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Food-web structures link multi-scale processes in complex landscapes

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Abstract

Complex landscapes are challenging to study because both the higher level contextual and interacting lower level mechanistic processes underpinning their ecological characteristics occur simultaneously. However, food-web structures can provide process insight in such landscapes by identifying these processes in specific contexts. Here, we used stable isotopes to identify spatially separate resources and infer resource flows underpinning food-web structures in a braided river. We found that river resources used by mobile consumers, including birds and fish, were spatially heterogeneous. Consumer resource use was related to four key structural food-web attributes: (1) spatiotemporal variation in foraging, (2) subsidies, (3) omnivory, and (4) ontogenetic niche shifts. Thus, both physical heterogeneity (contextual physical processes) and adaptive characteristics of consumers (mechanistic processes) were likely contributing to important food-web structures. Identifying these food-web structures in landscapes, across scales of resource use and spatial distribution, provides a way to identify processes and scales likely contributing to food-web stabilization.

KEYWORDS
dynamic river, food web, food-web structure, landscape heterogeneity, stable isotope

INTRODUCTION

Complex systems are characterized by emergent properties, such as stability, that have difficult-to-identify drivers associated with a mixture of contextual (higher level) and mechanistic (interacting lower level) processes (Heffernan et al., 2014; Newman et al., 2019; Riva et al., 2023). Typically, contextual processes set the stage for mechanistic processes to play out. However, measuring those processes and untangling their respective influences in complex ecological systems is challenging (Newman et al., 2019; Riva et al., 2023). Food-web theory suggests specific food-web structures, which can occur across spatial scales and hierarchies of organization, should increase stability and thus lead to more persistent assemblages (Rooney et al., 2008). These structures potentially confer stability by dampening species interaction strengths via two key pathways: (1) connectivity of spatially or temporally isolated resources through predation and (2) resource variability across spatiotemporal scales (Kondoh, 2003; McCann et al., 2005; Rooney et al., 2008). Identifying such food-web structures in real food webs, in contrast to models, and the associated processes driving spatial resource variability and connectivity will improve understanding of complex ecological systems.

Investigating food-web structures across distinct habitats within landscapes could reveal the scales and levels at which processes operate (Gounand et al., 2018; Rooney et al., 2008). For example, structures relying on phenological changes in predation can be mechanistic processes occurring at taxon-specific spatial scales, whereas environmental resource heterogeneity can be driven by broader contextual processes such as cyclones, mosaic fires, or flooding occurring on vastly different spatial scales (Dietzel et al., 2021; Johnston et al., 2019; Turner, 2010). Gaining such scale-specific knowledge is important to ensure the persistence of dependent species and habitats, because many processes occurring within complex landscapes are likely mismatched with scales of management and protection (Hauer et al., 2016; Riva et al., 2023).

Since patterns of connectivity and resource heterogeneity encompass a range of specific food-web structures, the structures are useful starting points for identifying important processes. For example, key food-web structures include food-web asymmetry (Rooney et al., 2006) and omnivory (Wootton, 2017), adaptive consumer foraging or adaptive consumer avoidance (Kondoh, 2003; Uchida et al., 2007), and variation in resource availability in space and time (Lamy et al., 2020; Quévreux & Loreau, 2022; Rooney et al., 2008). These structures reduce interaction strengths, an important stabilizing mechanism whereby weaker interactions dampen cascading effects between consumers and their resources (Bellmore et al., 2015; Rooney et al., 2006). These food-web structures can also point to mechanistic processes controlling interactions, such as birds flying over water to catch fish (a physiological/behavioral process creating connectivity), and contextual processes, like varying resources between the land and water where the bird forages (driven by environmental heterogeneity).

Physically dynamic systems, such as braided rivers, are tractable landscapes for investigation of such food-web structures (Datry et al., 2016; Hauer et al., 2016; Ward et al., 1998). Braided rivers have mobile and differentially disturbed channels spread across extensive lateral floodplains, creating distinctive habitat types (Gray et al., 2016). Consequently, braided rivers are a nexus of aquatic and terrestrial biodiversity linked to the intricately connected habitat mosaic (Harris et al., 2023; Hauer et al., 2016; Tockner et al., 2006).

Resource coupling in braided rivers, one form of connectivity, is due to a variety of processes that connect different habitats that vary strongly in their productivity and species composition (Gounand et al., 2018; Quévreux & Loreau, 2022). First, different resources can move between spatially different habitats or systems (such as terrestrial to aquatic). For example, spiders can couple terrestrial and aquatic environments by feeding along their boundaries and capturing emerging aquatic insects (Greenwood, 2014). We refer to these resource movements as subsidies (Polis et al., 1997; Terui et al., 2018). Alternatively, resources from spatially distinct habitats are coupled by mobile consumers moving between these habitats. Resource coupling by mobile consumers typically depends on their size and physiological constraints (Keppeler et al., 2021; Rooney et al., 2006). For example, fish can swim between physically connected but considerably different aquatic environments, and birds can travel large distances bringing in and using resources from vastly different systems (Hauer et al., 2016). By assessing energy flow between locations in complex landscapes, potentially stabilizing food-web structures can be identified across these scales of consumer movement.

