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Land-Water Connections

A Gradient of Wildlife Subsidies Alters Riverine Food Web Structure

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ABSTRACT

1. Terrestrial subsidies play a key role in freshwater food web structure and ecosystem function. Animal-mediated subsidies in particular provide high quality resources that shape aquatic food webs. We know little about how the magnitude of wildlife subsidies affects food web structure and stability, and how this relationship is affected by abiotic factors such as river flow. We use a wildlife subsidy gradient (hippo dung and wildebeest carcasses) in the Mara River, Kenya, to quantify the effect of subsidy magnitude on consumer use of allochthonous resources and degree of omnivory. Furthermore, we examined this relationship across seasons and flow rates to determine whether discharge affected the relationship between wildlife subsidy magnitude and allochthonous resource use.
2. We selected three sites along the Mara River wildlife gradient with no, medium, and high wildlife input and obtained stable isotopes from dominant basal resources and consumers across invertebrate functional feeding groups and fish feeding guilds. Samples were collected across varying flows and seasons. We used Bayesian mixing models, with consumer gut contents as priors, to assess changes in the consumption and assimilation of dominant food sources by invertebrate and fish consumers across the subsidy gradient and flow rates.
3. The Mara River food web shifted from being driven by autochthonous basal resources to being increasingly driven by allochthonous resources along the wildlife subsidy gradient. Aquatic insects and fish increased their allochthonous resource use from 27% to 52% and from 2% to 73.5%, respectively, mostly through increased consumption of hippo dung and vertebrate material during the wildebeest migration season. This diet shift led to a higher level of omnivory and a decrease in mean trophic position for invertebrates. River flow affected isotope values of consumers but not their resources at the no and medium wildlife input sites. Flow had little impact on stable isotopes at the high input site.
4. Our results suggest that wildlife input provides an important resource for aquatic consumers and that its importance in the aquatic food web increases with its relative magnitude. Higher levels of animal-mediated subsidies also increased consumer reliance on multiple resource pathways, suggesting higher wildlife input may increase food web stability. Abiotic factors like river flow can affect the relationship between allochthonous resource use and consumers by altering the quantity of wildlife input, but our results suggest that this is only the case when there is medium to no wildlife input. We propose that in areas with high wildlife input, subsidies are sufficiently abundant that flow has little effect on the ability of organisms to access the resource.

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5. Our results show that the magnitude of wildlife subsidies helps shape aquatic food web structure and provide the basis for the ecological theory that increasing magnitude of resource subsidies increases food web stability.

1 | Introduction

Aquatic ecosystems often receive large inputs of subsidies from the surrounding terrestrial ecosystem, due in part to their location in the landscape, their concave shape, and their linkage through downhill flows of water (Hynes 1975; Leroux and Loreau 2008). Several decades of research show that these terrestrial subsidies can play an important role in shaping food web structure and ecosystem function (Polis et al. 1997; Nakano and Murakami 2001; Tank et al. 2010). Characteristics of both the resource subsidy and the recipient ecosystem can be important in shaping how an aquatic ecosystem responds to a subsidy (Marczak et al. 2007; Richardson et al. 2010; Subalusky and Post 2019). These characteristics are particularly important for shaping the quantity and quality of resource subsidies relative to in situ resources (Marcarelli et al. 2011).

The relative importance of autochthonous resources (those produced within the system) and allochthonous resources (those produced outside the system) to aquatic consumers is a function of resource quantity and quality as well as abiotic factors such as river flow (discharge). Much research has focused on large quantity subsidies that tend to be relatively low quality, such as riparian leaf fall into streams (Bartels et al. 2012). These subsidies can play an important role in ecosystem energetics, driving an aquatic ecosystem to net heterotrophy (Marcarelli et al. 2011), but they have fairly low nutritional quality and are less important in driving secondary production (Brett et al. 2017; Marks 2019). Smaller subsidies of higher quality, such as deposition of terrestrial insects, can be disproportionately important in aquatic food webs (Nakano and Murakami 2001). Autochthonous algal production can also play a disproportionately important role in aquatic food webs despite often being a fraction of terrestrial carbon inputs (Brett et al. 2017), due to its high concentration of elemental nutrients and long-chain polyunsaturated fatty acids (Twining et al. 2019). In rivers, flow can act as an important variable to determine the relative balance of allochthonous and autochthonous resources. Discharge can concentrate allochthonous inputs during low flows and disperse inputs during high flows, potentially influencing their availability to consumers (Humphries et al. 2014; Frauendorf et al. 2019). Following floods, autochthonous resources can be scoured and consumers can become more reliant on allochthonous resources (Larsen et al. 2016; Frauendorf et al. 2019).

The magnitude of a resource subsidy in particular can play an important role in determining food web structure and stability. A robust body of theory suggests that low to intermediate levels of coupling across multiple resource pathways (allochthonous/autochthonous, brown/green, plant/animal, or across multiple trophic positions; often referred to as omnivory) can stabilize food webs and increase community persistence, whereas strong coupling and high levels of subsidies decrease food web stability and increase the strength of trophic cascades (McCann et al. 1998; Post et al. 2000; Takimoto et al. 2002; Moore et al. 2004). Empirical studies have shown that subsidy magnitude can influence food web stability through functional changes in recipient communities (Jones and Lennon 2015; Muscarella et al. 2016), and by coupling of resource pathways (Cross et al. 2013, https://www.zotero.org/google-docs/?sjCyko; Wolkovich et al. 2014, https://www.zotero.org/google-docs/?sjCyko). However, the influence of subsidy magnitude can be difficult to disentangle from other variables in natural systems, in which drivers of subsidy input may covary with factors such as rainfall, temperature, and discharge.

We used a natural gradient of resource subsidies along the Mara River in East Africa to test the influence of subsidy quantity and quality across varying river discharge on food web structure and feeding across multiple resource pathways as a potential indicator of food web stability. This gradient is created by the input of organic matter by large wildlife, with the highest concentrations of allochthonous inputs found along the most downstream reaches of the Mara River. Hippopotamus (*Hippopotamus amphibius*, hereafter hippos) feed in the grasslands at night and spend the day in water where they defecate and urinate, moving 36,000 kg/day of partially digested and relatively low quality organic matter and associated nutrients from the land to the water (Subalusky et al. 2015, 2018). Research in other systems has shown that hippo inputs are a resource subsidy for aquatic food webs (Grey and Harper 2002; Stears et al. 2018; Dawson et al. 2020). Hippo inputs are relatively consistent throughout the year; however, river discharge can influence hippo faeces distribution and accessibility to consumers, as it aggregates on the river bottom during low flows and stays more suspended in the water column during high flows (Subalusky et al. 2018). The distinct stable isotope value ($\delta^{13}C$) of C4 savanna grasses consumed and defecated by hippos allows these detrital inputs to be parsed from autochthonous aquatic production in consumer diets. Prior research in the Mara River notes that C3 can be a significant source of energy for parts of the river, but it is mostly from autochthonous production (e.g., periphyton, Masese et al. 2022). The Mara River is also part of the migratory route of the Serengeti wildebeest (*Connochaetes taurinus*). Annual river crossings occasionally result in mass drownings of hundreds to thousands of individuals (Subalusky et al. 2017). Associated carcass inputs provide a high quality (i.e., low C:N) terrestrial input at the most downstream sites when the migration is in the region between July and November. Drownings are unlikely to occur at very low flows, as the wildebeest can easily wade across the river, so these inputs tend to occur under medium to high flow conditions. The same savanna grasses that hippos consume are also consumed by wildebeest, giving both inputs a similar $\delta^{13}C$; however, isotopic fractionation during assimilation into wildebeest body material leads to ^{15}N enrichment, which allows carcass inputs to be further differentiated from hippo inputs using $\delta^{15}N$ values (Subalusky et al. 2017). Although wildebeest

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have the enriched $\delta^{15}N$ of a primary consumer, their carcasses represent a detrital input at the base of the river food web.

