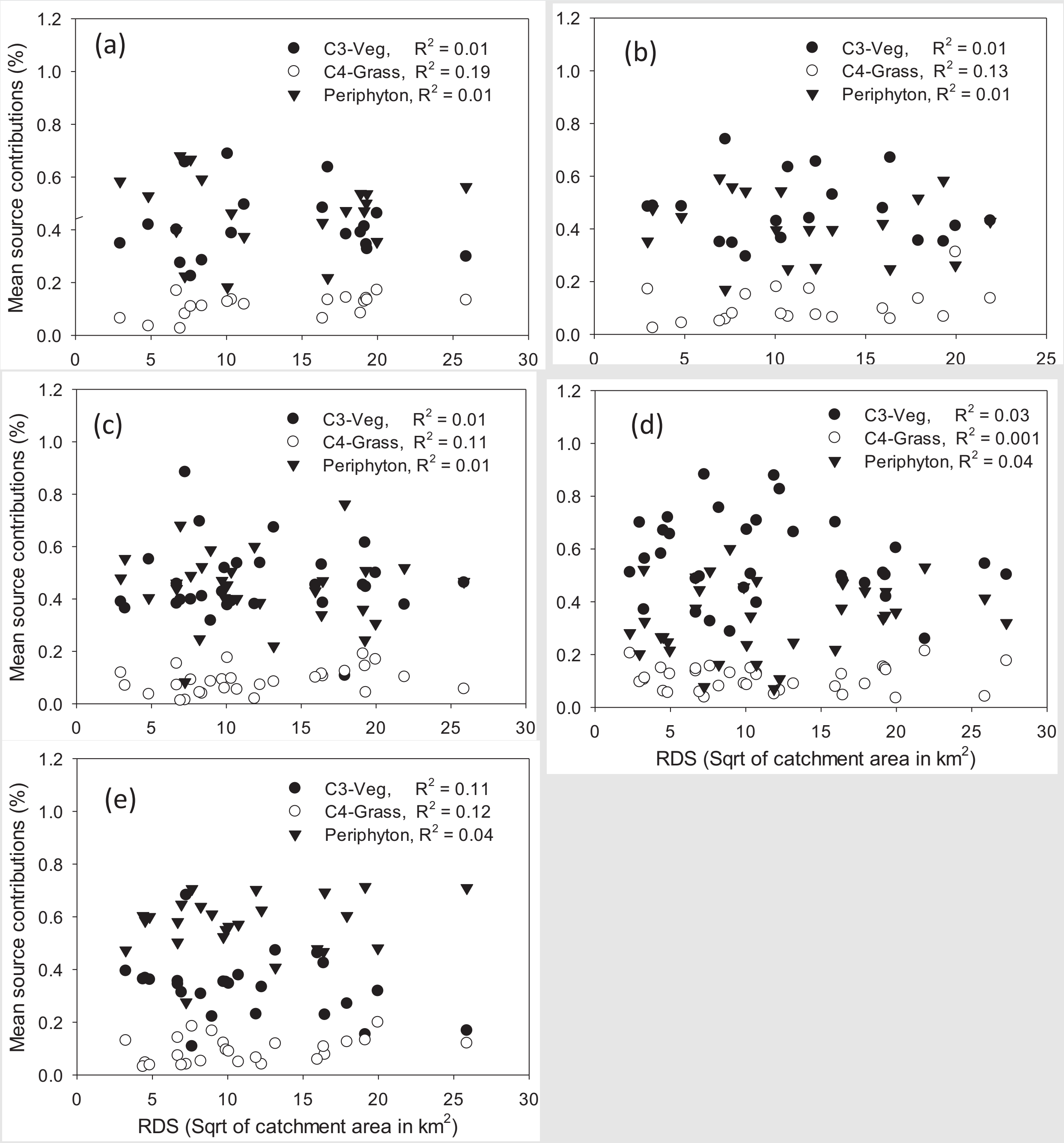

FIGURE 20.1 Source contributions to FFGs in forested sites. Longitudinal trends in source (C3 vegetation, C4 grasses and periphyton/algae) contributions to macroinvertebrate functional feeding groups (FFGs) in forested streams. Source contributions are assessed in response to changes in river distance (RDS) (stream size, measured as the square root of catchment area in km^2), density of large mammalian herbivores and percentage of land use under grasslands. (a) Collector-filterers, (b) collector-gatherers, (c) scrapers, (d) shredders, and (e) predators.

INBOX 20.1 Longitudinal trends in different sources of energy for riverine consumers.—cont'd

depended on the FFG considered. For instance, periphyton and C3 vegetation were equally important for collector-filterers (Fig. 20.1a) and scrapers (Fig. 20.1c). Periphyton was the most important source for predators (Fig. 20.1d), while C3 vegetation (trees) was the main source of energy for collector-gatherers (Fig. 20.1b) and, as expected, shredders (Fig. 20.1e). This also showed that the importance of trophic sources was related to the trophic position of the consumers, with autochthonous production becoming more important at the highest trophic level of the macroinvertebrate community (predators). Overall, periphyton was the major source of energy for most invertebrates in forested streams, except for obligate shredders that rely on coarse particulate organic matter from C3 vegetation; facultative shredders that are omnivorous, such as Potamonautidae (freshwater crabs), obtain a significant amount of energy from periphyton (Masese et al., 2022).

There were significant positive relationships (linear regressions, $P < .05$) between RDS and the importance of the three sources of carbon, although the rate of increase in the importance of C4 carbon sources with an increase in stream size (RDS) was low compared with that of C3 vegetation and periphyton (Fig. 20.2). In addition, an increase in stream size (RDS) was positively correlated with an increase in the importance of periphyton while negatively correlated with the importance of C3 carbon from terrestrial vegetation for macroinvertebrates (Fig. 20.2). While C3 vegetation and periphyton were equally important in these streams, C4 carbon contributed minimally (<10%) to consumers in low-order streams. As hypothesized by the river continuum concept (Vannote et al., 1980), the importance of C3 vegetation for invertebrates declined in mid-sized rivers as that of periphyton increased.

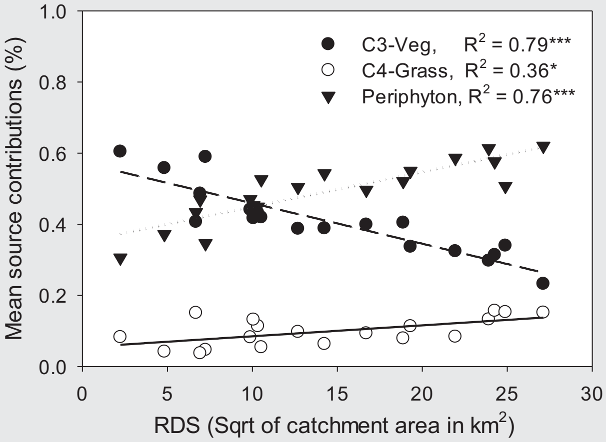

FIGURE 20.2 Longitudinal trends in source contributions to FFGs in forested streams. Longitudinal trends in the contribution of different sources of energy (C3 vegetation, C4 grasses and periphyton/algae) to macroinvertebrates in forested streams in the Mara river basin in response to changes in river distance from the source (RDS), which is a measure of stream size. RDS was measured as the square root of the catchment area in km^2.

livestock, congregate near watering points with increased inputs of organic matter and nutrients into aquatic ecosystems (Ogutu et al., 2010; Masese et al., 2014b; Iteba et al., 2021). In the Mara River, detritus was the major energy source for consumers during the wet season, while algal resources were more important during the dry season (Masese et al., 2015). In contrast, in the Boteti River in the Lower Okavango Delta, Bokhutlo et al. (2021) found that fishes derived the bulk of their energy from seston and terrestrial C4 grasses during the dry season, which agrees with the river wave concept that postulates that under low-flow conditions, aquatic food webs are supported by both in-stream primary production and allochthonous material from terrestrial vegetation (Humphries et al., 2014).

In addition to seasonal changes in trophic dynamics, seasonal, interannual or even decadal differences in the size and duration of flooding have an impact on the habitat structure, water physicochemistry and productivity of biota of floodplain rivers (Junk et al., 1989; Davies et al., 1994; Tockner et al., 2000; Boulton et al., 2006). A study in the Okavango Delta shows that small floods resulting from low precipitation in the headwater in Angola create shallow floodplains (Lindholm et al., 2007). This limits circulation and causes eutrophic conditions (e.g., high primary production), dominance of bottom-up processes and low fish reproduction. In contrast, large floods inundate extensive areas, allowing fish movement to important spawning sites on the floodplain and high fish production (Lindholm et al., 2007). Similarly, fish catches in the Niger River, and other African large rivers with extensive floodplains are a function of flooding extent (floodplain area) and duration (Welcomme, 1979, 1986b; Moses, 1987; Lae, 1992).