Following this approach, we investigated if and how a braided river food web was connected across the varying spatial foraging scales of different consumer types. We used stable isotopes to track energy flow from different resources in space, including the different channel types and the terrestrial parts of the floodplain. We expected that (1) physical heterogeneity would drive spatial differences in resources between distinct habitats, and (2) mobile consumers would exploit that spatial resource variability. In connection with the above, we also expected that despite the dynamism of these types of rivers, (3) food-web connectivity and resource heterogeneity should be present across the different spatial scales at which different consumers operate, and (4) these food-web structures would be those associated with dampened interaction strengths. Importantly, if the food-web structures identified are the same as those typically associated with dampened interaction strength, they could be used to identify the relative significance of mechanistic or contextual processes and therefore glean insight into potentially important scales for stabilizing processes. For example, if movement is a primary mechanistic process driving connectivity, the scale of species movement is likely to be important.

METHODS

We sampled the lower Te Awa-a-Takatamira | Cass River, Takapō, Aotearoa | New Zealand (−43.876675, 170.484123, ~700 m above sea level) between October 2021 and June 2023 (Figure 1). Our 3.5-km long by 1.5-km wide area study contained braiding channels flanked by vegetated areas of cushion plant-dominated communities (raoulia, *Raoulia haastii*, *Raoulia hookeri*, *Raoulia tenuicaulis*, and *Raoulia australis*), wetland, and grassland (total area ~370 ha), and frequent bed-moving floods changed wetted channel locations, creating spatially distinct and dynamic terrestrial and aquatic habitats (Figure 1). Despite this flow dynamism, Te Awa-a-Takatamira has supported persistent populations of rare river birds, fish, and plants since at least the 1970s (Lalas, 1977; NZ Freshwater Fish Database, 2023; Sanders & Maloney, 2002). Moreover, the indigenous (i.e., Māori) name of this river translates as "the river of Takatamira." Takatamira was a local chief of the South Island iwi (indigenous group), Ngāi Tahu, also indicating the river's significance. Overall, this river maintains relatively persistent ecological properties that are characteristic of a dynamic and highly valued landscape. Sampling comprised two components: (1) spatiotemporal sampling of physical channel characteristics and periphyton resources and (2) tissue collection from a variety of terrestrial and aquatic organisms for analyses of stable isotope composition. We describe these below, with additional details on isotope handling in Appendix S1.

Site attribute measurements

We delineated five braided river aquatic habitat types using physical attributes, periphyton abundance, and isotopic signatures of aquatic resources: (1) lateral springs, (2) lateral tributaries, (3) minor channels, (4) major channels, and (5) mid-channel springs (sensu Gray & Harding, 2007). To investigate spatial and temporal variability of these habitat types, especially the degree of resource heterogeneity, depth, width, temperature, dissolved oxygen (in milligrams per liter, YSI EcoSense ODO200), and turbidity (Eutech TN100) were measured from up to three channels of each habitat type selected from four 1-km transects (Figure 1) every second month from May 2022 to June 2023 ($n = 240$ total sites sampled). Aerial images (Phantom 4 drone) were taken in November 2021, March and May 2022, and every second month from June 2022 in conjunction with channel sampling using 60% front and side overlap, and orthomosaics created using Agisoft Metashape Professional (v1.6.5 build 11249, 2020). We calculated channel presence as the number of images a wetted sampled channel was present in,