Aquatic consumers in the Mara River incorporate an increasing proportion of terrestrial resources at sites with greater magnitude of wildlife and livestock input (Masese et al. 2015; Subalusky et al. 2017). These inputs were correlated with decreased trophic diversity and decreased trophic niche width in aquatic consumers, although the results varied by taxa and by season (Masese et al. 2018). Dry season consumption tended to be more balanced between autochthonous and allochthonous production, possibly due to the fertilizing effect of concentrated wildlife inputs on benthic biofilm, and wet season production tended to be more subsidized by allochthonous inputs, possibly due to the negative effect of increased water column turbidity on in stream production (Masese et al. 2015, 2018). The impacts of wildlife subsidies on insect diversity and consumption suggest there could be strong impacts on food web structure and stability. Furthermore, these impacts may be influenced by differences in river discharge between seasons, which modulates the availability of both autochthonous production and allochthonous resources. Here we use the natural gradient of wildlife inputs in the Mara and seasonal variations in river discharge to investigate relationships between inputs and food web structure. This study builds on previous work by asking how flow influences basal resource and consumer isotope ratios, if the animal subsidy within the food web is derived from direct (e.g., consuming hippo dung, wildebeest) or indirect consumption (e.g., consuming periphyton from hippo dung/wildebeest waters), and parsing out spatial and temporal differences in the relative contribution of dominant resources for consumers. Lastly, we incorporate invertebrates and vertebrates as food sources into our results to determine how the degree of omnivory and multichannel feeding changes across a magnitude of animal subsidies.

We conducted food web sampling at three sites in the Mara River, Kenya, along a gradient of subsidy input including no hippo input, medium hippo input, and high hippo input with and without wildebeest carcasses available (Subalusky et al. 2018). We collected samples of autochthonous resources and aquatic macroinvertebrates monthly throughout a hydrological year, and samples of fish seasonally, to capture the influence of discharge on allochthonous inputs and food web structure. It can be difficult to parse wet and dry seasons in the tropics, particularly in regions with bimodal rainfall peaks, so monthly sampling becomes important to understand discharge effects. We used both direct diet and stable isotope analyses of aquatic insects and fishes, in concert with Bayesian mixing models, to quantify consumption and assimilation of different food resources. We then analysed the spatial and temporal variability in food web structure in response to different quantities and qualities of subsidies and discharge. We hypothesized there would be an increase in multichannel feeding due to the influence of allochthonous inputs from hippos and wildebeest from upstream to downstream sites, corresponding with a shift towards a detrital-based food web along this gradient. We also hypothesized a larger reliance on plant material with increasing wildlife inputs, leading to a decrease in mean trophic position of aquatic macroinvertebrates and fishes. Finally, we hypothesized that seasonal variation in discharge would influence the degree of allochthony and animal resource use by changing the availability of subsidies from both hippos and wildebeest.

2 | Methods

2.1 | Site Description

The Mara River is a 5th order river that flows from forested headwaters in Kenya through the Maasai Mara National Reserve (MMNR) and Serengeti National Park into Lake Victoria, Tanzania. In this region the seasons are characterized by wet periods (March–June and October–December) and dry periods (January–February and July–October). We established three study sites along the Mara River. Emarti Bridge is near the confluence of the two tributaries that form the Mara River, has virtually no large wildlife population upstream, and therefore has no wildlife inputs (hereafter the no input site). Old Mara Bridge is 51 river km downstream of Emarti and at the northern border of MMNR. There are ~1400 hippos upstream of this site, creating an intermediate loading of organic matter and nutrients (medium input site). New Mara Bridge is 125 river km further downstream, near the Kenya-Tanzania border, and represents our high input site. There are a total of ~4000 hippos upstream of this site and numerous wildebeest crossings between the Old Mara Bridge and the New Mara Bridge from July–November. The median Mara River discharge (recorded at New Mara Bridge, 2011–2020) is 9.33 m^3/s with a maximum discharge of 318.46 m^3/s and a minimum of 0.02 m^3/s. The variation in land cover between our no input and high input site is 58%–65% agriculture, 18%–22% forest, 9%–10% shrub, and 3%–13% grassland, indicating that there are no major differences in land cover between sites.

2.2 | Impacts on Resource Pathways

We conducted three intensive sampling events during a typical dry (25–27 February 2014, avg. discharge = 2.35 m^3/s), wet (28–30 June 2016, avg. discharge = 16.75 m^3/s), and wildebeest wet (27–30 November 2013, avg. discharge = 7.52 m^3/s) season month. Wildebeest wet season indicates a time during the wet season when wildebeest cross the Mara River, occasionally resulting in mass drownings (Subalusky et al. 2017). We sampled across this discharge gradient because we expected it to influence the importance of allochthonous inputs and food web structure. It also allowed us to capture the seasonal variation in $\delta^{13}C$ of basal resources that might emerge from the impact of flow variation on boundary layer thickness and carbon diffusion (Keeley and Sandquist 1992; Finlay et al. 1999). We measured the stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of common basal resources (biofilm, coarse particulate organic matter (CPOM), fine particulate organic material (FPOM), and wildebeest tissue (WB)) and from consumers (dominant fish and macroinvertebrate taxa) in the river. As results will show, hippo dung is the dominant component of CPOM at medium and high input sites (composed of C4 grasses), while C3 leaf material is the dominant component of CPOM at the no input site. Additionally, we measured the degree of allochthony, animal resource use, and trophic position along our wildlife input gradient to determine how wildlife resources can impact multiple resource pathways.

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We analysed gut contents from consumers to use as priors informing Bayesian mixing models to determine the degree of allochthony and animal resource use shifts along the wildlife input gradient.

2.2.1 | Stable Isotope Collection and Analysis

We measured the $\delta^{13}C$ and $\delta^{15}N$ of biofilm by scraping Mara River bedrock and boulders ($n = 3–5$ per site, per season) and filtering each sample through a 25 mm pre-combusted GF/C filter paper. We collected CPOM (> 1 mm, $n = 2–4$ per site per season) within the river using a 1000 μm kicknet (Wildco, Yulie, FL, USA). We collected samples of C4 (grasses, forbs, sedges, and rushes) and C3 (leaves from *Acacia*, *Warbugia*, and other riparian trees) plants ($n = 2–4$ each per site per season) from the riparian zone at each site, as well as fresh hippo faeces from the medium input and high input sites ($n = 6–8$ per site), to examine their potential contribution to CPOM within the river. Lastly, we collected muscle tissue from 9 freshly drowned wildebeest (3 males, 3 females, and 3 subadults) during November 2012.

We used a kicknet to collect dominant invertebrate taxa from each of the functional feeding groups (FFG) (collectors (Co), scrapers (Sc), and predators (P)). Shredders were not common at our sites, and we were not able to obtain enough mass from this FFG to run stable isotopes. Depending on the size of the invertebrates, we collected between 1 and 45 individuals per sample and we analysed 2–11 replicate samples per site and per season (Table S1). Secondly, we obtained 20–50 fish tissue samples per site and season from the lateral muscle of common insectivorous (In) and omnivorous (Om) fishes. These included *Barbus nyanzae*, *Clarias gariepinus*, *Labeobarbus altianalis*, and *Labeo victorianus*.

All samples were dried at 60°C for at least 2 days, ground, and analysed for $\delta^{13}C$ and $\delta^{15}N$ on a ThermoFinnigan Delta Plus Advantage stable-isotope mass spectrometer (Thermo Scientific, Boca Raton, FL, United States) coupled to a Costech ECS 4010 Elemental Analyser (Costech Analytical Technologies Inc., Valencia, CA, United States). To account for lipids in our stable isotope data, we applied a mathematical correction for samples that had a C:N above 3.5 following recommendations from Post et al. (2007).

2.2.2 | Direct Diet Analysis

Macroinvertebrate and fish gut contents were collected at the same time as the stable isotope samples. We obtained 2–5 replicates of each invertebrate functional feeding group and fish guild (Table S1) for each season and site and preserved them in ethanol. The entire gut tract was removed and analysed for each invertebrate. We removed and analysed stomach contents for fish species with a defined stomach (*Barbus nyanzae*). For fish without a stomach (all other species), we took a homogenized sub-sample from the front, middle, and end of the fish tract, which was on average 21.5% of the total gut tract. All fish gut samples had to be diluted by 300:1 in order to use the same filter pore size between the invertebrates and fish, to capture diatoms, and to have little overlay of material.

