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Monsoonal impacts on the community trophic niches in two temperate headwater tributaries across a land use continuum

Hee Yoon Kang[1,2], Byeong-Gweon Lee[2], Jae-Ki Shin[3], Changseong Kim[1], Hyun Je Park[4] & Chang-Keun Kang[1]✉

Pulsed flows following heavy monsoon rain events alter riverine food webs, but their impact on headwater stream food webs across the continuum from forested canopy to open agricultural land use remains unclear. We investigated carbon and nitrogen stable isotopes in macroinvertebrates and fish in two tributaries of the Suyeung River, Korea, before and after heavy monsoon rains to assess changes in community trophic niches. Basal resources (leaf litter and biofilms) exhibited consistent δ^{13}C and δ^{15}N values across seasons, with biofilms showing higher δ^{13}C values. δ^{15}N values increased from forested to agricultural reaches, indicating varied nutrient inputs. Consumer isotope values remained stable over time but varied longitudinally, reflecting reliance on local resources. Trophic niches differed between watershed locations but overlapped seasonally. Despite a decrease in consumer δ^{13}C ranges after heavy rainfalls, variations in their δ^{15}N ranges and the ellipse centroid (SEAc) of isotopic niches between sites resulted in broadly consistent SEAc across locations and seasons. This indicates limited evidence for directional reshaping of food-web properties across channel reaches following monsoon rains. Downstream isotopic shifts suggest substantial agricultural influences on food webs. Overall, our findings highlight that monsoon rains may have minimal effects on the community trophic niches of stream food webs.

Keywords Food web, Stream ecosystem, Nitrogen source, Stable isotopes, Hydrological connectivity, Agricultural streams

Lotic ecosystems are shaped by environmental gradients, such as organic matter type, stream and channel morphology, and light penetration, which all generate spatial patterns in the functional composition of biological communities along a river continuum[1,2]. Ecological models, such as the river continuum concept[1], the flood pulse concept[3], and the riverine productivity model[4], outline the processes contributing to the structure and function of riverine ecosystems. These models suggest that riverine food web processes depend on the fluxes of nutrients, detritus, and organisms across environmental gradients[2,5], which all affect resource availability and predator abundance, and so ultimately govern spatial[5–9] and temporal[10–12] food web dynamics. However, generalizations about spatiotemporal variabilities in food web topology may be limited because biological organization (species distributions and their interactions) is driven by multiple abiotic factors in different geographic areas, namely climate, geomorphology, hydrology, and disturbance[13,14]. Therefore, the structure and function of riverine ecosystems are complex and context-dependent, driven by the interaction between food webs and specific environmental factors.

Temperate East Asia, which encompasses the Korean peninsula, has a monsoon climate leading to seasonal changes marked by heavy summer rains and dry winters[15]. The rivers in Korea are connected with tributaries that drain watersheds spanning montane forests to agricultural lands along a declining elevation gradient[16]. The summer monsoon (June to August) rains markedly increase the availability of terrestrial and riparian organic matter in river systems[17,18]. The large downstream river channels, along with dam and weir reservoirs, act as

[1]School of Earth Sciences and Environmental Engineering, Gwangju Institute of Science and Technology, Gwangju 61005, Republic of Korea. [2]Department of Oceanography, College of Natural Science, Chonnam National University, Gwangju 61186, Republic of Korea. [3]Limnoecological Science Research Institute Korea (THE HANGANG), Miryang 50440, Republic of Korea. [4]Department of Marine Ecology and Environment, Gangneung-Wonju National University, Gangneung 25457, Republic of Korea. ✉email: ckkang@gist.ac.kr

major sinks for nutrients and organic matter from upstream watersheds[19–21]. Following summer monsoon rains, pulsed flows in tributaries provide allochthonous resource subsidies to consumers, thus modifying trophic diversity in the downstream food webs of large rivers[11,12,22,23]. Consequently, mechanistic processes that modify the availability of terrestrial and aquatic resources and support the food webs within tributaries may reorganize the role of tributary inputs to the downstream ecosystems of large rivers[1,11,24].

It is widely agreed that there are distinct ecological differences between streams in forested and agricultural lands. In temperate forested headwater streams, riparian trees provide shade and inputs of particulate organic matter such as woody debris and leaf litter[25]. Conversely, agricultural land streams retain dense benthic biofilms due to a lack of canopy shading[26,27] and nutrient influx from catchments[28,29]. This spatial dichotomy may result in a shift at the food web base from leaf litter detritus to algal biofilm[25,30]. With the transition in landscape geomorphology from forest to agricultural lands and the differences in seasonal flow patterns, it is expected that the relative availability of terrestrial matter compared with stream biofilm matter would change from the dry to the rainy season along river corridors. In this context, to better understand riverine food-web networks in this climate zone, it is essential to examine the effects of the summer monsoon on the relationship between resource supply and food web patterns in upstream tributaries.