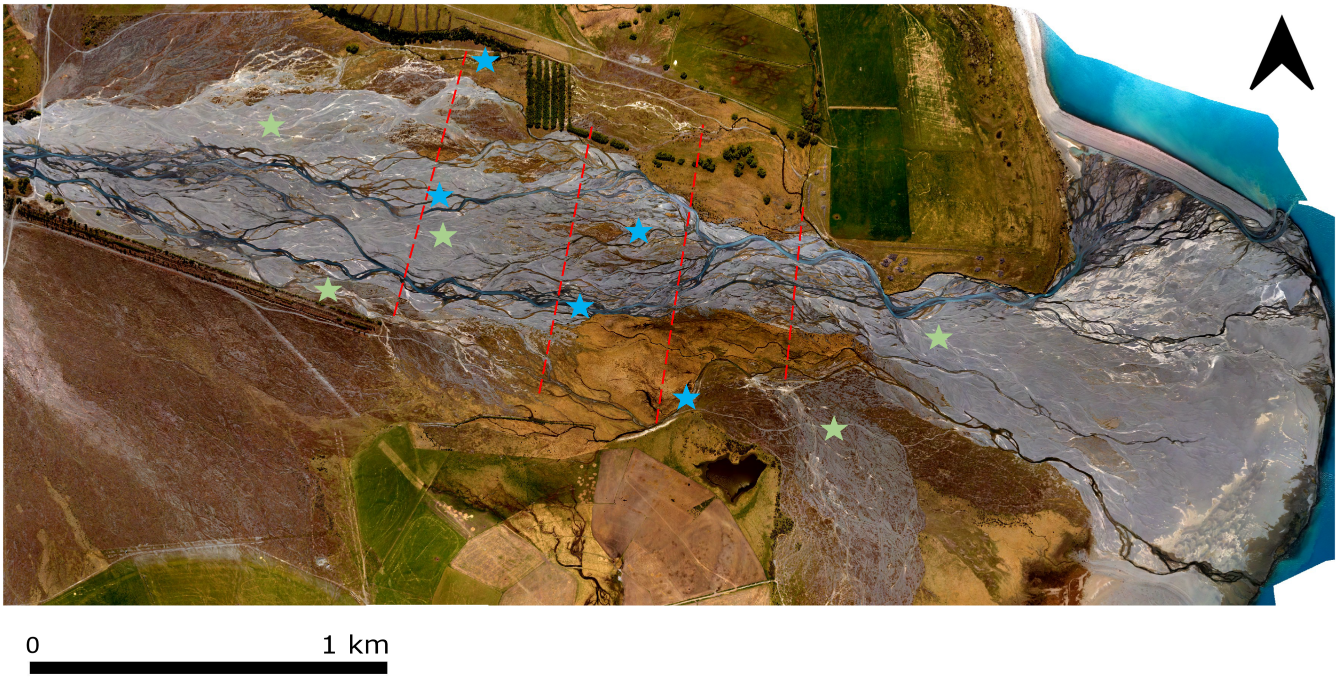

FIGURE 1 Te Awa-a-Takatamira | the Cass River (−43.876675, 170.484123, ~700 m above sea level) study area depicting channel measurement transects (red dashed lines) 250–300 m apart with examples of locations used for aquatic (blue stars) and terrestrial isotope tissue collection (green stars) from different habitat types. The river feeds into Lake Takapō at the east end. River imagery was taken by Fish Futures Technical Staff.

divided by the total number of images that had been taken (since November 2021) at the time of sampling. Channel presence was used as a proxy for channel disturbance; sites less impacted by flooding were present for longer throughout the image series. We also measured periphyton chlorophyll *a* (chl *a*) during this sampling using a BenthoTorch (bbe BenthoTorch by Moldaenke) on each of three representative small- (<5 cm) and medium- (5–15 cm) sized rocks from each channel. This efficiently quantified broad changes in algal resources (Kahlert & McKie, 2014), giving 1344 measurements across 8 months from 240 channels.

We delineated two terrestrial floodplain habitat types based on vegetation cover: (1) raoulia habitat (>20% ground covered by *Raoulia* spp.) and (2) gravel habitat (less than 10% vegetation). Raoulia cover comprised three species: *R. tenuicaulis*, *R. haastii*, and *R. hookeri*. Other plants included *Epilobium melanocaulon*, *Muehlenbeckia axilaris*, and *Echium vulgare*, an exotic herb. All these plants flower spring to summer (Ward, 1982; Woolmore, 2011), providing consistent resources to resident invertebrates (Primack, 1983; Ward, 1982).

Isotope tissue collection and processing

To assess mobile consumer resource use across habitats, we collected tissue for stable isotope analysis (SIA) from consumers and potential prey across floodplain habitats, predominantly during 2021–2022 austral spring and summer when birds were on the river (Appendix S1). For baseline source isotope values, we sampled aquatic invertebrates in the five aquatic habitats using a kick net, and other invertebrates using hand nets and pooters (species list: Appendix S1).

We chose birds, fish, and hunting spiders as our mobile consumer species. We took blood samples from adult birds and chicks of three riverine nesting species, including: tarapirohe | black-fronted tern (*Chlidonias albostriatus*; life stage and number: adults, 15; chicks, 10), ngutu pare | wrybill (*Anarhynchus frontalis*; adults, 3; chicks, 10), and pohowera | banded dotterel (*Charadrius bicinctus*; adults, 11; chicks, 10). These birds vary in river dependency (Hughey, 1998; Lalas, 1977), ranging from close aquatic association (wrybill) to wide foraging across all habitat types (tern). We collected ~50 μL of blood using passive capillary transport from adults caught with nest traps and chicks over 15 days old caught with a hand net (following Ardern et al., 1994). Isotope ratios in blood have a high tissue turnover, so reflect recent food sources (~13-day half-life for a 50-g bird, Vander Zanden et al., 2015). We sampled tissue from three fish species (*N*): kōaro (*Galaxias brevipinnis*, 66), upland bully (*Gobiomorphus breviceps*, 10), and common bully (*Gobiomorphus cotidianus*, 13), caught using electric fishing (Smith-root LR-24) with replicates from each of the five aquatic habitats. Muscle tissue, fin clips, and length measurements were taken from the first 15 individuals of each species to create muscle-fin SIA regressions (following Tronquart et al., 2012), and additional individuals were fin clipped only. Mobile hunting spiders, *Dolomedes* spp. and lycosids (12) were collected from gravel habitats. Thus, we sampled consumers encompassing a wide range of possible energy flow pathways, including all common species on the river.

We used isotope mass spectrometry (GNS, Wellington) to measure the ratio of heavy to light stable isotopes of carbon and nitrogen, δX (Appendix S1). Models from Post (2002) were used to calculate the trophic position and resource pool (lipid correction, dietary sources, fractionation, trophic enrichment factors [TEF], and baselines and equations in Appendix S1).

Statistical analysis

We investigated habitat differentiation and consumer foraging in analyses using R version 4.3.1 (R Core Team, 2023). We assessed how channel types differed in physical properties with principal components analysis (PCA) using "prcomp" in base R. We tested how these properties related to resource availability in different channel types with a generalized linear mixed model (GLMM, Poisson distribution) to predict chl *a* biomass (summed over the six rocks) from physical channel attributes measured across habitat types. We used the "glmmTMB" package for this model, testing for overdispersion (not detected) with the "performance" package, which checks Pearson's residuals against residual df (Brooks et al., 2017; Lüdecke et al., 2021).