Using methods described in Frauendorf et al. (2013) and Rosi-Marshall et al. (2016), we suspended gut contents from each invertebrate and fish in water and sonicated them for 30 s after which we filtered the content onto a nitrocellulose membrane filter (0.45 μm pore size, Millipore Sigma, Burlington, MA). Filters were dried at 60°C, placed on microscope slides, and cleared with Type B immersion oil. Ten photos were taken from random areas of each slide at 200× magnification for fish and 400× magnification for invertebrates. We then used the Fiji image processing program to identify particles and measure the area of individual particles (μm^2) (Schindelin et al. 2012). After summing individual particle areas of each food type from the ten pictures, we calculated the percent of each food type consumed relative to total food cover in ten pictures for each individual. Particles were classified as biofilm (includes fungal hyphae, filamentous algae, diatoms, and non-algal biofilm), leaf and grass, vertebrate, insect, and inorganic material.

2.2.3 | Bayesian Mixing Model

We used the Bayesian mixing model MixSIAR to estimate how much of each resource type was assimilated into invertebrate and fish tissue based on the $\delta^{13}C$ and $\delta^{15}N$ of the resources and consumers (Stock et al. 2018). We added informative priors to our models that were based on our diet data (Code S1). We rescaled the importance of the priors for fish because our analysed gut contents represented only 0.06%–2.5% with dilutions of the entire gut tract by dividing the priors by our number of sources (4, Stock et al. 2018), while we did not downscale our priors for the invertebrates since we used 100% of the gut contents. To have a meaningful model output, we narrowed our sources for the models to the four following categories: biofilm, CPOM (comprised of leaf and grass detritus from riparian vegetation and hippo faeces at downstream sites), fish, and invertebrates. We added wildebeest tissue as a fifth source to our model at the high input site during the wildebeest wet season. We did not include FPOM as a separate diet source because it is an amalgamation of biofilm and CPOM. We also used MixSIAR to examine any compositional changes in FPOM and CPOM along the gradient of hippo input, using biofilm and CPOM as FPOM sources, and C4 and C3 plants as CPOM sources for the model. We used a nitrogen discrimination factor of 2.3‰ (SD = 0.18‰) for insects and 3.4‰ (SD = 1‰) for fish, and we used a carbon discrimination factor of 0.4‰ (SD = 0.12‰) for both insects and fish (Post 2002; McCutchan et al. 2003; Bunn et al. 2013).

Using the results from our Bayesian mixing models, we estimated percent allochthony for each fish and invertebrate FFG at each site and season by dividing the percent CPOM and wildebeest tissue (when available) assimilated by the sum of materials assimilated (biofilm, CPOM, and wildebeest tissue). These calculations are likely conservative, as they do not include indirect allochthony, in which invertebrates or fish consume prey that themselves consumed allochthonous resources. However, that is beyond the scope of what we could determine using our diet methods. These estimates indicate the frequency of multichannel feeding, as wildebeest tissue and CPOM both represent detrital/brown food web pathways and biofilm represents an algal/green food web pathway.

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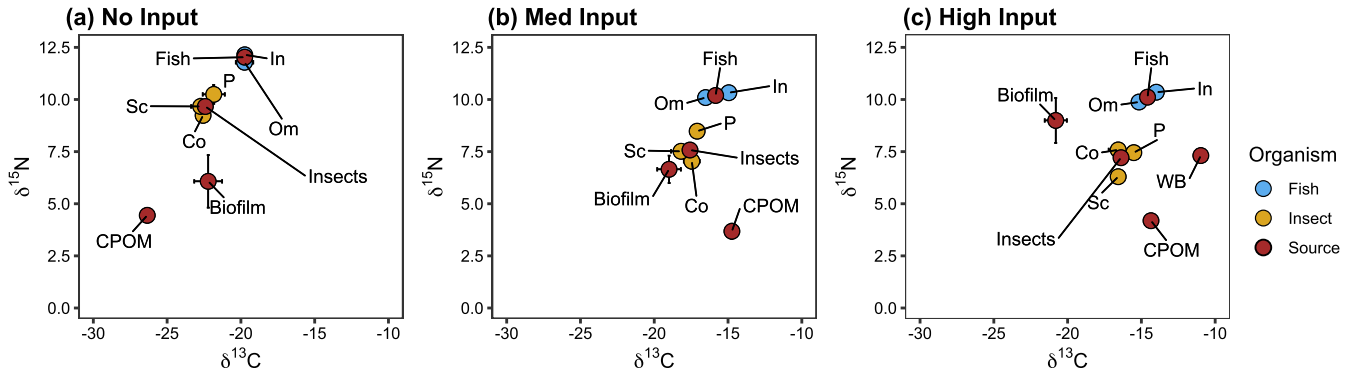

FIGURE 1 | Average isotope values (±SD) from consumers (omnivorous (Om) and insectivorous (In) fish; invertebrate scrapers (Sc), collectors (Co), and predators (P)) and dominant resources (biofilm, coarse particulate organic matter [CPOM], wildebeest tissue [WB]) across three sites that increase in wildlife input along the Mara River. These averages are a composite of values across wet and dry seasons.

We also calculated the percent animal vs. plant consumption for fish and invertebrate FFGs for each site and season, because these represent two distinct resource pathways within this system. The percent animal resources consumed was calculated by dividing the sum of percent invertebrate and vertebrate material assimilated by the sum of all sources that were included in our mixing models. Lastly, we calculated the trophic position of each FFG using methods described in Post (2002). For the trophic position of N_{base} (λ), we selected 2 if consumers had a diet containing > 80% algal or detrital resources and 3 if the consumer diet contained > 80% fish or invertebrate resources based on the MixSIAR results. A trophic position of 2.5 was selected for any consumers that fell in between.

2.3 | Effects of River Flow

2.3.1 | Stable Isotope Collection and Analysis

To examine the influence of discharge variability on stable isotope ratios of primary producers and invertebrates, we opportunistically collected resources and macroinvertebrate consumers across a range of discharge between June 2011 and June 2016, and we analysed those samples for stable isotopes. Biofilm (n = 2–7 at 8 different discharge levels per site) was scraped from ceramic tiles placed in the river at least 1 month prior to sampling, and the sample was filtered through a 25 mm pre-combusted GF/C filter paper. CPOM (> 1 mm, n = 3–6 at 12 different flow rates per site) was collected within the river using a Wildco 1000 μm kicknet. We sampled FPOM (< 1 mm, n = 1–4 at 10 different flow rates per site) from the water column using grab samples of water from a well-mixed portion of the river. We pre-filtered the sample through a 1 mm sieve to remove any accumulated CPOM. Samples were then filtered through a 25 mm pre-combusted GF/C filter paper. A portion of these filter papers was acid fumigated (HCl for 24 h) due to high sediment loads in the river, but analysis indicated minimal impacts on isotopic values due to low levels of carbonates in the system. Therefore, we combined fumigated and non-fumigated samples for further analysis. We collected common macroinvertebrate taxa from each functional feeding group (except shredders) using a 1000 um Wildco kicknet across 13 different flow rates at each of the three sites (n = 1–5 per site). All samples were dried at 60°C for at least 2 days, ground and analysed for $\delta^{13}C$ and $\delta^{15}N$ on a ThermoFinnigan Delta Plus Advantage stable-isotope mass spectrometer coupled to a Costech ECS 4010 Elemental Analyser.

2.3.2 | Discharge Statistics

We measured discharge continuously every 15 min using a Eureka Manta2 sonde with an installed depth probe (Eureka Water Probes, Austin, TX, USA) at a rated cross-section at the high input site (Dutton et al. 2018) from May 2011–July 2016. We calculated the average flow, peak flow (Q_{10}) and baseflow (Q_{90}), and flow variability (Q_{10}/Q_{90}) for the 2 weeks before each sampling event. We ran generalized linear models to determine the relationships between each flow variable and the $\delta^{13}C$ and $\delta^{15}N$ values of the resources and invertebrate consumers. We used the "lme4" and "pscl" (to extract R^2 values) packages from the statistical program R (Bates et al. 2015; Jackman 2017; R Core Team 2023, https://www.zotero.org/google-docs/?0vm3y6).