Here, we employed stable isotope of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) to investigate seasonal and spatial variations in food web characteristics (such as trophic base, diversity, niche, and pathways) in tributaries down a forest to agricultural land gradient. The isotope values of aquatic and terrestrial producers are distinguishable and can be reflected in the tissues of stream consumers, with a predictable change of ≤ 1‰ for $\delta^{13}C$ and 2–4‰ for $\delta^{15}N$ at each trophic level[31–33]. Therefore, stable isotope analysis is a reliable tool for determining the relative contributions of autochthonous (stream) and allochthonous (terrestrial) sources to consumer production[34], and for validating river ecological models[24,30,35]. In addition to identifying the dietary sources and trophic positions of species using individual isotope measurements, community-wide metrics based on species positions in a niche space (i.e., $\delta^{13}C$–$\delta^{15}N$ space) can provide quantitative response variables (e.g., trophic diversity, total niche space and width, and niche similarity) within and between food webs in response to environmental variations[36,37].

In this study, we investigated the contribution of terrestrial and stream carbon sources to the nutrition of consumers, and the spatial and seasonal patterns of food web attributes in two tributaries of the Suyeung River, South Korea (Fig. 1), before and after the monsoon. Based on the observed dramatic increases in fluxes of terrestrial and riparian plant debris through river corridors during monsoonal flooding[17,18,24], we anticipated that monsoonal rains would cause flood disturbances that mobilize more organic matter further downstream as a result of increased erosion (sweeping with no sedimentation) and habitat degradation in upstream areas. This would be followed by a rapid recovery of biofilms in the open, agricultural upstream reaches[26–29]. Consequently, we expected that the reduction in available trophic resources (i.e., trophic diversity) would result in the upstream-reach food webs relying more on local resources following the monsoon. We hypothesized that consumer isotopic niches, based on their $\delta^{13}C$ and $\delta^{15}N$ values, would shift consistently between forested and agricultural upstream reaches from pre- to post-monsoon. Furthermore, we used $\delta^{15}N$ values to compare nitrogen sources between two contrasting stream locations to examine the incorporation of forest and agricultural watershed-derived nutrients into stream food webs. We compared food web attributes (community-wide metrics) to test for spatial and seasonal patterns and to relate them to hydrological features. Our goal was to evaluate the impact of monsoon flow pulses in resource supply from montane forests and agricultural land on the food web attributes in upstream locations, and to understand tributary processes in association with variability of downstream food webs.s

Results

Topographic and hydrological features

The forest stream sites (F1 and F2) and the agricultural land sites (M1 and M2) exhibited distinct topographic and hydrological characteristics (Table 1). The elevations at the forested headwater stream sites, F1 and F2, were 167 m and 270 m, respectively, with gentle gradients to downstream. The mean full water widths varied from 2.0 to 4.0 m at the forest sites to 20–60 m at the agricultural stream sites. The wetted width, in which water flows, showed very narrow ranges from 0.4 to 2.1 m in the forested headwaters to 5.5–17.0 m in the agricultural reaches, with a shallow water depth of ~ 0.1–0.4 m at base flow. In contrast to the forested channel sites with their overhead canopy, the agricultural stream sites (elevations: 70 m at M1 and 50 m at M2) had 52–88% of the full levee area covered by dense riparian grasses, without any shading from a canopy. In the agricultural stream, the mean water discharge at base flow was much higher (1.4–2.2 $m^3 s^{-1}$) than in the headwater stream sites (< 0.09 $m^3 s^{-1}$). Water quality parameters, including turbidity, chlorophyll *a*, suspended particulate matter (SPM), particulate organic matter (POC), and particulate nitrogen (PN) concentrations, were generally higher at the M1 and M2 sites than at the forest stream sites, F1 and F2. For biofilms, chlorophyll *a* content was consistently higher at the agricultural stream sites (29.5–45.8 mg m^{-2}) than at the forest stream sites (2.84–4.06 mg m^{-2}). However, ash-free dry weight, POC, and PN contents did not show significant longitudinal trends. The C:N molar ratios of both SPM and biofilms were much lower at both the agricultural stream sites (M1: 7.0–8.2 and M2: 6.1–7.1) than at the forest stream sites (F1: 16.4–21.6 and F2: 12.1–14.2).