To determine spatial use of prey through SIA, we needed to first investigate if spatial variation existed between the resource isotope signatures. Prior to estimating how resources contributed to consumer diets (as dietary proportions inferred from SIA), we tested for differences between the isotope signatures of the resource groups. We used multivariate ANOVA (MANOVAs) for each set of potentially contributing resources from different habitats, with post hoc evaluation with linear discriminant analysis (LDA) to evaluate differences between potential dietary sources.

Finally, we created stable isotope mixing models ("simmr" v 0.5.1.212; Govan and Parnell, 2023) to investigate energy flow between food resources from across the floodplain and consumers (five fish spp., two spider genera, and adults and chicks of three bird spp.). In the models, sources were grouped spatially where possible, and by taxa where sources were not sufficiently spatially distinct (e.g., fish and lizards, see Appendix S1).

Consumers were also split by sample location (fish) or life stage (bird) where possible. When using mixing models, it is important that all likely sources are included and that TEFs are appropriate. We checked these assumptions, and whether consumer isotope values fell within the geometric area created by sources included in the model (Parnell et al., 2013; Appendix S1: Figure S1). We excluded terrestrial prey sources from fish dietary mixing models because of the paucity of structural riparian vegetation and low number of land-based invertebrates adjacent to channels, meaning fish diets typically contain low proportions of terrestrial prey (e.g., <5% in kōaro, McIntosh, 2000; Appendix S1). These models generated likelihood distributions of the contributions of sources to consumer diet.

RESULTS

Physicochemical conditions varied considerably among aquatic habitats. The first two PCA axes described ~60% of physical attribute variance across channel types (Appendix S2: Figure S1). These different physical properties of channels were associated with variability in algal resource abundance (full Poisson GLMM model; Appendix S2: Table S1). Channel width–depth ratio had a strong positive correlation with periphyton abundance (estimate: 0.20, SE ± 0.09, $z = 2.201$, $p = 0.0278$; Appendix S2: Table S1) and turbidity had a strong negative influence (estimate: −0.06, SE ± 0.12, $z = -5.465$, $p < 0.001$; Appendix S2: Table S1). Thus, river algal resources varied spatially among habitat types, tied to channel physical properties.

Mixing models revealed that isotopic composition of dietary resources differed across floodplain habitats, indicating that invertebrate isotopic signatures were distinct enough to use as spatially explicit sources (MANOVAs: fish sources, $F = 13.44$, df = 6, 114, $p < 0.001$; tern sources, $F = 26.6$, df = 8, 160, $p < 0.001$; other consumer sources, $F = 13.99$, df = 4, 88, $p < 0.001$; Appendix S2: Table S3). Thus, the distinct physical habitats were reflected in the isotopic signatures of resources, facilitating mixing model use based on resource habitats reflecting these isotopic and physical differences, including: (1) lateral channels, (2) central plain gravel channels, (3) raoulia, and (4) gravel.

Fish mixing models

Isotopic mixing models indicated fish likely used resources from different aquatic habitats (Figure 2). Kōaro from stable side springs, for example, likely obtained two-thirds of their resources from lateral sources (mean dietary proportions ± SD, hereon; 0.65 ± 0.044; Figure 2A), whereas kōaro from central floodplain channels (minor, major, and mid-channel springs) rarely used lateral channel sources (mean contribution of less than 0.13; Figure 2B–D). However, kōaro from a lateral tributary likely used dietary sources from both lateral channels and the central gravel channels (0.43 ± 0.086 and 0.57 ± 0.23, respectively), indicating that kōaro from these areas were likely foraging from multiple distinct areas (Figure 2E).

Upland bully mostly had similar feeding movements to kōaro, with most fish predicted to have fed from locations where they were caught (Figure 2). However, upland bullies from central gravel springs likely gained over 60% of their diet from the central floodplain, and individuals from a lateral spring also used more of an even split of resources (0.44 ± 0.12 local; Figure 2I). Local sources contributed most to common bully from lateral areas and central channels (mean contributions of >0.8 in both cases), indicating that this species was only feeding from locations similar to where they were found (Figure 2F,G).

Spider mixing models

Riparian spiders were evenly connecting aquatic and terrestrial food sources through predation. Predicted spider diets were split between aquatic (0.44 ± 0.06) and terrestrial (0.56 ± 0.19) sources. This indicates that spiders were preying evenly on invertebrates such as other spiders and beetles (0.3 ± 0.09) compared to invertebrates from the raoulia habitat such as moths (0.26 ± 0.1; Figure 3F).

Bird mixing models

The birds fed across habitats, differing in resource use among species and life stages. Banded dotterel adults fed differently to chicks (Figure 3A,B); aquatic invertebrates contributed to 0.6 (±0.07 SD) chick diet, compared to 0.34 (±0.05 SD) to adult diets. Adults fed more evenly across the floodplain, likely eating more gravel-sourced invertebrates such as spiders (0.49 ± 0.09). Wrybill used resources from shallow channels, such as those from minor braids and mid-channel springs (0.82 ± 0.3) compared to gravel and major braid invertebrates (Figure 3E). Overall, wrybill fed between different channel types but only within the aquatic habitats of the central floodplain. Terns, the largest and most mobile bird, showed little variation between adults and chicks with even amounts of all sources likely consumed (Figure 3C,D). A relatively high proportion of lizards (0.13 ± 0.07 and 0.13 ± 0.08, respectively) and