3 | Results

Overall, resources and consumers became more enriched in ^{13}C and slightly more depleted in ^{15}N with increases in wildlife input in the Mara River (Figure 1). The $\delta^{13}C$ value of the CPOM became less negative by around 12‰ from the low input site to the high input site, indicating that hippo inputs shifted the carbon composition of CPOM from that of C3 plants to that of C4 grasses. Consumers (fish and insects) reflect the shift in carbon resources, as their $\delta^{13}C$ increased by 5‰–6‰ with high wildlife input. In contrast, the $\delta^{13}C$ of biofilm shifted comparatively little across the three sites. The $\delta^{15}N$ of resources and consumers showed comparatively small declines, around 2‰ for most groups, from the no input to the high input site. The exception to this trend is the $\delta^{15}N$ of biofilm, which increased by around 3‰ along the loading gradient.

3.1 | Shifts in Resource and Consumer Composition

We examined the composition of CPOM and FPOM across sites with varying degrees of wildlife input to quantify shifts

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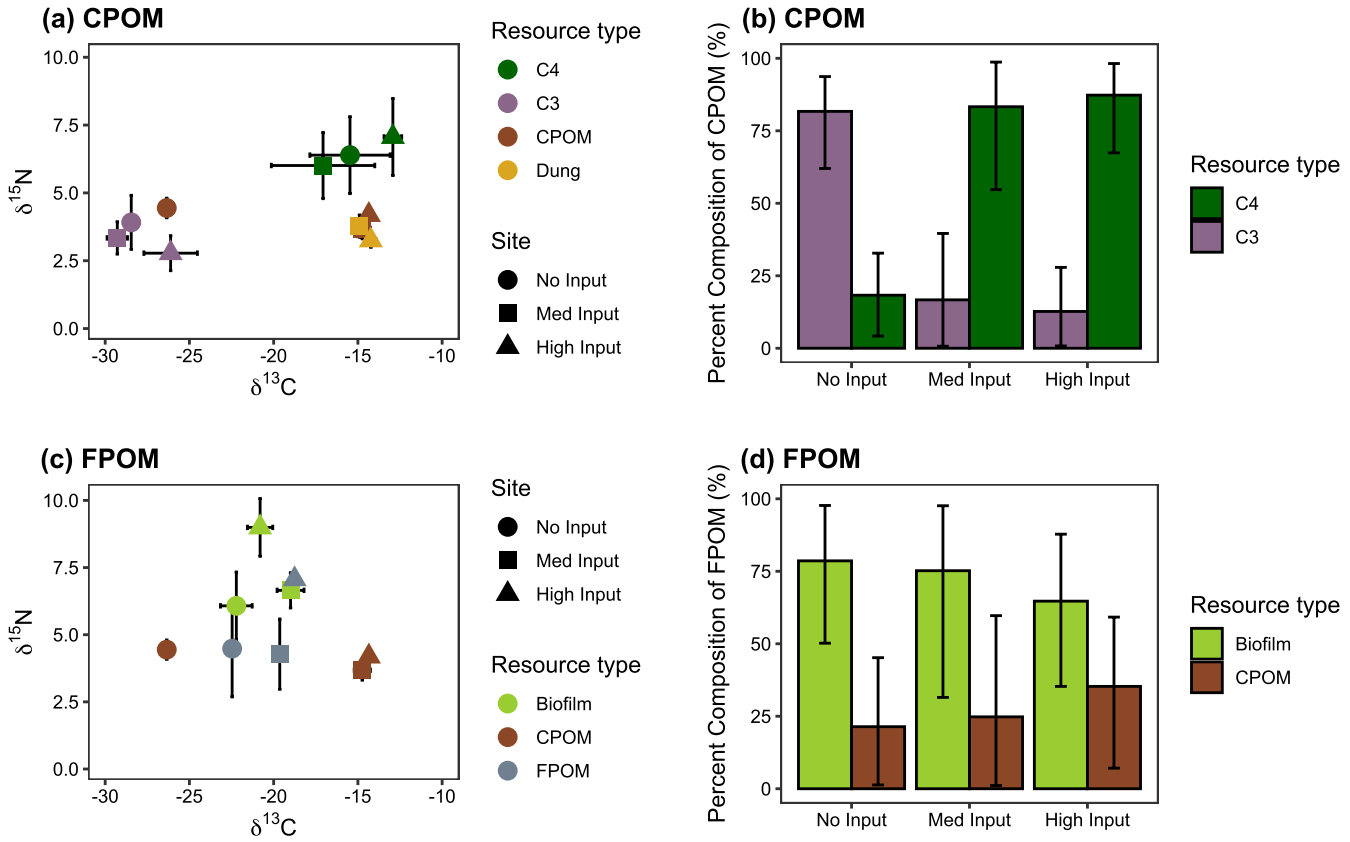

FIGURE 2 | Isotope values of coarse (a; CPOM) and fine (c; FPOM) particulate organic material in relation to other resource types across three sites in the Mara River with varying degrees of wildlife input. Using MixSIAR to estimate the composition of CPOM (b) and FPOM (d), we found that on average (95% CI) CPOM was composed mostly of C3 leaves at the no input site and C4 grass at sites with medium and high input by wildlife. FPOM was composed mostly of biofilm across all three sites.

in their isotope signature and composition. The $\delta^{13}C$ of CPOM at the no input site was −26.3‰, similar to that of C3 riparian leaves, while the $\delta^{13}C$ of CPOM at the medium and high input sites was −14.7‰ and −14.4‰, respectively, similar to that of C4 grasses (Figure 2a). Based on MixSIAR results, we estimated that CPOM is composed primarily of riparian leaf vegetation (81.7%, 95% credible intervals (CI) at 62.0% and 95.8%) at the no input site, and mostly C4 grasses at the medium and high input sites (83.3% with CI at 54.7% and 99.3%; 87.3% with CI at 67.4% and 99.2%, respectively; Figure 2b). The isotope values of CPOM at both medium and high input sites overlap with that of hippo dung (Figure 2a), supporting our hypothesis that CPOM at these sites primarily originates from hippo dung. FPOM on the other hand is largely composed of biofilm with an average composition of 72.8% (CI: 39.8%, 96.8%) biofilm across sites, although with a slight decline in proportion of biofilm and increase in proportion of CPOM as hippo inputs increased (Figure 2d).

Invertebrates and fish assimilated less biofilm and more CPOM as wildlife inputs increased from the no input to the high input site. Based on MixSIAR results, the percent biofilm assimilated in invertebrate tissue declined by 17.4%, while the amount of CPOM assimilated increased by 7.7% between the no and high input sites (Figure 3a). Fish had similar but larger increases in CPOM and decreases in biofilm across the wildlife input gradient. The percent of biofilm assimilated by fish declined by 40.8% at high input sites, while the amount of CPOM assimilated increased by 25.3% (Figure 3b).

Invertebrates and fish showed little variation in assimilation of invertebrate material across the wildlife input gradient, but both assimilated larger percentages of vertebrate material at the high input site (Figure 3). Invertebrates increased fish and wildebeest assimilation at the high input site (up to 8% each) while fish doubled the vertebrate assimilation at the high input site (from 14.1% (CI: 7.4%, 21.8%) to 30.5% (CI: 8.1%, 41.7%)), which was driven by higher assimilation of wildebeest material (up to 39.5%). Overall, fish had a large degree of variation across sites, likely driven by the relatively smaller sample sizes for fish compared to invertebrates. We note that, while the stomach content data are often aligned with stable isotope results, there were several occasions where these results diverged (Table S2). As a result, MixSIAR results more or less reflected the divergent data depending on the weighting of the priors.