Isotopic characterization of terrestrial and instream basal resources

The $\delta^{13}C$ values of basal resources spanned a wide range from − 34.7‰ (terrestrial plant *Erechtitis hieracifolia* at F1 in spring) to − 15.7‰ (biofilms at M2 in spring). Similarly, the values for $\delta^{15}N$ ranged from − 6.6‰ (terrestrial plant *Chamaecyparis obtusa* at F2 in summer) to 11.1‰ (riparian grass *Miscanthus sacchariflorus* at M1 in spring) (Fig. 2; Supplementary Tables S1 and S2). There were significant differences in isotope compositions among resource groups (3-way PERMANOVA, Pseudo-$F_{4,69}$ = 62.1, P = 0.001) and between sites (Pseudo-$F_{3,69}$ = 131, P = 0.001), but not between seasons (Pseudo-$F_{1,69}$ = 1.87, P = 0.163). There were no interaction effects for the

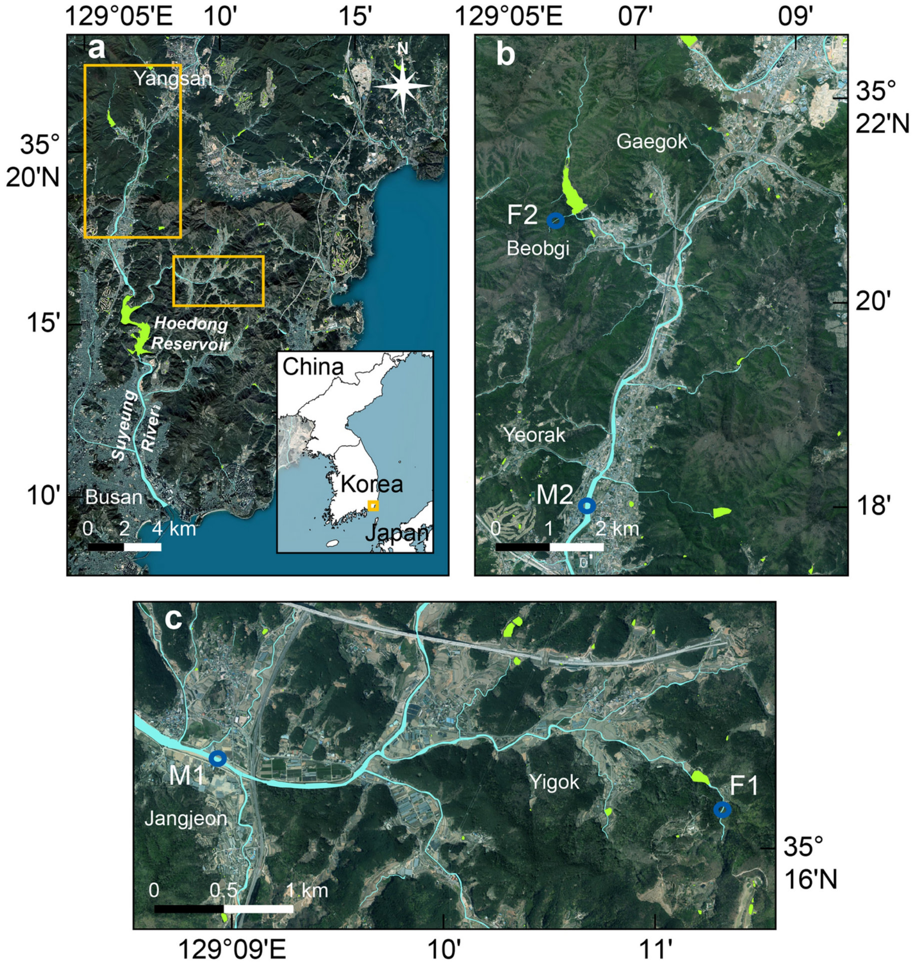

Fig. 1. Map showing the location of the Suyeung River system and its tributaries (**a**), and the sampling sites in the Beopgi (**b**) and Cheolma (**c**) tributaries. F1 and F2 are the montane forest stream sites; M1 and M2 are the agricultural stream sites. Green spots indicate reservoirs. The map was created using the Tile Map Service for Korean plugin (ver. 3.0.4; https://plugins.qgis.org./plugins/tmsforkorea/) in QGIS software (ver. 3.22.1).

main factors ($P > 0.05$) (Supplementary Table S3; Fig. S2). Subsequent pairwise comparisons showed significant differences in isotope composition between the basal resource groups ($P < 0.005$) except for coarse benthic organic matter (CBOM) vs. suspended particulate organic matter (SPOM) ($t = 0.61$, $P = 0.662$). Moreover, the isotope compositions of basal resources were identical between forest stream sites (F1 vs. F2, $t = 1.75$, $P = 0.055$) and agricultural stream sites (M1 vs. M2, $t = 0.57$, $P = 0.725$) but differed significantly between the forested (F1 and F2) and the agricultural streams (M1 and M2) sites ($P = 0.001$).