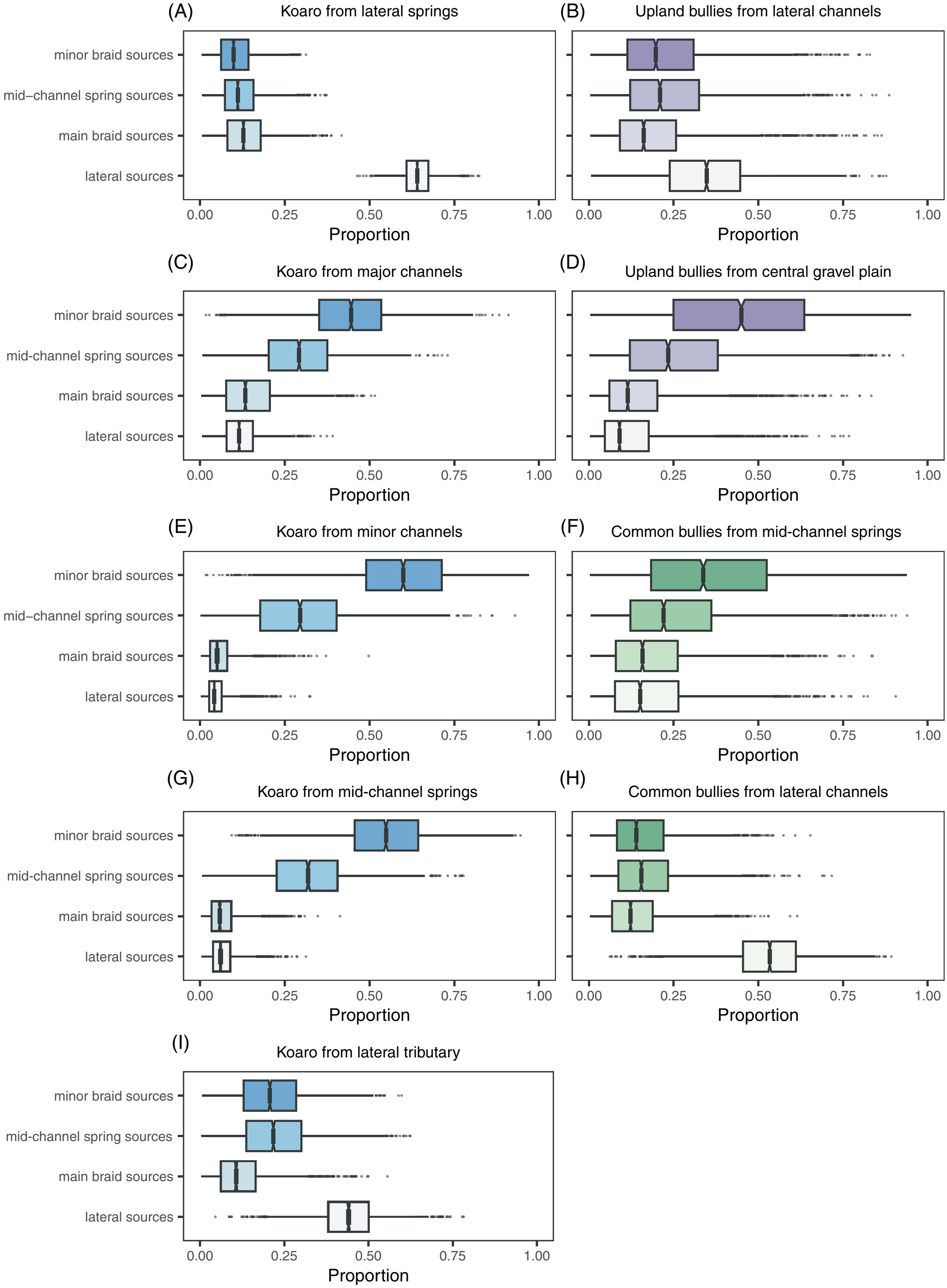

FIGURE 2 Dietary proportion outcomes from Bayesian mixing models run for fish species found in different channel types of Te Awa-a-Takatamira with boxes representing posterior distributions of dietary sources contributing to a given consumer's isotopic signature, the *y*-axis showing food sources from different areas, and contribution to dietary proportion on the *x*-axis. Habitats where fish were located are shown in separate plots (A–I) and fish species are depicted in different colors; kōaro (blue), upland bullies (purple), and common bullies (green).