3.2 | Allochthony, Animal Resource Use, and Trophic Position

We saw an increase in allochthonous resources assimilated at sites along the gradient of wildlife inputs. Invertebrate allochthony increased from 27% ± 3.5% at the no input site to

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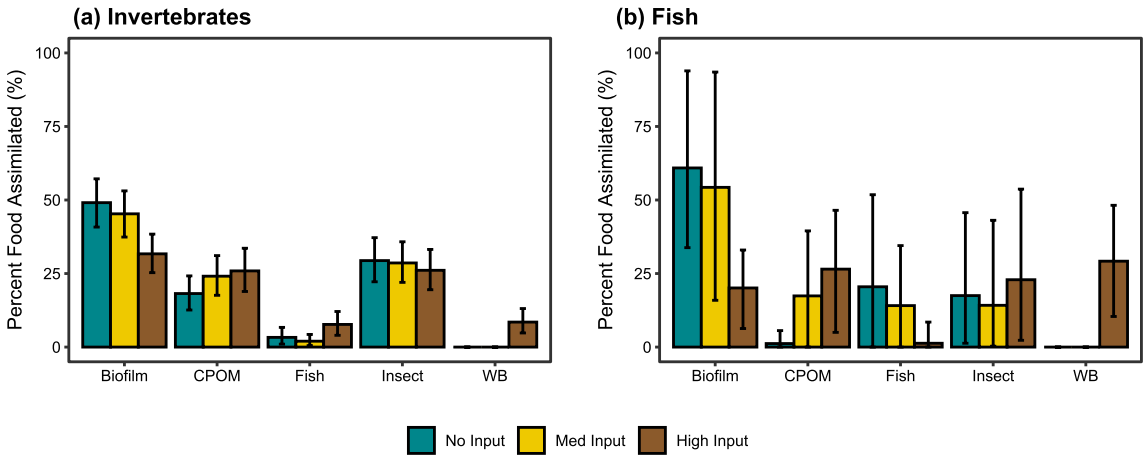

FIGURE 3 | MixSIAR results showing the average % assimilated (95% CI) biofilm, coarse particulate organic matter (CPOM), insect, and fish and wildebeest (WB) in invertebrate (a) and fish (b) tissue.

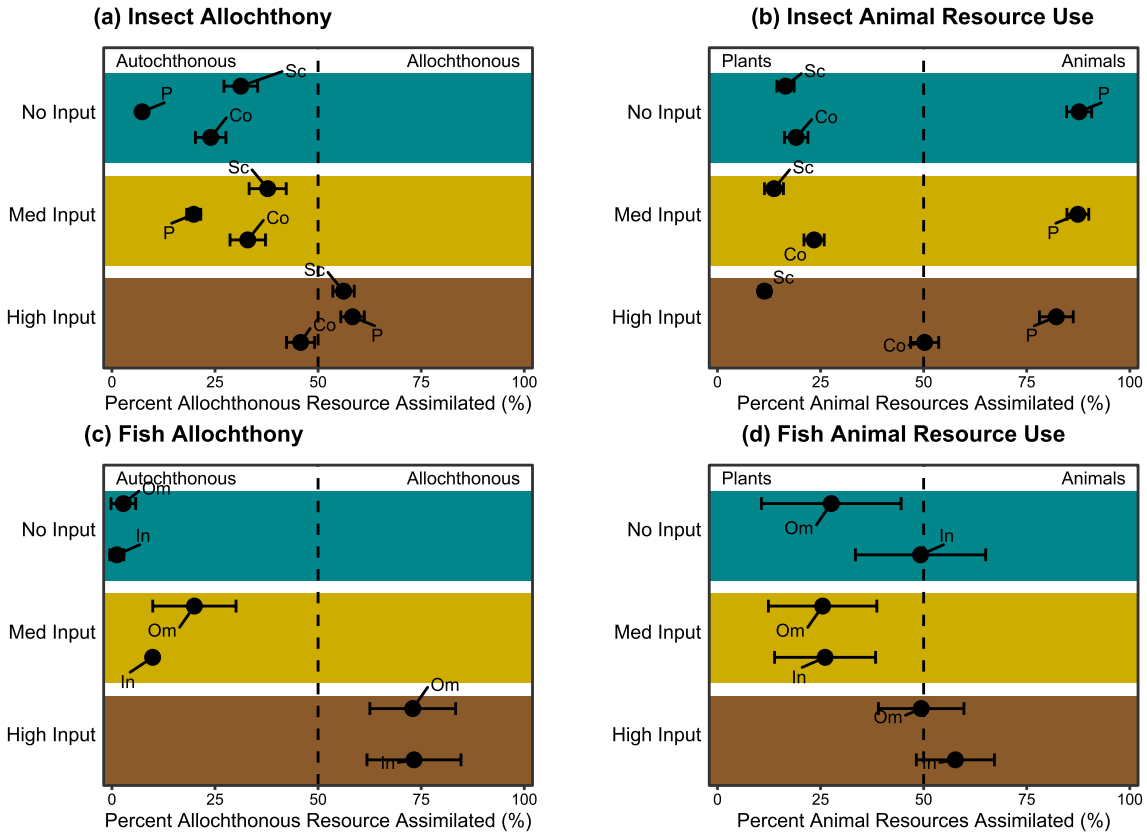

FIGURE 4 | Average percent (±SD) of allochthonous resources assimilated in insect (a; scraper [Sc], collector [Co], and predator [P]) and fish (c; omnivore [Om], insectivore [In]) tissue across three Mara River sites that varied in the amount of wildlife input. The average percent of animal resources assimilated (±SD) is shown for different insect (b) and fish (d) feeding groups.

52.0% ± 3.5% at the high input site, and the increase was consistent across all functional feeding groups (Figure 4a). Fish displayed a much larger increase from 1.9% ± 2.2% at the no input site to 24.3% ± 14% at the medium input site and 73.5% ± 11.6% at the high input site (Figure 4c). These shifts were similar between both fish feeding guilds.

Overall the degree of animal resource use did not shift significantly as the magnitude of wildlife input increased. We only saw a clear shift towards increased animal assimilation for invertebrate collectors at the high input site (Figure 4b, from 19.1 ± 2.8 at no input to 50.3 ± 3.4 at high input). Omnivorous fish increased their percent of animal material assimilated at the high input site (from 27.6% ± 17.0% at no input to 49.4% ± 10.4% at high input), but there was considerable variation across all the data (Figure 4d).

As wildlife inputs increased, the trophic position of invertebrates decreased on average by one trophic level, but there was little directional change in the overall trophic position of

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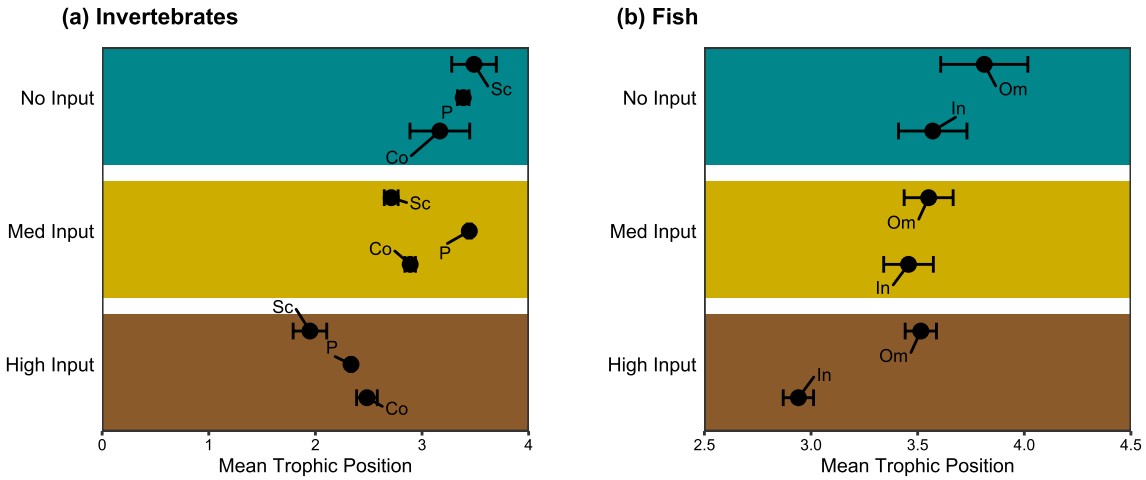

FIGURE 5 | Mean trophic position (±SD) of invertebrates (a; scraper [Sc], collector [Co], and predator [P]) and fish (c; omnivore [Om], insectivore [In]) across three sites in the Mara River that increased in wildlife input. Note that the x-axes are on different scales.