In addition to seasonal changes in inputs of terrestrial organic matter and abundance of aquatic producers such as periphyton and filamentous green algae, shifts in the feeding habits of consumers, especially omnivorous species, can also occur seasonally in response to these changes. For instance, phytodetritivorous tilapias such as *Oreochromis mossambicus*, *Oreochromis niloticus* and *Coptodon rendalli* have flexible diets and feed on either detritus or algae depending on availability (Lowe-McConnell, 2000). In the Rianila River in Madagascar, these fishes feed mainly on algae during the dry season when algae resources are readily available, rather than relying on less nutritive terrestrial detritus, leading to seasonal changes in the relative importance of allochthonous and autochthonous sources of energy (Abrantes et al., 2013).

The IRES systems in arid and semiarid regions experience transitions in flow levels from flooding to extended periods of dry seasons when flow ceases or remains interstitial (Fig. 20.3). These flow changes drive varied responses in trophic interactions and dynamics (Fig. 20.3). When flow levels drop and access to the floodplain is restricted, shrinkage in aquatic habitats results in greater reliance of consumers on local sources of production (seston and

FIGURE 20.3 Pools of water in streams in the Mara river basin during the dry season. Upper—a tributary of the Amala river showing eutrophic conditions caused by livestock inputs of organic matter and nutrients. Lower—a tributary of the Talek river within the Maasai Mara Game Reserve showing remnant pools that had large populations of fish (small-sized cyprinids and *Clarias gariepinus*). These pools shrink further during prolonged droughts, intensifying predation pressure on fish by piscivorous birds and mammals.

INBOX 20.2 Spatial and seasonal differences in trophic structure.

Stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analysis was used to describe spatial and seasonal variation in trophic niches and trophic structure in river reaches in the Mara River (Kenya) that differed in environmental conditions (agricultural vs. forested) and amounts of organic matter and nutrients inputs by livestock and hippopotamus (*Hippopotamus amphibius*). The study sites included a forested site (fourth order); four agricultural sites: Nyangores (fifth order), Amala 1 (fourth order), Amala 2 (fifth order) and Mara 1 (sixth order); and one hippo-influenced site: Mara 2 (sixth order). The study sites represented a gradient of C3- to C4-dominated vegetation. The forested site was located in the Mau Forest, where C3 vegetation dominated both the riparian and terrestrial areas of the catchment, while the most downstream site (Mara 2) was located in a savanna ecosystem dominated by C4 grasses and strongly influenced by hippo inputs of organic matter and nutrients from the terrestrial environment. The agricultural sites receive mixed inputs of both C3 and C4 carbon and increased amounts of nutrients under the influence of agricultural lands, human settlements

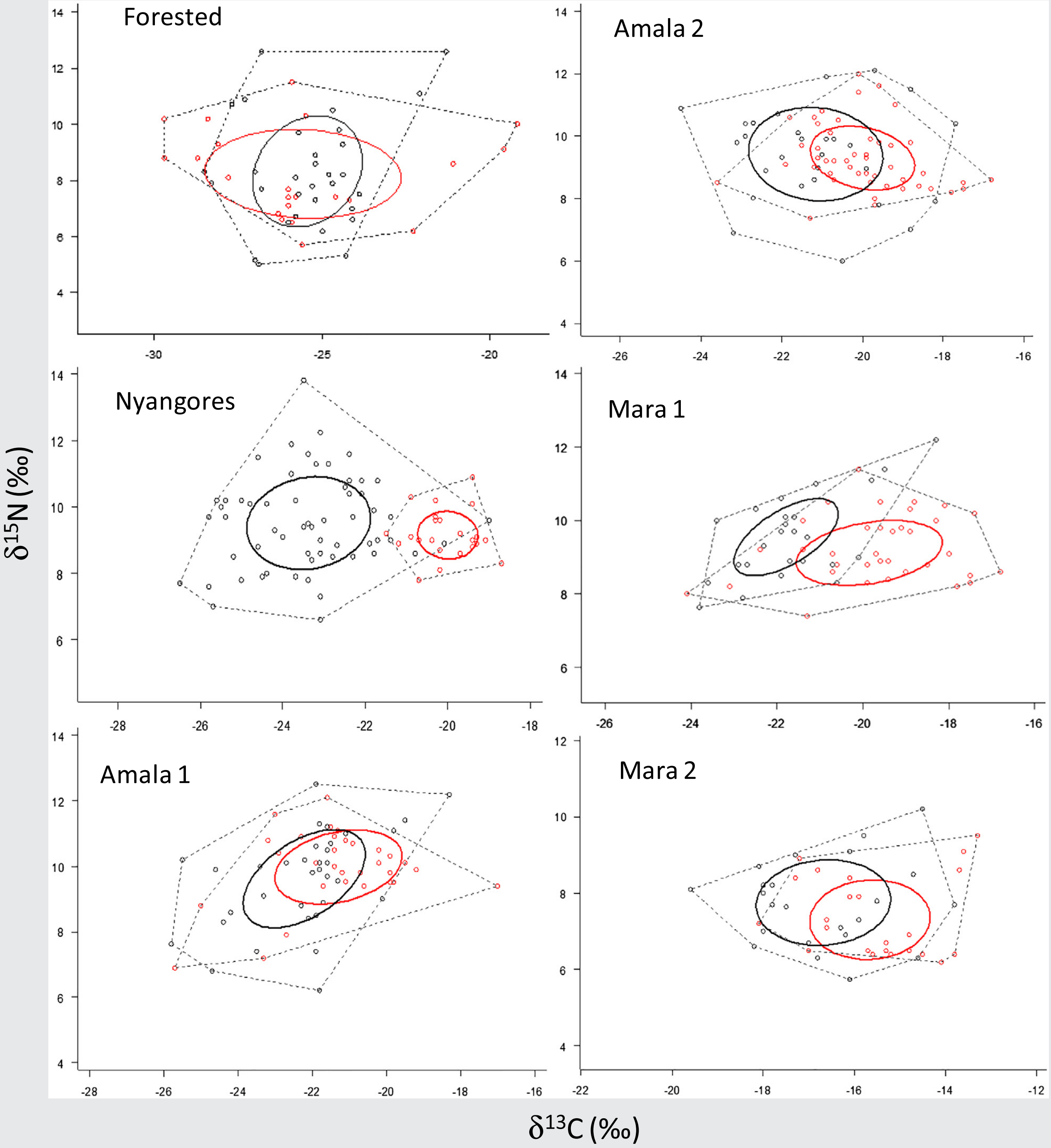

FIGURE 20.4 Site-by-site comparison of standard ellipse areas (SEA), representing the core isotopic niche space of invertebrates from the seven sites during the dry (red solid line) and wet (black solid line) seasons. Dotted lines are each site's convex hull areas of invertebrate communities, corresponding to the area encompassing all invertebrates in the $\delta^{13}C$—$\delta^{15}N$ plot. Note the changes in the *x*-axis values.

Continued

INBOX 20.2 Spatial and seasonal differences in trophic structure.—cont'd

and varying densities of livestock. To investigate differences in community trophic niche size among sites and seasons, stable isotope niches were quantified and compared using standard ellipse areas (SEAs; expressed in ‰2) using the SIBER (Stable Isotope Bayesian Ellipses in R) of SIAR (Stable Isotope Analysis in R) (Parnell et al., 2010; Jackson et al., 2011). Ellipse sizes were based on SEA_B, a Bayesian small sample size-corrected SEA (Jackson et al., 2011).