Both the $\delta^{13}C$ and $\delta^{15}N$ values differed significantly among basal resource groups between geographical locations (F1–F2 vs. M1–M2) (univariate PERMANOVA, Pseudo-$F_{6,90} = 154$ and 103, $P = 0.001$ for both; Supplementary Table S4). The $\delta^{13}C$ values of biofilms (-17.4 ± 1.1‰, $N = 12$) and SPOM (-18.7 ± 2.1‰, $N = 12$) at M1–M2 were significantly (pairwise comparisons, $P = 0.001$) higher than those of the matching items (-27.8 ± 1.2‰, $N = 12$; -28.5 ± 1.2‰, $N = 12$) at F1–F2 (Fig. 2). In contrast, the $\delta^{13}C$ values of riparian grass leaf litter (-28.3 ± 1.3‰, $N = 20$) at M1–M2 were close to those of CBOM (-28.9 ± 1.7‰, $N = 9$), biofilms, and SPOM at F1–F2 ($P = 0.294$ and 0.630). The $\delta^{13}C$ value of terrestrial tree leaf litter (-30.6 ± 1.8‰, $N = 20$) was lowest of all resource groups ($P < 0.05$). The mean $\delta^{15}N$ values of basal resources (6.6 ± 0.8‰, 6.0 ± 0.6‰, and 6.5 ± 2.5‰ for biofilms, SPOM, and riparian leaf litter, respectively) available at M1–M2 were much higher than those (-0.1 ± 1.0‰, -1.3 ± 1.1‰, -1.2 ± 1.6‰, and -3.4 ± 2.0‰ for biofilms, SPOM, CBOM, and terrestrial leaf litter, respectively) at F1–F2 ($P < 0.05$). The area-pooled mean $\delta^{13}C$ and $\delta^{15}N$ values of the respective basal resources were used as end-member values in the subsequent isotope-mixing model for consumers (Table S5).

Consumer isotope values and basal resources supporting aquatic food webs

A total of 51 consumer taxa (47 invertebrates and four fish) at the forest stream sites and 45 taxa (30 invertebrates and 15 fish) at the agricultural stream sites were analyzed (Supplementary Tables S6 and S7). Among them, the whirligig beetle (*Gyrinus japonicas*) and Japanese stick insect (*Phraortes elongates*), which had very negative $\delta^{13}C$ values indicating feeding on terrestrial insects, were excluded from the PERMANOVA test. The $\delta^{13}C$ values of consumers, with a few exceptions, overlapped with or were slightly higher than those of SPOM and biofilms in

	Forested headwater channel		Agricultural-land channel	
	F1	F2	M1	M2
Elevation (m above sea level)	167	270	70	50
Bankfull width (m)	2.0–3.0	2.0–4.0	20–30	50–60
Wetted width (m) at base flow	0.6/1.4	0.8/1.7	7.4/12.3	8.4/15.6
Water depth (m) at base flow	0.2/0.2	0.2/0.3	0.3/0.4	0.3/0.4
Average water velocity (m s^{-1})	0.05/0.09	0.05/0.11	0.15/0.50	0.25/0.60
Mean discharge (m^3 s^{-1})	0.05/0.07	0.06/0.08	1.5/1.7	1.6/2.0
Water				
Water temperature (°C)	15.8/21.7	15.1/22.8	17.7/23.2	18.6/23.4
Turbidity (NTU)	0.5/0.7	0.3/0.8	2.6/6.2	7.2/15.2
Chlorophyll *a* (mg l^{-1})	0.35/0.81	0.32/0.78	1.95/3.42	2.16/6.14
Suspended particulate matter (mg l^{-1})	0.34/7.83	3.56/9.66	14.79/24.64	20.44/30.47
Suspended POC (mg l^{-1})	0.28/0.46	0.37/0.72	0.97/1.24	1.28/1.48
Suspended PN (mg l^{-1})	0.02/0.03	0.03/0.04	0.16/0.18	0.19/0.23
C:N (molar ratio)	16.4/20.8	17.1/21.6	7.0/8.2	8.0/7.4
Biofilms				
Chlorophyll *a* (mg m^{-2})	2.84/3.73	4.06/3.68	36.84/32.23	29.48/45.76
Ash-free dry weight (g m^{-2})	47.3/25.6	33.6/18.4	28.4/42.4	32.5/35.7
POC (mg m^{-2})	38.44/31.28	28.64/41.13	42.46/36.58	30.06/37.45
PN (mg m^{-2})	3.25/3.02	2.57/3.38	8.08/6.28	4.92/6.62
C:N (molar ratio)	13.8/12.1	13.0/14.2	6.1/6.8	7.1/6.6