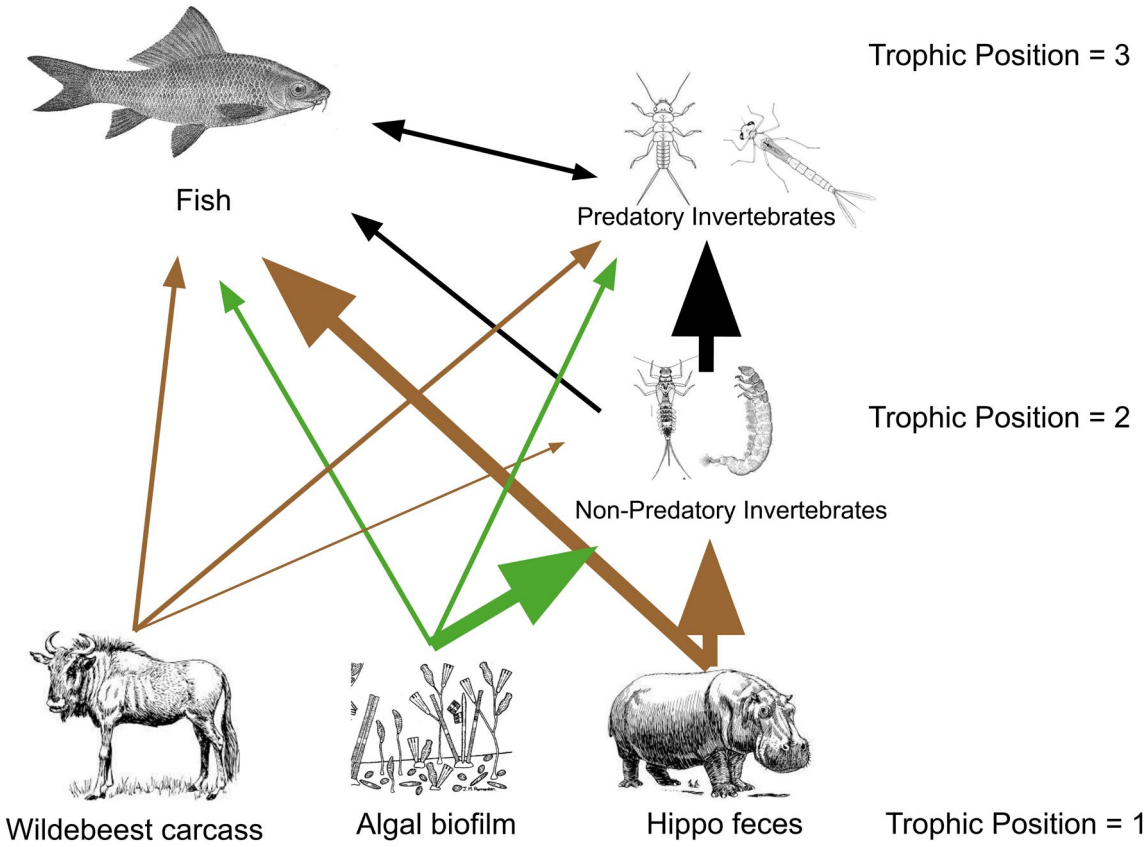

FIGURE 6 | Food web diagram for the Mara River with high input of wildlife, illustrating the multiple resource pathways through omnivory and multi-channel feeding. Brown arrows = detrital food web; green arrows = algal food web; black arrows = secondary consumption, which may be comprised of both detrital and algal consumers. Arrow widths are proportional to % assimilation as indicated by Figure 3, where the smallest arrow represents 5%–10% assimilation, medium sized arrow 11%–25% assimilation and the largest arrow 26%–50% assimilation of a food source.

fish (Figure 5). The trophic position of invertebrates decreased from 3.17 ± 0.28 to 2.48 ± 0.1 for collectors, from 3.39 ± 0.06 to 2.33 ± 0.02 for predators, and from 3.49 ± 0.21 to 1.95 ± 0.16 for scrapers. Fish had an overall mean trophic position of 3.47 ± 0.29 across all sites. Insectivorous fish decreased their trophic position from 3.6 ± 0.16 to 2.94 ± 0.07 with increases in wildlife inputs, while omnivorous fish remained relatively stable across the input gradient.

To illustrate the frequency of muti-channel feeding at the high input site, and the influence of the algal vs. detrital and animal vs. plant components, we diagrammed the river food web with

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arrows weighted relative to assimilation estimates from our Bayesian mixing models (Figure 6).

3.3 | Influence of Seasonality and River Flow

We examined the degree of allochthony and omnivory by season for our three intensive sampling seasons (dry, wet, wildebeest wet). Insects consumed more allochthonous resources during the wet season compared to the dry season, especially at the high input site (Figure 7a). There was seasonal variation in allochthony by fishes, but the patterns were not consistent by site (Figure 7c). The percent animal resources assimilated did not vary much between seasons across sites for either insects or fish, possibly due to a large degree of variability in the data (Figure 7b,d). However, insects did have a higher degree of animal resource use at the high input site during the wildebeest-wet season when carcasses were in the river.

River flow had little effect on the stable isotope values of food sources in the Mara River, but it did change the $\delta^{13}C$ and $\delta^{15}N$ of insect consumers. On average, base flows (Q_{90}), peak flows (Q_{10}), and flow variability did not show significant correlations with $\delta^{13}C$ and $\delta^{15}N$ of biofilm, FPOM, or, for the most part, CPOM at any of the sites in the Mara River (Figure 8, Table S3). The only exception was the $\delta^{15}N$ of CPOM, which decreased slightly from 4.1‰ to 2.4‰ as baseflow increased at the medium input site ($R = 0.34$, $p = 0.048$).

In contrast, the $\delta^{13}C$ of insect tissue increased from −23.6‰ to −21.9‰ with increasing flow at the no input site (Figure 8d, $p < 0.001$), but decreased from −16‰ to −18.2‰ with flow at the medium input site ($p < 0.001$), and had no change at the high input site ($p = 0.39$). When examined by functional feeding groups, this pattern was largely driven by collectors, while predators only showed the decrease in $\delta^{13}C$ with increasing flow at the medium input site ($p = 0.009$, Figure S1). Scrapers did not vary in $\delta^{13}C$ across flow levels at any sites (Figure S1). The $\delta^{15}N$ of insects decreased from 10.8‰ to 9.4‰ with increasing flow rates at the no input site ($p < 0.001$, Figure 7h), but increased from 6.6‰ to 8.8‰ with higher flow at both the medium and high input sites (both $p < 0.001$). There were few significant relationships between $\delta^{15}N$ and flow across functional feeding groups (Table S3).

4 | Discussion

The Mara River food web shifts from being primarily based on autochthonous resources to being increasingly based on allochthonous resources along a gradient of inputs from large wildlife. Aquatic insects consumed a larger proportion of allochthonous basal resources along this gradient, from 27% to 52%, mostly through increasing consumption of CPOM (largely hippo derived), as well as vertebrate material during the wildebeest migration season. This diet shift led to an increasing degree of animal resource assimilation and a decrease in trophic position