The results showed that at the C3-dominated Forested site, there were no seasonal differences in food web structure for

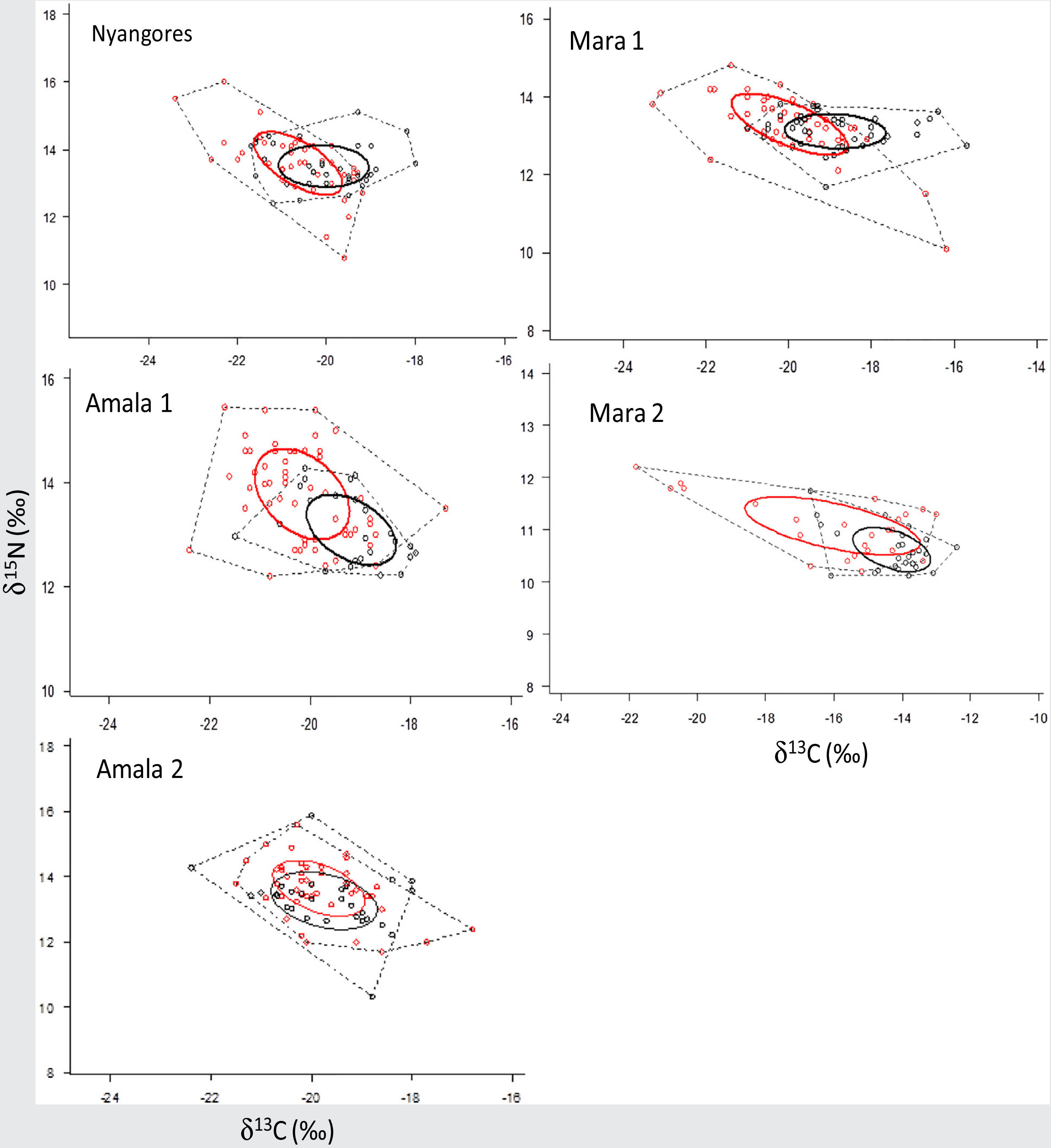

FIGURE 20.5 Site-by-site comparison of standard ellipse areas (SEA) for insectivorous fishes, representing the core isotopic niche space of invertebrates from the seven sites during the dry (red solid line) and wet (black solid line) seasons. Dotted lines are each site's convex hull areas of invertebrate communities, corresponding to the area encompassing all fish groups in the $\delta^{13}C-\delta^{15}N$ plot. The forested site had no fish; hence, it is missing from the image. Note the changes in the *x*-axis values.

INBOX 20.2 Spatial and seasonal differences in trophic structure.—cont'd

the invertebrates: standard ellipse area (SEA_B) did not differ in size between seasons (Fig. 20.4), and the overlap in SEA_B between seasons was high (52‰**²**). Similar patterns were observed for the Amala 1, Mara one and the C4-dominated Mara two sites. However, for the Nyangores and Amala two sites, there were considerable seasonal differences in food web structure, with the dry season food webs much smaller (Fig. 20.4), with the Nyangores recording the lowest overlap (14‰**²**) in SEA_B between the dry and wet seasons. Notably, the SEA_B was right-shifted for all sites except the Forested site, indicating enrichment in $\delta^{13}C$ values of invertebrates during the dry season. This suggests a shifting basal energy resource during the dry season.

For insectivorous fishes, there were minimal seasonal differences in trophic structure: SEA_B sizes did not differ between seasons at most sites (Fig. 20.5), and overlaps in SEA_B were high for four of the five sites, ranging from 46‰^{2}–63‰^{2}. The C4-dominated and hippo-influenced Mara two site recorded the smallest overlap (32‰^{2}) between the seasons, and 99.9% of SEA_B were larger during the dry than the wet season (Fig. 20.5). In addition to the slightly enriched $\delta^{13}C$ values for most insectivorous fishes at most sites during the dry season, the $\delta^{15}N$ values were enriched for most fishes at all sites (Fig. 20.5). The hippo-influenced Mara two site showed SEAs with the highest $\delta^{13}C$ values for both invertebrates and fish. This suggests a strong influence of C4 carbon sources supporting aquatic consumers. Contrary to the C3-dominated Forested site, the C4-dominated Mara two site had a compact and less diverse food web. This can be partly explained by high levels of suspended sediments that limit both primary production and the diversity of sources available to consumers (Masese et al., 2015). Moreover, the dominance of the C4 pathway and lower isotopic trophic diversity at the Mara two site is also likely a result of the annual mass drownings of wildebeest (*Connochaetes taurinus*) whose carcasses have the same $\delta^{13}C$ value as the C4 grasses they feed on (Subalusky et al., 2017). Wildebeest carcasses have recently been shown to have both short- and long-term ecosystem effects directly through the mineralization of soft tissue by fish or indirectly through biofilm growth on bones that are later fed on by insects and fish after soft tissue decomposition (Subalusky et al., 2017).

algae), a pattern observed in other tropical dryland rivers (Taylor et al., 2006; Jardine et al., 2012). During low flow levels, predation levels also increase due to increased species interactions in reduced habitats. Further reduction in flow reduces river reaches into disconnected pools in which instream primary production dominates trophic pathways, although this can be supplemented by fish feeding on terrestrial insects at the water's edge. As the pools further shrink, predation pressure on fish and other aquatic animals by piscivorous birds, mammals (e.g., otters), and reptiles (e.g., Nile crocodile, water monitor) intensifies, creating strong top-down pressures. In river reaches with livestock and hippos, there is often an excessive build-up of animal-vectored organic matter within riverine pools (Wolanski and Gereta, 1999; Dutton et al., 2021). These inputs of terrestrial organic matter and nutrients can influence the structure and function of aquatic communities by shaping the feeding ecology of aquatic consumers, altering macroinvertebrate community structure and depressing microphytobenthic biomass (Grey and Harper, 2002; McCauley et al., 2015; Dawson et al., 2016; Stears et al., 2018). In the Great Ruaha River in Tanzania, Stears and McCauley (2018) noted that the loading of hippo dung accelerates fish predation by terrestrial consumers during the dry seasons when river flow ceases and water remains in disconnected pools. In these pools, fish display aerial respiration and swim close to the surface where dissolved oxygen concentration is highest, exposing fish to predators, which included yellow baboons (*Papio cynocephalus*) that are not normally piscivorous and many species of piscivorous birds (Stears and McCauley, 2018).

Are Afrotropical streams and rivers different?

Within the global context of organic matter processing, trophic dynamics and food web structure in riverine ecosystems, there is a raging, and yet unresolved, debate on the position of tropical streams and rivers (Boulton et al., 2008; Boyero et al., 2009; Dudgeon et al., 2010; Masese and McClain, 2012). From long-term studies in the tropics, some shared attributes are emerging. These include a high degree of autochthony, widespread omnivory, short food chains and dominance of macroconsumers (Mantel et al., 2004; Douglas et al., 2005; Coat et al., 2009; Dudgeon et al., 2010). The degree to which Afrotropical riverine ecosystems fit into these characteristics or differ has not been widely explored. Here, we examine how Afrotropical streams and rivers compare or differ from their tropical counterparts and those in the temperate region.