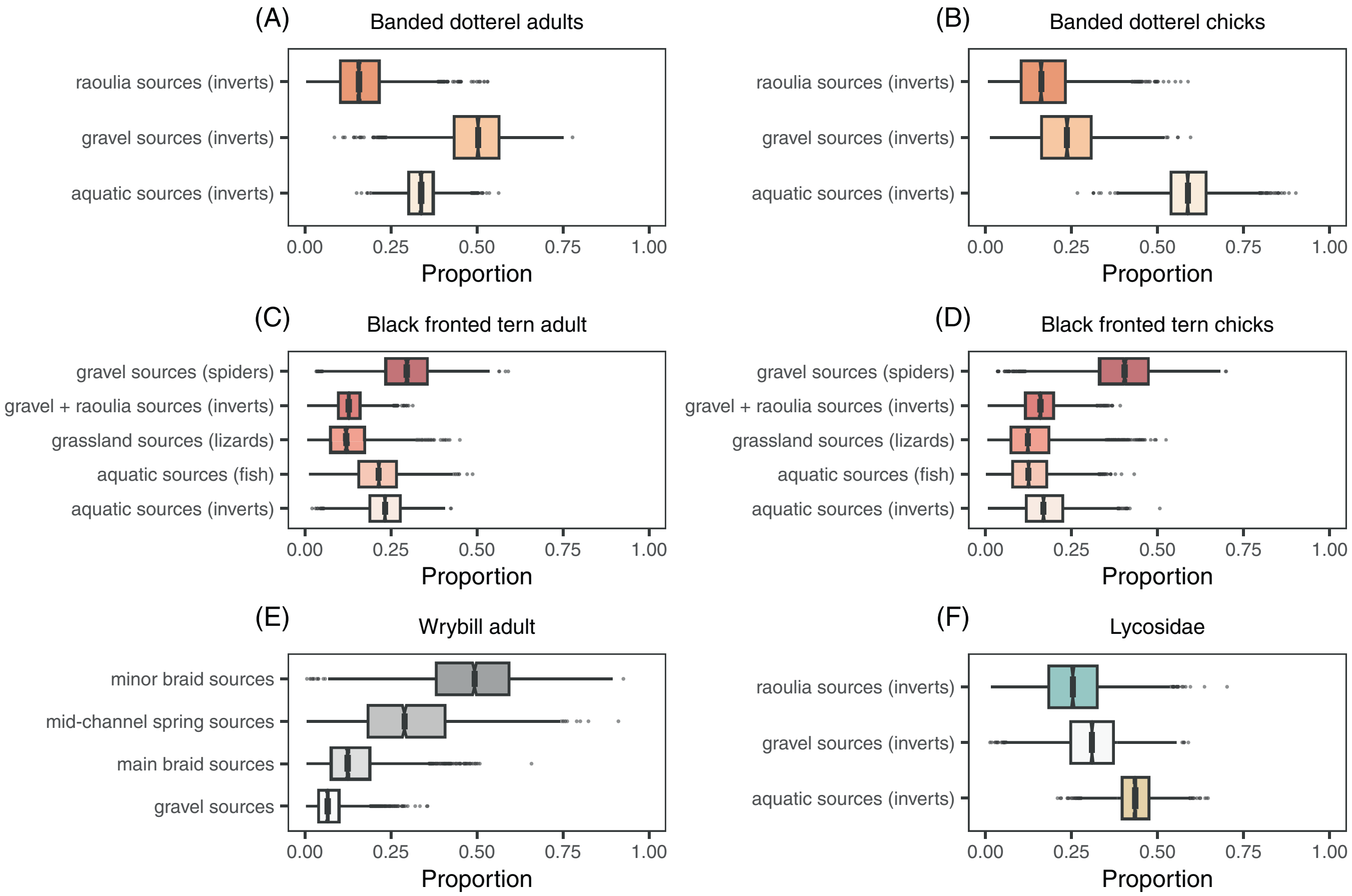

FIGURE 3 Dietary proportion outcomes of Bayesian mixing models run for different terrestrial based consumers across Te Awa-a-Takatamira with boxes representing posterior distributions of dietary sources contributing to a given consumer's isotopic signature, the *y*-axis showing food sources from different areas, and contribution to dietary proportion on the *x*-axis. Consumers are depicted in separate plots; (A) banded dotterel adults, (B) banded dotterel chicks, (C) black-fronted tern adults, (D) black-fronted tern chicks, (E) wrybill adults and chicks, and (F) Lycosidae spiders.

gravel spiders (0.3 ± 0.09 and 0.41 ± 0.1, respectively; Figure 3C,D) likely contributed to tern diets. Although our model had difficulty distinguishing both lizard versus spider sources, and invertebrates from vegetated areas versus aquatic sources, the tern diets were undoubtedly broad. Overall, these results show that bird foraging connected aquatic and terrestrial food-webs in this river as a floodplain meta-food web.

DISCUSSION

We investigated the spatial distribution of distinct resources in a highly disturbed complex landscape (a braided river) and their potential connection by mobile consumers (fish, birds, and spiders) that differed in life history and foraging spatial scale. We found food-web structures indicating spatial variability between resources in different areas, and consumer movements and resource subsidies that connected habitats. Variability in river resources was controlled by physical differences in the landscape driven by flow-related factors (such as differences in turbidity and depth) across the river (contextual processes). Fish and birds coupled resources through movement and life-stage shifts, and subsidies from aquatic resources supplemented terrestrial spider and bird diets (mechanistic processes). These results indicate that structural food-web patterns likely arising from both contextual and mechanistic processes can be identified across a complex landscape. These processes underlying food-web structure can help identify potentially important scales for stabilizing mechanisms. For example, mechanistic processes, such as species interactions and adaptive behaviors, occur at a scale relative to the species in question, and clarifying where they feed elucidates that scale. Contextual processes, such as disturbance-driven spatial resource variability, will likely be important if the heterogeneity matches the scales of resource coupling. We consider the properties and roles of these structural patterns below, noting that identifying such food-web structures in complex landscapes, such as river networks, fire impacted forests, or coral reefs, could help to identify the scale at which potential structurally stabilizing mechanisms may occur.

Spatial resource variability

Source isotope values varied between habitat types, allowing us to delineate resources from different habitats. While many rivers have local variations in δC^{13} values, the ability to consistently spatially distinguish between different riverine aquatic food-web resources with stable isotopes is uncommon (Alves et al., 2017). Our successful differentiation likely reflects the characteristic combination of spring and main-channel flow types occurring in the same braided river floodplain (Alves et al., 2017; Gray & Harding, 2007). This variation, in combination with the physical characteristics of aquatic channels, highlights the spatial resource variability of the Te Awa-a-Takatamira floodplain, a dynamic floodplain with a persistent combination of species observed since the 1970s. These spatial resource differences underpin the first predicted pattern of naturally stable food webs: that resources in different habitats will be spatially variable (Rooney et al., 2008).