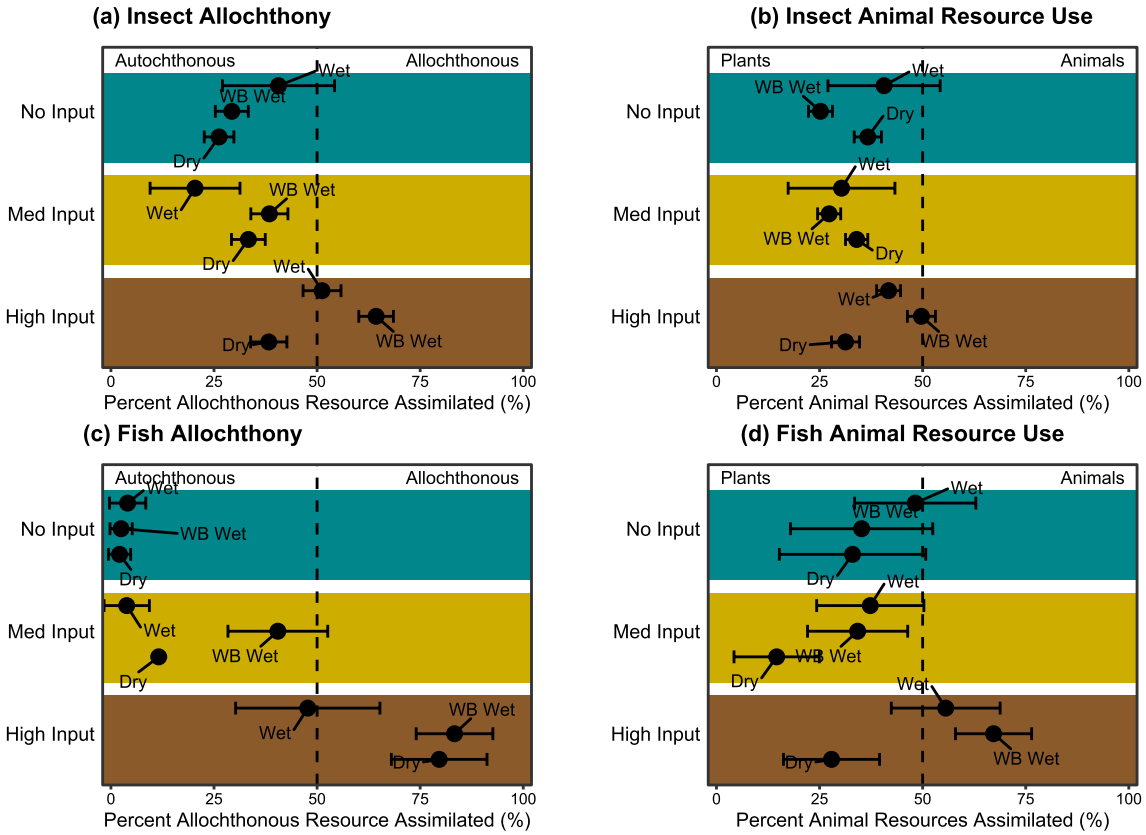

FIGURE 7 | Average percent (±SD) of allochthonous resources assimilated in insect (a) and fish (c) tissue during the dry and wet season, as well as the wet season during which wildebeest drownings occurred (WB Wet) across three Mara River sites that varied in the amount of wildlife input. The average percent of animal resources assimilated (±SD) is shown for insects (b) and fish (d) across the same seasons.

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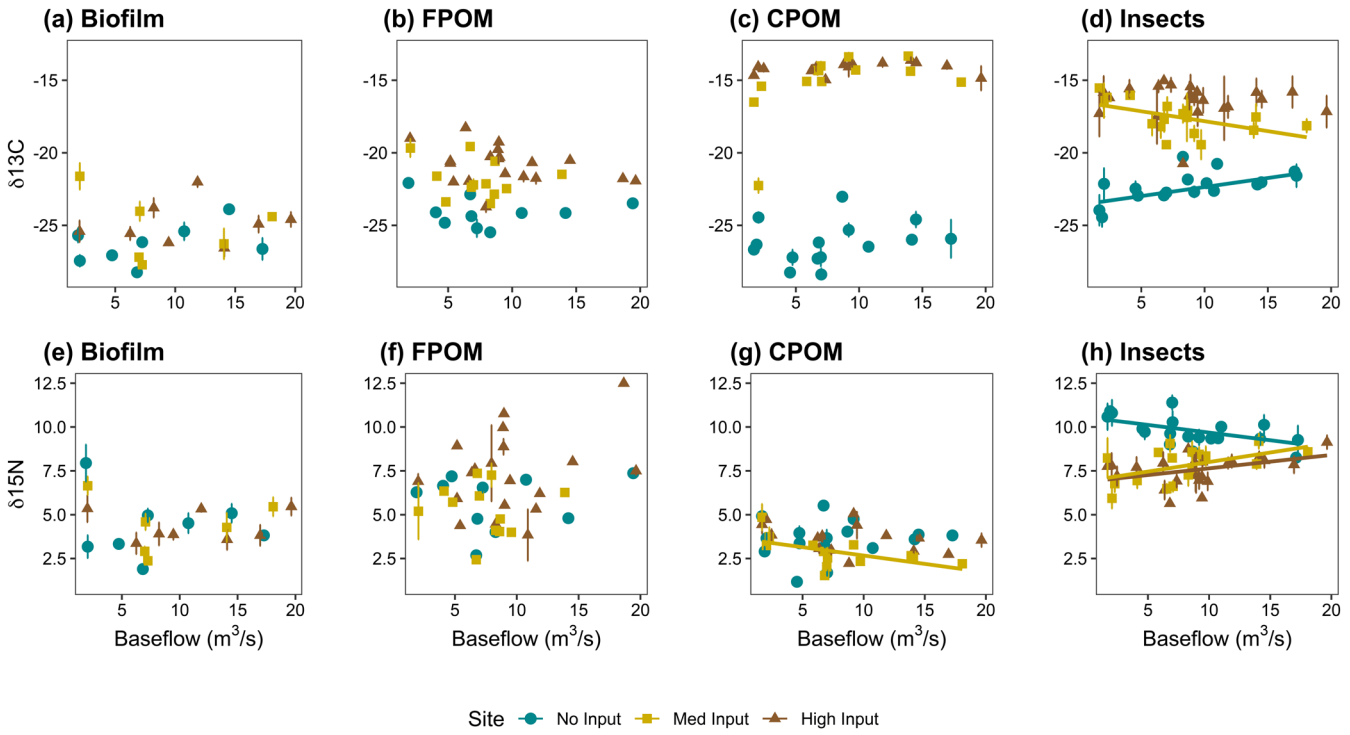

FIGURE 8 | Average (±SD) stable isotope carbon (δ13C, panels a–d) and nitrogen ($\delta^{15}N$, panels e–h) across baseflow (m^3/s) at sites with No, Medium, and High wildlife input in the Mara River for dominant food sources likely consumed directly by insects (biofilm, fine particulate organic matter (FPOM), and coarse particulate organic matter (CPOM)) and insect consumers.

for invertebrates. Likewise, there was a large shift in reliance on allochthonous resources by fishes, from consuming 2% to 73.5% allochthonous resources along our wildlife subsidy gradient. This shift is largely due to a decrease in biofilm consumption and an increase in CPOM consumption. As a result, the amount of animal resources assimilated and mean trophic position among fishes did not change. Lastly, we saw shifts in $\delta^{13}C$ and $\delta^{15}N$ values for invertebrate consumers, but not for resources, with changes in river discharge. Interestingly, these shifts were not apparent at the site with large amounts of wildlife input, suggesting that wildlife inputs are large enough to mute effects of river flow.

Large wildlife inputs primarily influence the river food web through changes in basal resources. CPOM, which is primarily allochthonous material, shifted from being almost entirely composed of C3 riparian plants at the no input site (uppermost site) to being almost entirely composed of C4 terrestrial grass at the high input site (lowermost site). Prior research in this system has shown a significant increase in the magnitude of CPOM in the river along this gradient, due to large inputs of C4 vegetation (grass) by hippos (Subalusky et al. 2015, 2018), and an increase in C4 vegetation in the river food web corresponding with increasing density of large mammalian herbivores (Masese et al. 2015, 2018). This was confirmed by our stable isotope analysis, where the isotopic values of CPOM from the medium and high input sites aligned with the isotopic value of hippo dung. Fine particulate material (FPOM), which is a composite of autochthonous and allochthonous sources, became increasingly composed of CPOM along this gradient, although biofilm remained a dominant source of FPOM. These impacts illustrate the bottom up pathways through which large wildlife inputs strongly alter the river food web.