Relative importance of trophic resources

Allochthony

The earliest food web studies in African streams and rivers focused on food composition and feeding habits of fishes based on gut content analysis (GCA). Findings from these studies showed that most species feed on plant material, including detritus, and some appreciable amounts of insects (e.g., Corbet, 1961; Okedi, 1971; Balirwa, 1979; Ochumba and Manyala, 1992). In the Sondu-Miriu River in the Lake Victoria basin, Kenya, while 14 fish species fed on plant materials, phytoplankton/algae were detected in the guts of only four species, which also had large quantities of plant materials and detritus in their guts (Ochumba and Manyala, 1992). On comparing the food of *Barbus* spp. from Lake Victoria and tributary rivers, Balirwa (1979) showed that in rivers, the fish ingested more plant material than those in the lake, which is in agreement with earlier findings by Corbet (1961).

Stable isotope analysis of carbon (δ^{13}C) and nitrogen (δ^{15}N) have also confirmed the predominance of terrestrial plant material in riverine food webs. A study investigating local watershed influences on energy sources for riverine fishes in the Lake Victoria basin, Kenya, found that when indigenous riparian vegetation was replaced with grasses (notably sugarcane), the C4 signature of the grass appeared in two fish species investigated (*Labeo Victorianus* and *Barbus altianalis*) (Ojwang et al., 2007). Other studies have reported the incorporation of C4 carbon from terrestrial grasses into food webs or consumers in African rivers (Masese et al., 2015, 2022; McCauley et al., 2015; Bokhutlo et al., 2021). Significant incorporation of C4 carbon sources into food webs in riverine ecosystems in Africa is unexpected, contrary to some previous tropical studies (Hamilton et al., 1992; Forsberg et al., 1993; Clapcott and Bunn, 2003). However, large African rivers receive copious amounts of C4 carbon from terrestrial grasslands deposited in rivers by large populations of hippos and livestock (Subalusky et al., 2015; Masese et al., 2020a; Voysey et al., 2023). These carbon resources are then incorporated into food webs either directly through consumption by insects and fish or indirectly through microbial biofilms and macroinvertebrate food chains (Masese et al., 2015, 2022; McCauley et al., 2015).

Autochthony

Recent studies suggest that instream primary production, while not contributing the greatest biomass toward the total carbon budget, supports most metazoan production in streams and rivers (Lewis et al., 2001; Thorp and Delong, 2002). Both the river continuum (RCC; Vannote et al., 1980) and the riverine production model (RMM; Thorp and Delong, 1994, 2002) concepts predict that in mid-sized rivers, the most important sources of organic matter fueling food webs are autochthonous algal-based resources. Although algae may be less abundant in large and turbid rivers than detritus derived from terrestrial vegetation, algae are more nutritious, have higher energy densities, and contain more labile organic molecules than terrestrial primary producers, and, therefore, they are disproportionately assimilated into consumer biomass (Thorp and Delong, 2002).

A growing number of studies in the tropics indicate that even in headwater streams, autotrophic production is an important energy source for aquatic consumers (Boyero et al., 2009; Dudgeon et al., 2010 and references therein). While research is limited on gross primary production in African streams and rivers (Fugère and Masese, 2024, Chapter 13), studies in upland Kenyan and Ugandan streams indicate the presence of some primary production that can be incorporated into food webs (Fugère et al., 2018a; Fugère and Masese, 2024). However, much of this production is in open canopy agricultural streams, as most forested streams are net heterotrophic (Masese et al., 2014b; Fugère et al., 2018a). Consequently, increased primary production in agricultural streams increases the incorporation of algal resources into consumers' diets in agricultural streams. In Madagascar, Benstead and Pringle (2004) reported increased use of biofilm as a food resource for macroinvertebrates in agriculture compared with forested streams. In many African rivers, quantitatively, the most important food item consumed by fish and macroinvertebrates is amorphous detritus (Palmer et al., 1993; Ochumba and Manyala, 1992; Masese et al., 2014b), which contains significant amounts of microalgae and cyanobacteria. Gut contents analysis of fishes in different African rivers has also reported filamentous algae or diatoms as some of the main food items in the diets (e.g., Corbet, 1961; Balirwa, 1979; Eccles, 1985; Kraiem, 1996; Nakangu et al., 2023). In one Rift Valley Kenyan stream, diatoms were part of the detritus consumed by freshwater crabs - *Potamonautes* spp. (Lancaster et al., 2008). Omnivores and species that consume large quantities of detritus derive most of their energy from algal components of the detritus (March and Pringle, 2003; Winemiller, 2003; Brito et al., 2006) because of differential assimilation of the various components therein. Consequently, the contribution of autotrophic production to secondary production in African rivers could be higher than implied using GCA methods. Indeed, studies using stable isotopes and fatty acids analysis of consumers and their putative food resources in African streams and rivers have highlighted the importance of autochthonous food resources for metazoan production (Masese et al., 2015, 2022; Dawson et al., 2016).

Dominance of macroconsumers

Macroconsumers are defined as large-size consumers excluded by 2-mm mesh in litter decomposition experiments (*sensu* Pringle and Hamazaki, 1998; Rosemond et al., 2001). Many studies have reported a dominance of macroconsumers in tropical stream food webs in the tropics (Rosemond et al., 2001; Douglas et al., 2005; Coat et al., 2009; Moulton et al., 2010; Yang, 2023). In low-order African streams, macroconsumers include small-bodied fish such as barbs (*Enteromius* spp.) and catfishes (*Clarias* spp.), freshwater crabs (e.g., *Potamonautes* spp.), crayfish and shrimps. Decapod crustacean macroconsumers are quite dominant in headwater African streams, where they exert significant influences on both leaf litter processing and population dynamics of invertebrates (Abdallah et al., 2004; Dobson, 2004; Lancaster et al., 2008). In the many African large rivers, shrimps such as the African river prawn, *Macrobrachium vollenhovenii* and the atyid shrimp *Caridina* spp. are present. However, studies that have examined the ecological role played by prawns and shrimps in streams in African streams and rivers are limited. Most of these macroconsumers are omnivorous, potentially increasing leaf processing when eaten either in concert with smaller macroinvertebrates or as a substitute for smaller macroinvertebrates. There is evidence of top-down control exerted by freshwater crabs on macroinvertebrates in streams too. In a Kenyan Rift Valley stream, the high abundance of *Potamonautes* sp. coupled with the low abundance of macroinvertebrates in the same stream has been identified as an example of top-down control exerted by crabs on stream macroinvertebrates (Lancaster et al., 2008). Similarly, fish and shrimps can exert a strong influence on benthic sediments, detritus, nutrient demand, and algal and invertebrate assemblages (Pringle et al., 1999; Flecker and Taylor, 2004; Souza and Moluton, 2005).

Widespread omnivory

Studies show that tropical communities feed on diverse food resources at more than one trophic level (Winemiller and Jepsen, 1998). Omnivory is thought to be an adaptive response to the strong seasonal hydrology that governs the availability of food resources in tropical riverine food webs (Lowe-McConnell, 1985; Winemiller, 1990, 2004; Winemiller and Jepsen, 1998; Huang et al., 2007). This is also the case in many studies in African streams and rivers, showing that most species are omnivores that feed at more than one trophic level. In the Lake Victoria basin, analysis of gut contents indicates that almost all fish species feed on different food items, including insects, detritus and algal components (Corbet, 1961; Ochumba and Manyala, 1992; Raburu and Masese, 2012; Nakangu et al., 2023). In the Sondu-Miriu River most fish species feed on three or more food items (Ochumba and Manyala, 1992). The most important food items consumed are detritus (including mud), insects (adults and larvae), macrophytes and phytoplankton/algae, consumed by 54%, 54%, 50% and 14% of the 28 fish species, respectively (Ochumba and Manyala, 1992). Gut content analysis of macroinvertebrates has also shown that most stream taxa feed on different food items, either by accident or deliberately, including animal material, algae and amorphous detritus (Benstead and Pringle, 2004; Masese et al., 2014a). A study in Mt Kenya streams indicated that omnivory is common in a freshwater crab (*Potamonautes* sp.), which relies on a terrestrial subsidy of ants and detritus to meet its energy needs (Lancaster et al., 2008).