Following spatial delineation of resources, we found that almost all isotopic signatures of mobile consumers indicated that they fed from multiple areas, fulfilling the second expectation linked to food-web stability: habitat connectivity at large spatiotemporal scales relative to the resources (Rooney et al., 2008). The variety of ways that fish, birds, and spiders connected these spatially distinct resources underpinned diverse food-web structures. These depended on mechanistic processes, the phenology, physiology, and behavioral ecology of the consumers as well as physical resource accessibility, as we describe next.

Consumer movement and resource use

Fish evidently accessed spatially separated resources by moving between the lateral and central floodplain, leading to spatially varying consumer–resource interactions. Some (but not all) fish sampled likely obtained less than 55% of their diet from local sources, such as species in lateral channels. Moreover, the lateral tributary was the most physically disconnected from the central braided channels, but we estimate both upland bully and kōaro found there obtained around 50% of their food from central gravel channels. Our results suggest that fish movement is occurring between habitats in some cases at large distances, such as over a kilometer of movement between the central and lateral channels. Studies of kōaro (Young, 2002), other galaxiids (Cadwallader, 1976; Górski et al., 2014), and common bully (Górski et al., 2014) movement suggest that our findings are plausible but highlight the need for more research into drivers of fish movement and resource acquisition. Resource coupling by consumer movement, as some fish must have been doing in this study, is likely a common process in many systems where consumers forage on larger spatial scales (Gounand et al., 2018; Rooney et al., 2008).

Spiders also fed across a variety of resources, with their terrestrial food being spatially subsidized by aquatic sources. Despite model difficulties distinguishing between terrestrial sources, these results concur with *Dolomedes* spider diets on another New Zealand braided river (Greenwood, 2014) and the large contributions of aquatic resources to adjacent riparian predators like spiders observed globally (Baruch et al., 2021). Subsidies can be an important component of consumer diets that sustain consumer populations where persistence would otherwise be infeasible (e.g., Roffler et al., 2023). While our SIA results demonstrate wide-ranging fish foraging movement and spider use of aquatic subsidies, there is a need for future work quantifying the spatial and temporal extent of these processes.

Collectively, fish and spider foraging illustrate food-web structures involving two forms of spatial variation in resource acquisition. First, subsidy use from different resources (Baruch et al., 2021; Nakano et al., 1999; Uno, 2016), exemplified here by spiders supplementing terrestrial food with aquatic food, is a mechanism that can occur across many systems including marine to terrestrial (Gutgesell et al., 2022). Secondly, spatial variation in the interactions between the consumer and spatially distinct prey (Uchida et al., 2007), demonstrated here by individual fish moving about the river. This second mechanism is a key component of resource variability across many systems including lacustrine fishes moving from benthic to pelagic food sources (Vander Zanden & Vadeboncoeur, 2002). Some fish of the same species did not move as much as others, introducing another layer of variation in interactions between consumers and their resources (individual level or local scale instead of population level or regional scale). Functionally, subsidies and foraging-based spatial variability in resource acquisition are quite different mechanisms affecting interaction strength, but structurally, they provide the same outcome (Figure 4). Both mechanisms likely dampen individual consumer–resource interaction strengths because consumers can only interact with one resource at a time, thus alleviating pressure on others (Bellmore et al., 2015; Marcarelli et al., 2020).

Asymmetry and feeding strategies

We also identified structurally asymmetric feeding pathways of mobile consumers, arising from generalist feeding strategies across trophic levels (i.e., omnivory) and habitats. Omnivorous feeding strategies can reduce interaction strengths due to resources (such as algae or pollen) going through multiple different feeding pathways to get to a consumer (such as terns or dotterels). Banded dotterels, for example, preyed on spiders and fish which feed on mayflies, as well as the mayflies themselves. Such omnivory has the potential to limit the effect of trophic cascades, because omnivores prey-switch with changing resource abundance (Benkendorf & Whiteman, 2021; He et al., 2021; Wootton, 2017), as occurs in other flood-prone river environments and ecosystems with temporally shifting resource availability (Chanut et al., 2019; Gutgesell et al., 2022). These asymmetrical food-web structures are an important interaction-dampening mechanism identifiable across a multitude of species from fish to crabs to bears (Gutgesell et al., 2022).

Mobile generalist consumers also foraged on different resources across habitats, a much broader form of generalism. Generalism was observed when consumers had an array of prey to choose from. For example, black-fronted terns consumed relatively even dietary proportions of fish (21%) and aquatic invertebrates (23%), with models also indicating that they were likely eating spiders (29%) which were in turn splitting their resource use. Thus, these consumers display not only omnivory (feeding on both fish and invertebrates) but also generalism because of their diverse use of prey options. Such broad resource use can contribute to dynamically shifting food-web interactions that are stabilizing, in contrast to specialist species which may be more vulnerable to loss of specific prey (e.g., Machado et al., 2023). For example, shifting wolf predation pressure from deer to otters following sea otter reintroduction (Roffler et al., 2023) alleviates pressure on exploited prey populations, potentially stabilizing food webs.