These terrestrial inputs from large wildlife increase rates of allochthony (i.e., subsidy consumption) among consumers, particularly fishes. Both omnivorous and insectivorous fishes shifted from consuming < 5% allochthonous resources at the no input site to consuming > 70% allochthonous resources at the high input site. Other research in this system has suggested autochthonous production declines along this gradient (Subalusky et al. 2018). Together, these results suggest that terrestrial subsidies from large wildlife may provide a particularly important resource to consumers, despite being of relatively lower quality than autochthonous sources (average Mara River C:N biofilm = 7.0 vs. average C:N CPOM = 31.0) and their difference in essential biomolecules such as Omega-3 fatty acids (e.g., Hixson et al. 2015; Twining et al. 2019, 2025). This pattern also supports the general prediction that the magnitude of resource subsidy relative to autochthonous production is important in determining consumer diet and that terrestrial subsidies can increase stability in the river food web by decreasing predation pressure on in situ prey (Takimoto et al. 2002).

Overall, insects and fish increased their reliance on multiple resources pathways as wildlife subsidies increased (Figure 6), which should increase food stability and community persistence (McCann et al. 1998; Post et al. 2000; Takimoto et al. 2002; Moore et al. 2004). Aquatic macroinvertebrates and fish generally increased their dependence on allochthonous and animal resources. The collector functional feeding group had the most pronounced change, increasing from a primarily plant-based diet at the no input site to a 50% plant: 50% animal diet at the high input site. This increase was largely driven by increasing consumption of vertebrate material during the wet wildebeest season, when wildebeest carcasses were present in the river.

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This diet change was not evident in the trophic position of collectors, which decreased from 3.17 at the no input site to 2.48 at the high input site. This discrepancy may be because we set the trophic position of wildebeest at 1 due to its detrital nature, which places this animal tissue at the same trophic position as plant material. In addition, the consumed wildebeest carcass evident in gut content analysis may not have been evident in the invertebrate tissues due to turnover time needed for assimilation. Fish also assimilated a higher proportion of animal material at the high input site in the wet and wildebeest wet season, when animal assimilation exceeded 50%. Increasing presence of animals in their diet at the high input site was driven by increased consumption of both insects and vertebrate material along the river gradient. Trophic position stayed relatively consistent at around 3.6 across all sites for omnivorous fish, although the trophic position of insectivorous fish declined at the high input site from 3.6 to 2.9, following the decline in trophic position of invertebrates.

Flow levels do not appear to change the stable isotope values of basal food web resources. The $\delta^{13}C$ and $\delta^{15}N$ of biofilm, FPOM, and CPOM were all fairly consistent across an order of magnitude difference in baseflow values (Q_{90}: 2–20 m^3/s; Table S3 for further values). We expected that changes in boundary layer dynamics at varying discharge would change the $\delta^{13}C$ of at least biofilm (Keeley and Sandquist 1992; Finlay et al. 1999), but the $\delta^{13}C$ of biofilm at all three sites overlapped with one another across the whole range of discharge. FPOM values showed some differentiation in $\delta^{13}C$ by site, due to the increasing contribution of CPOM at downstream sites, but this pattern also did not vary significantly with discharge. Finally, the $\delta^{13}C$ of CPOM values was strongly differentiated among sites, but not impacted by discharge.

In contrast to the pattern among resources, there were significant changes in consumer use of allochthonous resources with discharge. When examined by season, allochthonous resource use increased during the wet and the wildebeest wet season for insects and during the wildebeest wet season for fishes. Discharge level may alter availability of resources, as wet season discharge may scour autochthonous resources, while allochthonous inputs from hippos are relatively constant over time (Subalusky et al. 2015), and inputs from drowned wildebeest are likely to be higher during high flows (Subalusky et al. 2017). When examined over a range of discharge, the $\delta^{13}C$ of insects at both the no input and the medium input sites appeared to shift from CPOM to FPOM as discharge increased, perhaps reflecting a shift in resource availability. At the high input site we see little differences across flow, which could indicate that the high wildlife input provides a continuous food source for invertebrates independent of flow. The $\delta^{15}N$ of insects at all sites converged to similar values, with values at the no input site decreasing with flow and values at the medium and high input sites increasing with flow, perhaps suggesting a potential shift to more similar food resources across all sites at higher flows. These patterns were largely driven by changes in the collector functional feeding group, and we hypothesize they may have arisen from shifts in food resource availability in response to flow in addition to shifting community composition of insects. These different interpretations illustrate the importance of analysing food web dynamics over a range of flow conditions, rather than solely during single seasonal time points, particularly in tropical systems with dynamic seasonality.

Although not the focus of our study, this research illustrated challenges in using direct diet data versus stable isotope values in understanding food web dynamics, as the two analyses may reflect different dietary niches (Petta et al. 2020). The maxim that "you are what you eat" is often applied to use of stable isotopes in diet reconstruction. While this holds true for some species like predators who consume prey as a whole, for other species, like detritivores, a more accurate maxim is "you are what you assimilate". Consumers eating a diet dominated by a high quantity-low quality food source may have gut contents that mostly reflect use of that food resource, while their stable isotope signature may reflect a greater proportion of whatever high quality food is available, regardless of its low quantity. Indeed, studies have shown that algal resources may be present disproportionately in consumer diets even in systems with low primary production (Marcarelli et al. 2011). These challenges raise questions about the use of priors in diet analysis, particularly in highly heterotrophic ecosystems in which a large amount of potentially low quality organic material is available for consumption. Priors will have a greater weight in mixing models when the isotopic data poorly resolves the source contributions, which highlights the potentially important role of direct diet priors to improve model learning about consumer diet (Brown et al. 2018). However, if diet data do not accurately reflect assimilated food resources, they might produce misleading results. This area is an important topic for future investigation in animal diet analysis.

The substantial shifts in aquatic food web structure along the Mara River gradient suggest that terrestrial resource inputs from large wildlife play a significant role in driving energy flux and food web dynamics in this river ecosystem and may impact overall community structure and stability. Ecological theory predicts that feeding across multiple resource pathways, including those produced by resource subsidies, should increase food web stability up to a certain point, particularly when they provide complementary resources to autochthonous production, as they may stabilize consumer populations when in situ resources are rare (Takimoto et al. 2002). However, high levels of subsidies may destabilize food webs by elevating consumer populations beyond their carrying capacity, with impacts on other in situ communities (Leroux and Loreau 2008). Our results form the basis for further investigation into how the magnitude of wildlife subsidies influences the stability of river food webs.

Author Contributions

Conceptualization: A.L.S., T.C.F., D.M.P., C.L.D., E.J.R., L.N. and E.N. Developing methods: A.L.S., T.C.F., D.M.P., C.L.D., E.J.R., L.N., E.N. and A.R. Conducting the research: A.L.S., T.C.F., C.L.D. and A.R. Data analysis: A.L.S., T.C.F., C.L.D. and A.R. Preparation of figures and tables: T.C.F. and A.L.S. Writing: T.C.F, A.L.S., D.M.P., C.L.D., E.J.R., A.R., L.N. and E.N.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** fwb70208-sup-0001-Supinfo.pdf. **Figure S1:** Average (±SD) stable isotope carbon (d 13C) and nitrogen (d15N) of invertebrate functional feeding groups across baseflow (m3/s) at sites with no, medium, and high wildlife input in the Mara River. **Table S1:** Number of individuals in each functional feeding group (collectors, predators, scrapers) or feeding guild (insectivores, omnivores) analysed for the isotope and gut content data sets across sites and seasons (dry, wet, wildebeest (wb) wet). **Table S2:** Correlation *p*-values and associated correlation coefficients (if significant) between carbon (d13C) or nitrogen (d15N) signatures of food sources (biofilm, fine particulate organic material (FPOM), and coarse particulate organic material (CPOM)) and insect consumers (separated by functional feeding groups) and Mara River flow variables (average flow (Avg. Flow), peak flow (Q_{10}) and baseflow (Q_{90})), as well as flow variability (Q_{10}/Q_{90}). **Table S3:** Percent of each food source consumed (for gut contents results) or assimilated (MixSIAR results). MixSIAR results show % of each resource assimilated when including (w/) or excluding (w/o) gut content priors into the models for insects and fish across a wildlife input gradient. CPOM = coarse particulate organic material; WB = wildebeest. **Code S1:** MixSIAR code used for running the models across seasons and sites for fish and for invertebrates. The purple highlighted values were changed in the code for each functional group, site, and season. This example code is for fish from the High Hippo Input site at the wildebeest wet season. The MixSIAR_model.txt is a file provided by Stock et al. (2018).

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