Even though omnivory is an old attribute of tropical food webs, there has been a notable increased tendency toward greater omnivory displayed by many fish species (Ojwang et al., 2010). Three species in the Sondu-Miriu River, which were predominantly piscivorous, *Bagrus docmac*, *Clarias gariepinus* and *Lates niloticus,* have been reported to also incorporate a significant amount of other food items, including insects and molluscs (Ochumba and Manyala, 1992). If indeed increased omnivory is a recent attribute of riverine and other aquatic food webs, then it is of interest to identify its cause(s) in light of the persistent and myriad environmental challenges that currently plague many river catchments. It has been suggested that disturbance by human activities can alter the composition of aquatic communities and the availability of preferred food resources for consumers. Under such conditions, omnivory is the most appropriate ecological strategy, which takes advantage of whatever food is available. For instance, below industrial discharge points and in river sections that are severely degraded, omnivores are consistently higher than insectivores, with some fish species displaying different feeding preferences depending on the environmental condition of the site inhabited (Raburu and Masese, 2012). It has also been observed that even *Labeo victorianus* that is morphologically endowed with a subterminal mouth well suited for grazing aufwuchs from rocks in clearwater has shifted to occasionally feed on insects and organic matter in perturbed waters (Ojwang, 2006; Nakangu et al., 2023). Consequently, opportunistic and omnivorous fishes such as catfishes, cichlids and cyprinids are the most abundant in rivers (Ochumba and Manyala, 1992; Masese et al., 2014b).

Food chain length

Food-chain length denotes the number of energy transfers from basal resources to the apex predator in an ecosystem and is thought to be a function of available energy (Elton, 1927; Hutchinson, 1959), ecosystem size (Schoener, 1989; Post and

Pace, 2000), and ecosystem type (Vander Zanden and Fetzer, 2007). This aspect of vertical web architecture strongly affects community structure (Pace et al., 1999) and ecosystem function (Duffy et al., 2005). For this reason, food-chain length is considered a central characteristic of ecological communities (Post, 2002; Hall and Raffaelli, 1993), and identifying the factors that determine food-chain length is a fundamental issue of ecology (Mantel et al., 2004; Dudgeon et al., 2010).

Because of the wide diversity of food items consumed, tropical riverine food webs tend to be short, diffuse and with high connectance rather than long and linear chains (Winemiller, 2004; Douglas et al., 2005; Coat et al., 2009). This is also the case among consumers in large rivers in tropical Australia and the Neotropics, where food webs are dominated by relatively few strong interactors and macroconsumers that are often omnivorous (Winemiller, 1990; Jepsen and Winemiller, 2002; Pusey et al., 2010).

Terrestrial-river connectivity

One key attribute of African rivers is the strong connectivity between terrestrial and aquatic environments mediated by large wildlife (Jacobs et al., 2007; Subalusky et al., 2015; Benjamin et al., 2024, Chapter 14) and increasing livestock populations (Masese et al., 2020b; Iteba et al., 2021). The role of large animals in savannah river systems is particularly noteworthy because of the high numbers of large mammalian herbivores, both livestock and wildlife, that are residents of these landscapes and subsidize riverine food webs through excretion and egestion in rivers during crossings and watering (Fig. 20.6). The transfer of terrestrial organic matter and nutrients to these savanna rivers occurs during the dry and wet seasons. Animals congregate in perennial streams and rivers during the dry months, creating an opportunity to deposit large quantities of organic matter nutrients into the rivers (e.g., Jacobs et al., 2007; Iteba et al., 2021). During the rainy season, organic matter and nutrients deposited in riparian areas are washed into the river system. In addition, many African river

FIGURE 20.6 Subsidies linking terrestrial and aquatic food webs in African savannas. (a) Large herbivores visit water to feed and drink, and their excretions wash into the river. (b) Hippopotami graze on land at night and spend their days partially submerged, showering dung and urine into the river (Subalusky et al., 2015). Drowned wildebeest carcasses provide food for (c) vultures, which move nutrients back to land, and (d) crocodiles. (e) Uneaten soft tissue decomposes rapidly, releasing large pulses of carbon and nitrogen (Subalusky et al., 2017). (f) Bones take years to decay, slowly leaching nutrients (notably phosphorus) and providing a substrate where biofilms grow and are grazed by aquatic consumers. Nutrients in the water column can enter aquatic food chains through consumption by (g) zooplankton, (h) insects and crustaceans, and (i) fishes, or be conveyed back into the riparian zone by (j) floods, which fertilize the plants eaten by herbivores (a and b). (Inset) Map of the Serengeti wildebeest migration; triangles indicate major river crossings. *Figure designed by TerraCommunications.*

systems were historically inhabited by large populations of the common hippopotamus (Voysey et al., 2023). Although the distribution of hipps has shrunk because of human activities, many large river systems in central, eastern and southern Africa still host large populations. Hippos transport large amounts of organic matter from riparian areas into rivers daily. The wallowing of hippos also creates many pools and lagoons in rivers and floodplains, which provide refuge for fish during the dry season (Naiman and Rogers, 1997). The pools and lagoons are subsequently fertilized by hippo dung, which promotes primary and secondary production (Hoberg et al., 2002; Mosepele et al., 2009). Organic matter and nutrient inputs into streams and rivers contribute directly and indirectly to food webs and other ecosystem processes (Fig. 20.6).

Fish migrations may also be important in transferring energy within riverine environments in African large rivers. Many fishes in Lake Victoria make periodic runs into influent rivers and their floodplains for breeding and feeding (Lowe-McConnell, 1985; Ochumba and Manyala, 1992; Masese et al., 2020a). Some fish move up to 80 km upstream of the major rivers (Whitehead, 1959b). Even though limited information exists on the contribution of potamodromous fishes in the supply of organic matter and nutrients between lakes and rivers and within rivers, migrating fishes are known as nutrient transfers between lentic and lotic systems. Studies on anadromous salmonids have demonstrated the importance of migratory fishes in the recycling of elements between marine and freshwater habitats in North America (Kline et al., 1990; Cederholm et al., 1999). The excretion of ammonia, other nitrogenous wastes and eggs that die are consumed during spawning runs and incorporated into the heterotrophic pathways (Bilby et al., 1996; Wipfli et al., 1999).

Effects of human activities on African riverine food webs

Many streams and rivers in Africa are increasingly experiencing multiple stressors from human activities (Mpopetsi et al., 2024b, Chapter 25; Fouchy et al., 2019). Some persistent stressors include land use and land cover changes, nutrient and organic pollution, the introduction of exotic species, and alteration of flow regimes through excessive water withdrawals and damming. There is an increasing urgency to understand how these changes in environmental conditions influence the structure and functioning of riverine ecosystems, including biodiversity and energy sources and flow in food webs (Ormerod et al., 2010; Jackson et al., 2016; Reid et al., 2019). Here, we highlight some human-induced stressors that significantly impacts ecosystem structure and functioning, including food webs, in African rivers.

Land use and land cover changes

Land use and land cover (LULC) changes in catchments and the vicinity of streams and rivers have distal and proximal controls on community structure and trophic dynamics in streams and rivers. In African streams and rivers, changes in LULC have been linked to habitat loss and degradation, including deterioration in water quality, increased water temperature, concentrations of solutes and reduced dissolved oxygen concentrations, and the quality and flux of organic matter (Masese et al., 2024b,c, Chapters 10 and 12). These changes in habitat conditions alter assemblage characteristics (both primary producers and secondary consumers) and trophic interactions, leading to changes in trophic size and structure.

In the Mara River, land use change has been linked to changes in the relative importance of different carbon sources for consumers and isotopic trophic niche sizes (Masese et al., 2015, 2018). An increase in livestock populations after converting native forests and grasslands has been found to increase the fractional contribution of periphyton and C4 carbon for macroinvertebrates and fish in the river (Masese et al., 2015, 2022). Land use change from forestry to agriculture has also been noted to decrease trophic diversity and niches of consumers, with food webs at forested sites having the widest trophic niche size and highest trophic diversity compared with food webs in river reaches influenced by high densities of hippos (Masese et al., 2014b). This is mostly related to increased turbidity in hippo-dominated areas (Dutton et al., 2018), which limits aquatic primary productivity (Tamooh et al., 2012). For instance, in the Betsiboka (Madagascar) and Tana (Kenya) rivers, isotopic niche sizes were much smaller because of high turbidity compared with Zambezi (Mozambique) and Ambila rivers, whose clear waters allowed for a range of aquatic producers to occur (plankton, periphyton and epiphytes), hence increasing trophic diversity and niche sizes of consumers (Abrantes et al., 2014).