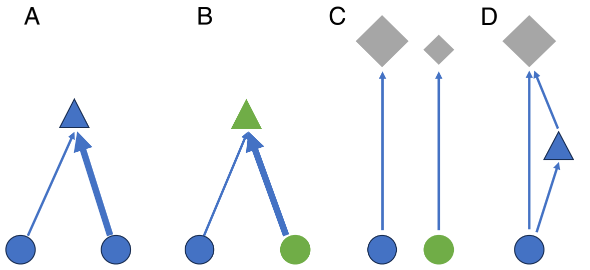

FIGURE 4 Food-web structural patterns that are associated with stability where circles indicate primary producers, triangles are primary consumers, and diamonds are secondary consumers, with small shapes indicating early life stage and larger shapes indicating adult life stage, colors indicating spatially distinct environments, and arrows indicating a predation interaction. (A) Consumer movement-driven spatial variation in feeding (depicted by line thickness) (B) subsidy-driven spatial variation in feeding (C) ontogenetic niche shifts, and (D) consumer generalism.

Some forms of generalism could weaken interactions in food webs even in spatially compressed environments because consumers can take advantage of both abundant but lower quality resources as well as more limited protein-rich resources (Gutgesell et al., 2022; Momot, 1995; Wootton, 2017). Here, differences in resources do not require spatial complexity, and thus, generalism can lower vulnerability to trophic cascades through adaptive foraging and offsetting of competition in a wide variety of circumstances (Liao et al., 2020; McCann et al., 2005; Sabo et al., 2009). For example, spatially compressed rivers suffer reductions in food-chain lengths, which can be partially attributed to switches in the degree of trophic omnivory (McHugh et al., 2015; Sabo et al., 2009). Thus, a system with generalists such as omnivores may require greater external pressures (such as flooding or land encroachment) to destabilize it, compared to systems relying solely on the spatial complexity-based structures discussed above.

The final food-web structure identified involved feeding interactions varying between consumer life stages. We found large differences in dietary composition of adult banded dotterel compared to their chicks, where adults fed to a higher degree on terrestrial invertebrates than their chicks. This variation in feeding strategy suggests that dotterels shift their feeding niche with life stage (an ontogenetic niche shift). Chicks of most braided river birds are precocial (i.e., independent) from just one day old (Maloney et al., 1999); thus, ontogenetic niche shifts are probably common in these ecosystems. These feeding shifts can increase individual interaction strengths due to the presence of specialists within a generalist population, creating non-substitutable food sources, potentially destabilizing individual dynamics (Nakazawa, 2014; Rudolf & Lafferty, 2011). However, ontogenetic shifts can also dampen interaction strengths and reduce competition at a population level (Sánchez-Hernández et al., 2022). Individuals from different cohorts can interact with spatially different resources (spatial dampening) and these interactions can shift as the younger cohort grows (temporal dampening) (Sánchez-Hernández et al., 2019, 2022). These interaction strength-dampening processes arise from species traits, indicating additional mechanistic processes that could increase stability.

CONCLUSIONS AND FUTURE CONSIDERATIONS

By empirically identifying structural patterns known to weaken food-web interactions, we have begun untangling potential stabilizing mechanisms operating across spatial scales and levels of biological organization in a complex landscape. These food-web structures are likely to be very common and important to the dampening of interaction strengths across landscapes (Bellmore et al., 2015; Chanut et al., 2019; Quévreux & Loreau, 2022; Rooney et al., 2006; Wootton, 2017). Such patterns likely occur in many heterogeneous systems, for example, spatial shifts in lake fish feeding from benthic to pelagic zones, or subsidies from marine-derived nutrients in forests (Naiman et al., 2002; Vander Zanden & Vadeboncoeur, 2002). The highly valued Te Awa-a-Takatamira ecosystem comprises many spatially variable and heterogeneous resources connected by mobile consumers foraging across a range of spatial scales. These facilitated food webs, where broader patterns of connectivity and spatial resource variability gave rise to several key food-web structures (Figure 4). The isotope mixing models applied are not quantitative estimates of interaction strengths, but they provide a good broad-scale estimate of energy flow and of how food sources potentially contribute to diets (Quevedo et al., 2009), and a starting point for future work into species interactions over space and time. Our observations provide an insightful snapshot of the spatial variation of diet in consumers moving at different scales within Te Awa-a-Takatamira. Collectively, they demonstrate the array of key structures that can arise from both contextual and mechanistic processes in complex landscapes.

The food-web structures we have identified encompass a broad array of ecological processes. Spatial resources variability can be driven by movement, disturbance, species interactions, and adaptive behaviors, physiology, and landscape heterogeneity; connectivity through predation interaction can be driven by these same processes (Abrahms et al., 2021; Lamy et al., 2021; McCluney et al., 2014). Structural patterns involving spatially varying interactions highlight the importance of preserving processes that create spatial variability and heterogeneity in the landscape. Understanding the relative importance of these processes is particularly important in complex, heterogeneous landscapes where homogenizing processes are significant global threats.

AUTHOR CONTRIBUTIONS

Data collection was conducted by all authors; data were analyzed by Holly A. L. Harris with inputs from all other authors, and Holly A. L. Harris also wrote the first draft. Conceptualization was by Holly A. L. Harris, Angus R. McIntosh, Jonathan D. Tonkin, and Tara J. Murray, and all authors contributed to manuscript editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Harris et al., 2025) are available in Figshare at https://doi.org/10.6084/m9.figshare.24848445.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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