Unlike temperate rivers, African rivers drain catchments with contrasting coverage of C3 and C4 vegetation (Abrantes et al., 2014). The amount of C3 and C4 vegetation in catchments and riparian areas also determines the abundance of large mammalian herbivores with high densities in C4-dominated catchments. These patterns in vegetation type and cover influence biogeochemical parameters, primary producers and consumer trophic ecologies, especially when subjected to land use changes and other developments such as agriculture and urbanization (Abrantes et al., 2013; Marwick et al., 2015, 2018). For instance, in the C3-dominated Zambezi River in Mozambique (catchment with a C3/C4 cover of 61/39%), C3 producers were the most important sources for many trophic guilds of consumers, while in the highly turbid and C4-dominated Betsiboka River (C3/C4 cover of 42/58%) in Madagascar where C3 producers are scarce and waters very turbid, C4 material was the most important contributor to animal nutrition (Abrantes et al., 2013). In contrast, in the Tana River, despite the dominance of C4 vegetation in the catchment (C3/C4 cover of 36/64%), the clear waters support primary production, and consumers rely on a combination of C3, C4 and phytoplankton (Abrantes et al., 2013) (Inbox 20.3).

INBOX 20.3 Effects of land use and large mammalian herbivores on source contributions to consumers in Afromontane-savanna rivers.

A study investigated the influence of land use change and subsidies by large mammalian herbivores (both livestock and large wildlife) on the importance of different sources of carbon/energy for macroinvertebrates in an Afromontane-savanna river, the Mara River, Kenya. Eighty (80) sites were sampled during the dry season in subcatchments draining different land uses and locally influenced by human activities, cattle and wildlife. Sites were then grouped into five broad categories: forested (19), agricultural (26), low-density livestock (15), high-density livestock (12), and wildlife (i.e., hippo) (10) sites. Forest sites had C3 vegetation dominating the catchment and riparian areas and were used as a reference for the human and LMH influences. For more details on sampling design, see Masese et al. (2022).

The results show that the importance of different sources of energy for consumers in Afromontane-savanna rivers is spatially variable in response to changes in land use, abundance and distribution of large mammalian herbivores, both livestock and wildlife, among other factors. The importance of C3 vegetation, C4 grasses and periphyton for invertebrates differed among the five site categories, but patterns were similar for scrapers and collectors (Fig. 20.7). Overall, periphyton was either the major or second-most important source of carbon for all FFGs at forested, agricultural and livestock sites and predators were more reliant on this energy pathway than the rest of the FFGs (Fig. 20.5). Except for shredders in forested streams, the importance of C3 vegetation was reduced for the rest of FFGs in the other regions and was lowest at the hippo sites. On the contrary, the importance of C4 carbon responded strongly to LMH density and was the most important source of carbon (>50%) for all FFGs at hippo sites, except shredders (Fig. 20.5). Source contributions followed similar patterns for all FFGs except predators and shredders (Fig. 20.5). Predators seemed to draw most of their nutrition from the periphyton pathway at all sites except those with hippos. Shredders, on the other hand, displayed an over-reliance on C3 vegetation as their main source of carbon at all sites, which is consistent with their feeding habits on coarse particulate organic matter, i.e., mostly leaves of C3 vegetation of terrestrial origin. The findings of this study show that land use has a strong influence on the importance of different sources of carbon for riverine consumers, but the strength of this influence depends on the nature of land use or human influence. For instance, livestock grazing had a greater influence on the importance of periphyton for macroinvertebrates than crop farming (agriculture)—probably because of increased primary production driven by nutrient inputs from livestock egestion and excretion (Masese et al., 2014b; Iteba et al., 2021).

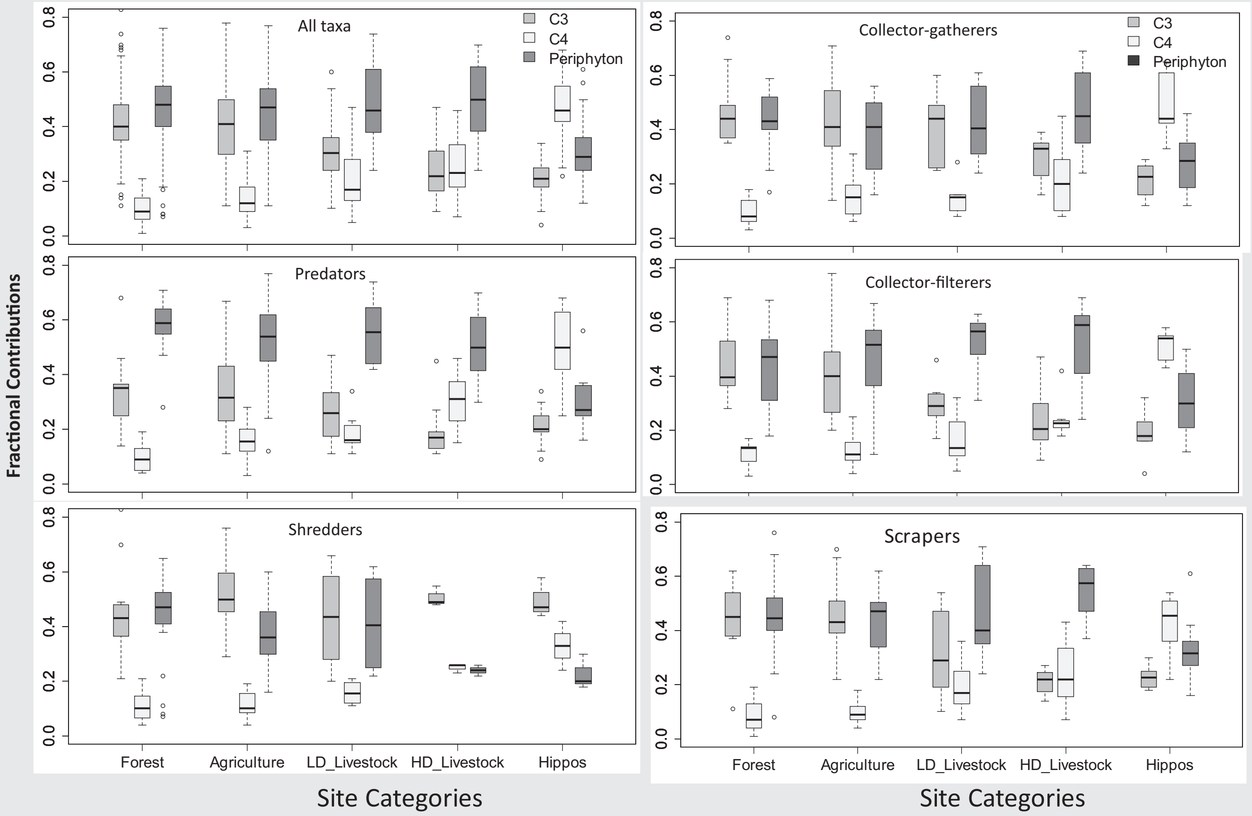

FIGURE 20.7 Box-and-whisker plots of fractional contributions of C3 vegetation (grey), C4 grasses (light grey) and periphyton (dark grey) to macroinvertebrates functional feeding groups across different site categories in the Mara river. (a) All taxa, (b) collector-gatherers, (c) predators, (d) collector-filterers (e) shredders, and (f) scrapers. C3 C3 plants; C4 C4 plants.

Exotic introductions

African streams and rivers and their catchments have sometimes witnessed reckless and uncontrolled introduction of plant and animal species that have affected their structure and functioning. Eucalyptus trees have been introduced into catchments and riparian areas of rivers in many countries. In riparian areas, Eucalyptus species alter the loading rates of leaflitter and its contribution to food webs. Studies comparing the decomposition rates of Eucalyptus and indigenous leaves show that Eucalyptus leaves decompose more slowly than native species (Masese et al., 2024c, Chapter 12). Replacement of native riparian vegetation with exotic species creates favorable light conditions for increased primary production and growth of aquatic macrophytes in previously unvegetated channels. This can alter energy sources for communities by reducing dependence on allochthonous energy sources from leaflitter to a reliance on autochthonously produced algal resources.

Streams and rivers in Africa have also witnessed the exotic introduction of many fish species. In the Kenyan rivers draining into Lake Victoria, nine exotic fishes (*Oreochromis niloticus*, *O. leucostictus*, *Coptodon zillii*, C. *rendalli*, *Gambusia affinis*, *Micropterus salmoides*, *L. niloticus*, Brown trout—*Salmo trutta*, and Rainbow trout—*Oncorhynchus mykiss*) have been reported (Masese et al., 2014b). The Nile tilapia, *Oreochromis niloticus*, is one of the most widespread exotic fish species in Africa, with successful invasions and/or introductions in southern Africa, the Lake Victoria basin, West and North Africa. This and other introduced cichlids, such as *O. leucostictus, Coptodon zillii, C. rendalli* pose extinction risks to indigenous congenerics through hybridization and competition exclusion (Kwikiriza et al., 2024). Brown and rainbow trout have also been successfully introduced to many rivers in countries in Eastern and Southern Africa (Weyl et al., 2017). Trout are generalist predators, and their introduction to highland cool streams and rivers has had many ecological effects. Trout primarily feed on aquatic invertebrates in their native range, but can also feed on fish, terrestrial invertebrates and vertebrates such as amphibians, reptiles and small mammals (Gillespie, 2001; Budy et al., 2013). In South Africa, they have been linked to the decline, and in some cases local extinction, of native invertebrates, frogs and fish (Karssing et al., 2012; Ellender, 2013; Rivers-Moore et al., 2013; Jackson et al., 2016). Potgieter (2014) found that brown trout reduced the abundance of shredding invertebrates, which caused a decline in leaf litter decomposition rates, indicating that trout can alter ecosystem function through trophic cascades. The introduction of trout in the upper reaches of the Rooikrantz Dam in South Africa decimated local populations of the Border barb (*Barbus Trevelyan*) through predation and competition for food (Gaigher, 1979). Brown trout have also been linked to the decline of *Pseudobarbus* spp. and *Sandelia capensis* in many South African rivers (Cambray, 2003). In Zimbabwe, negative impacts of introduced trout on native fish and macroinvertebrates have also been reported (Kadye et al., 2013). These ecological effects of introduced trout have mainly been reported in South Africa, but similar effects have likely occurred in other countries where trout introductions have been successful, such as Kenya, Lesotho, Madagascar and Swaziland (Welcomme, 1988).

Climate change

Our knowledge of how the functional diversity and food webs of African riverine ecosystems respond to climate change drivers is very limited. However, there is increasing evidence that climate change is affecting ecosystems, including the spatial and temporal distribution of water quality and quantity, as well as aquatic communities. In rivers and their catchments, the effects of climate change on the hydrology and water quality and aquatic communities are compounded by local human activities such as land use change and excessive water abstractions. Many rivers have reported changes in the natural flow regimes characterized by reduced dry season base flows and flooding and peak discharges during the wet season, and these changes have been linked to climate change (e.g., Shinhu et al., 2023). Increased runoff is a major driver of soil erosion, especially from converted lands, and this causes the siltation of streams and rivers with significant effects on primary production and the composition of aquatic communities, including invertebrates and fishes (Sayer et al., 2018). Some invertebrates, such as shredders living in their thermal optima in forested streams, face the greatest risk of extinction due to the warming of streams and rivers due to climate change and land use change (Yule et al., 2009; Boyero et al., 2011b, 2021). In the headwaters of the Mara River basin, seven species of invertebrates are restricted to colder forested streams, likely as a response to the warming and poor water quality in the nearby agricultural streams (Masese et al., 2014a). Loss of detritivorous shredders will impact organic matter processing, nutrient cycling, and, consequently, energy sources for food webs.

Loss of river connectivity

Because of the demand for water and hydropower, many large African rivers have been dammed, and many are earmarked for damming to meet these needs. The growing human population is also increasingly settling on riparian areas of large rivers. As a result, many have been dyked or channelled to manage floods. These developments have resulted in the loss of both longitudinal and lateral connectivity in many rivers. Longitudinal and lateral connectivity of rivers, wetlands, and lakes is critical to ecosystem function, given the interdependency of these spatially distinct ecosystems on energy and nutrient flows that sustain their functionality. Connectivity among habitats is an important component in the stability of food webs (McCann et al., 2005; Rooney et al., 2006). Migrations of fish between lakes, rivers and peripheral wetlands, as well as along river corridors, are critical for accessing habitats and food resources during specific phases of the life histories of many fish species (Cadwalladr, 1965; Junk et al., 1989; Winemiller and Jepsen, 1998; King et al., 2024). Access to such spatially discrete resources has played an important role in sustaining populations of threatened and vulnerable species. In the Lake Victoria basin (LVB), it has been long recognized that the use of fishing gears that prevent upstream migration of fish during spawning runs is detrimental to fish populations and the riverine fishery (Whitehead, 1959a; Cadwalladr, 1965).

Recent evidence suggests that the LVB rivers still maintain populations of basin-scale migratory fishes, such as *Labeobarbus altianalis* and *Labeo victorianus* (Masese et al., 2014b). The well-being of these and other migratory species in African rivers and lakes is at risk if longitudinal connectivity in the flow of energy, nutrients and organic matter is lost. Evidence shows that many populations are becoming locally extinct or reduced to small, fragmented stenotopic populations in rivers (Ojwang et al., 2007; Chemoiwa et al., 2013). Similarly, the diking of rivers or building of levees and draining of wetlands have limited lateral connectivity and exchanges of energy and other materials between the rivers and their floodplains (e.g., Junk et al., 1989; Winemiller and Jepsen, 1998). By confining rivers to their channels and limiting water and nutrient flows to floodplain lakes, depressions and wetlands, many species that are dependent on seasonal water level fluctuations for survival and reproduction are placed at a higher risk of becoming locally extirpated (e.g., Kishe-Machumu et al., 2018).

Knowledge gaps and future research needs

A synthesis of available data has identified some knowledge gaps in understanding the structure and function of riverine ecosystems in terms of trophic interactions and dynamics and the influence of human activities (Table 20.2). Although not exhaustive, the list of research needs and knowledge gaps aims to stimulate discussion on the information needed to better manage and protect African riverine ecosystems and safeguard ecosystem goods and services, including riverine fisheries relied upon by millions of people on the continent (see Dalu et al., 2024c, Chapter 29).

Data are limited on the effects of land use and land cover and the influence of flow regime components (base flows, floods and droughts) on the quality and supply of organic matter and trophic relationships in streams and rivers. As a corollary to this, there is a need for future studies to investigate spatial and temporal variations in food web structure. These studies should be tied to those investigating the role and influence of nutrient and organic matter loading from farmlands, wildlife, such as hippopotami, livestock and urban areas on aquatic communities and ecosystem processes, including trophic dynamics (Masese et al., 2018, 2020b; Stears et al., 2018; Subalusky et al., 2018).

Given the scarcity of data on tropical stream food webs and the potential for differences in food web attributes and energy flow between different-sized streams, the need for investigations on Afrotropical streams and rivers similar to those undertaken on other tropical and temperate counterparts. Similalry, food webs in large rivers are said to rely on organic matter derived from forested upper reaches (Vannote et al., 1980). However, longitudinal importance of the different sources of energy in African rivers require more investigation to clarify the emerging contradictions arising from studies in the tropics (e.g., (Hadwen et al., 2010b)). The climatic difference, seasonal heterogeneity and the role of large mammalian herbivores offered by large African rivers offer perfect conditions for contributing to the discussions.

Studies on the ecology, feeding habits, trophic and environmental guilds of riverine communities are needed to augment understanding of biotope preferences and flow requirements of threatened and vulnerable species. Some of the most comprehensive studies on diet composition and feeding habits of riverine fishes were done more than 50 years ago (Corbet, 1961; Jackson, 1961), and need to be updated in response to the changing environmental conditions in rivers (e.g., Olowo and Chapman, 1999). Although many studies are using biomarkers such as stable isotopes and fatty acids, the scale is still very limited. For instance, fatty acids have only been used in studies in South Africa, and the knowledge of their use seems limited in other countries. The use of stable isotopes is also limited by cost and expertise; most research is done through collaborations with researchers outside the continent where samples are being analyzed. Such studies will inform their management and conservation, considering that the feeding habits of many rivers are not clearly understood and may change because of changes in environmental conditions. Considering that most riverine fishes in African rivers incorporate insects to some extent in their diets (Corbet, 1961; Masese et al., 2014b; Nakangu et al., 2023), this points to the role a healthy river system must play for invertebrates as well as fish communities. Thus, insectivorous fishes occupy an important position in rivers and are a highly viable option for bioindication and other ecological studies.

TABLE 20.2 Research needs, gaps in knowledge and potential applicable tools in studies on trophic interations and trophic dynamics in aquatic ecosystems. Both lists of potential tools and related studies are not exhaustive.

Research needs	Knowledge gaps	Potentially applicable tools	Examples of similar studies
Ecosystem structure and function	- Energy sources and nutrient flows in food webs - Changes in dietary quality of basal resources - Drivers of species distributions - Long-term responses in fish community structure to land use and land cover change - Nutrient limitation and ecosystem productivity	- Trophic markers and stable isotopes - Stable isotopes, fatty acids, bioenergetic models - Population studies, ecological models - Population studies, ecological models - Nutrient additions experiments, nutrient diffusing substrates	- Masese et al. (2015, 2018). - Garcia et al. (2017), Jochum et al. (2017), Richoux et al. (2018). - Masese et al. (2014a, 2014b), Fugère et al. (2016, 2018a). - Fugère et al. (2018b), Leitão et al. (2018). - Subalusky et al. (2018).
Ecosystems connectivity	- Status of fish migrations, status of riverine fisheries and the importance of migratory species - Longitudinal importance of different sources of carbon/nutrients in rivers and effects of point sources, livestock and municipal and industrial discharges	- Acoustic telemetry, tagging studies, stable isotopes, otolith microchemistry, molecular biomarkers (fatty acid, DNA barcoding) - Trophic markers, ecological models, remote sensing	- Secor et al. (1995), O'Brien et al. (2013), Hart et al. (2015), Chemoiwa et al. (2013). - Ojwang et al. (2007), Hadwen et al. (2010b), O'Brien et al. (2013, 2024), Cross et al. (2013).
Effects of altered flow regimes	- Effects of reduced or altered flows on biodiversity and ecosystem functioning - Resilience and vulnerabilities of species and processes to altered or reduced flows - Determination of environmental flows for rivers - Effects of prolonged droughts and low flows on invertebrate and fish populations	- Ecological models, mesocosm experiments, physiological studies - Population surveys, ecological models - Population surveys, ecological models - Population surveys; mesocosm experiments; ecological models	- Bunn and Arthington (2002), Arthington et al. (2010). - Wildhaber et al. (2017). - McClain et al. (2014), O'Brien et al. (2018). - Bogan et al. (2015), Leigh et al. (2016), Calapez et al. (2017).
Taxonomy and systematics of species	- Enhancement of species collections from neglected habitats and regions in the LVB - Preponderance of genetic introgression in different fish groups in rivers, e.g., cichlids and cyprinids - Description of new species, development of new species identification keys and/or updating existing keys and schema	- Surveys for specimen collections - Molecular/genetic biomarkers - Morphometry, meristics & molecular biomarkers (genetics)	- Mugo and Tweddle (1999), Kishe-Machumu et al. (2018). - Angienda et al. (2011), Schmidt et al. (2017). - Schmidt and Pezold (2011), Schmidt et al. (2015).
Effects of carbon and nutrients loading	- Influence of nutrient loading by large wildlife and livestock on invertebrates and fish diversity and functional structure - Interaction between flow variation and nutrient loading on species diversity - Influence of carbon and nutrient loading on balance between autotrophy and allochthony	- Population studies, ecological modelling, experimental mesocosms - Population surveys, experimental mesocosms, ecological modelling - Nutrient additions, experimental mesocosms, ecological modelling	- Masese et al. (2015, 2018), Subalusky et al. (2018). - Dawson et al. (2016), Dutton et al. (2018), Masese et al. (2018). - Masese et al. (2017), Subalusky et al. (2018).

Continued

TABLE 20.2 Research needs, gaps in knowledge and potential applicable tools in studies on trophic interations and trophic dynamics in aquatic ecosystems. Both lists of potential tools and related studies are not exhaustive.—cont'd

Research needs	Knowledge gaps	Potentially applicable tools	Examples of similar studies
Determination of biotope requirements of species	- Establishment of environmental flow requirements of species - Effect of biotope availability on invertebrates and fish communities - Classification of species into environmental guilds	- Population surveys, ecological modeling - Population surveys, ecological models - Population surveys	- Muñoz-Mas et al. (2019a, 2019b). - Fausch et al. (2001), Dallas (2007), Leitão et al. (2018). - Welcomme et al. (2006).
Feeding habits, diet composition and trophic relationships	- Influence of water quality and habitat on diet composition of invertebrates and fishes - Influence of altered flows diet composition and condition of fishes - Niche overlaps and competition between exotic and indigenous species - Incidence and occurrences of parasites and diseases in riverine fishes and their influence on fish condition	- Stomach content analysis, trophic markers - Stomach content analysis, trophic markers - Stomach content analysis, trophic markers - Physiological studies, pathological studies	- Corbet (1961), Olowo and Chapman (1999), Masese et al. (2015). - Nakangu et al. (2023), Sommer et al. (2024). - Zengeya et al. (2015), Masese et al. (2018). - Susdorf et al. (2018).
Exotic introductions	- Mapping distribution of exotic species in streams and rivers - Population trends, ecology and impact of exotic species	- GIS tools (remote sensing), species distribution models - Individual and population surveys, community studies	- Jean-Nicolas et al. (2017), Aschonitis et al. (2018). - Shechonge et al. (2019), Masese et al. (2020a).
Biomonitoring and risk assessment	- Assessment of ecological state of rivers - Ecological risk assessment of rivers and the riverine fisheries	- Use of indices of biotic integrity utilizing invertebrates and fish - Ecological models	- Karr and Chu (2000), Raburu and Masese (2012), Masese et al. (2013). - O'Brien and Wepener (2012), O'Brien et al. (2018).
Emerging contaminants	- Risks associated with the occurrence of emerging contaminants (e.g., pharmaceuticals and personal care products (PPCPs), polychlorinated biphenyls (PCBs), PFAS and persistent organic compounds (POPs) - Evaluation of harmful effects of these chemicals using persistence, bioaccumulation, and toxicity (PBT) criteria, including ecological effects	- Testing the persistence, bioaccumulation, and toxicity (PBT) criteria - Use of standardized protocols to quantify sublethal effects - Study the biological activity, exposure, and ecological effects of the chemicals	- Rosi-Marshall et al. (2015), Ebele et al. (2017). - Richmond et al. (2017), Sardiña et al. (2019). - Kandie et al. (2020), Nantaba et al. (2020).

Comprehensive mapping of exotic species in streams and rivers is needed to determine their status and trends. These data should include population characteristics (abundance, reproduction) and distribution. For instance, red swamp crayfish and trout have been introduced to many streams and rivers in eastern and southern Africa, but studies on their ecological effects have mainly been done in South Africa. Other widespread exotic species that should be assessed and their threats to indigenous species evaluated include Nile perch and Nile tilapia, among others.

Conclusion

Studies on food webs and knowledge of how aquatic ecosystems are nourished have a lot to contribute to sustainable management and conservation of the increasingly threatened Afrotropical streams and rivers. However, the lack of comparable studies across regions and systems has restricted generalizations about determinants of ecosystem structure and function and predicting the likely impacts of global and regional human disturbances, notably land use change, anthropogenic climate change and the associated variations in the natural flow regimes of streams and rivers. In part, a limited understanding of the functioning of Afrotropical riverine ecosystems impedes their sustainable management. In most cases, limited time series data on environmental and ecological conditions leads to a reliance on studies done in the temperate zone and elsewhere in the tropics to interpret existing information and develop management guidelines. While Afrotropical streams and rivers share several structural and functional attributes with their tropical counterparts where a lot of riverine ecological research has been done (e.g., Hong Kong, Australia and the Neotropics), some clear differences exist. For instance, Afrotropical streams and rivers in arid and semiarid savanna climates tend to be less predictable, more prone to unexpected floods and droughts and display a flashier flow regime. Moreover, African savannas are among the remaining terrestrial ecosystems hosting the largest populations of large wildlife on Earth, including large populations of terrestrial and semiaquatic herbivores. Streams and rivers draining these landscapes experience strong connectivity with terrestrial ecosystems in terms of inputs of organic matter and nutrients mediated by these animals through excretion and egestion. These unique characteristics of Afrotropical streams and rivers confer unique structural and functional dynamics that must be explored and better understood to devise appropriate management strategies. This chapter has identified several research needs that need to be addressed to increase our understanding of trophic interactions and dynamics and, consequently, develop appropriate measures for biodiversity conservation and sustainability of ecosystem goods and services deriving to millions of people in Africa.

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