Table 1. Topographic and hydrologic characteristics of the study sites in the upstream tributary system of the Suyeung River. Data represent mean values of three replicate measurements taken in May and September, except for elevation and bankfull width, which were measured once. POC and PN refer to particulate organic carbon and nitrogen, respectively.

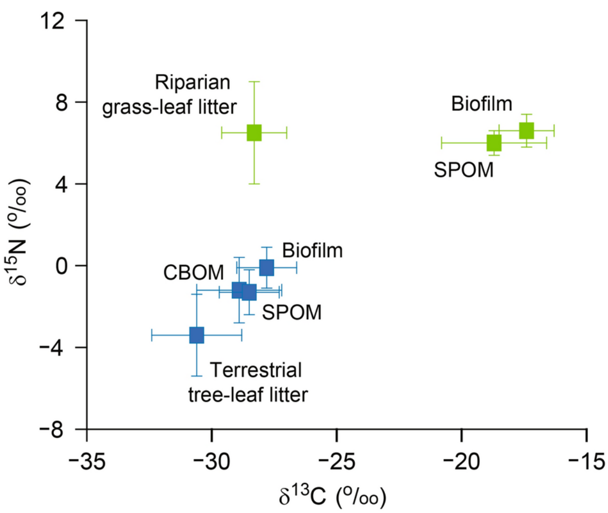

Fig. 2. Biplots of $\delta^{13}C$ and $\delta^{15}N$ values of putative basal food resources at the forest and agricultural land sites. Data represent mean $\delta^{13}C$ and $\delta^{15}N$ values (±SD) (see Table S5). Blue represent the forest channel reach sites and green the agricultural reach sites. SPOM, suspended particulate organic matter; CBOM, coarse benthic organic matter.

their respective watershed locations. In contrast, their $\delta^{15}N$ values were aligned vertically with the corresponding values of SPOM and biofilms, increasing with trophic level (Fig. 3).

There was a significant difference in isotope compositions of consumers between sites (2-way PERMANOVA, Pseudo-$F_{3,86}=166$, $P=0.001$) but not between seasons (Pseudo-$F_{1,86}=0.67$, $P=0.470$), with no interaction effect of site × season (Pseudo-$F_{3,86}=1.8$, $P=0.113$) (Table 2). Pairwise comparisons indicated that the isotope

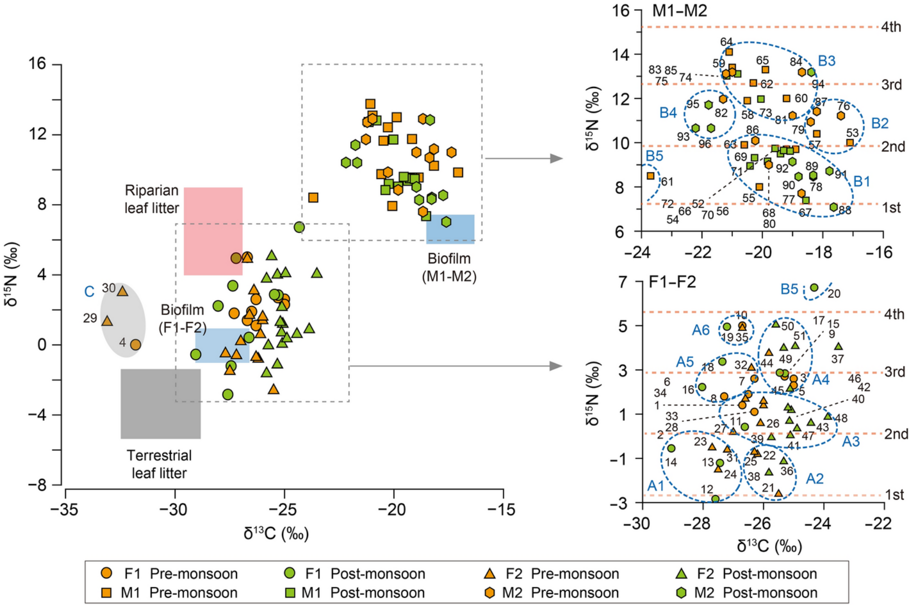

Fig. 3. Biplots of $\delta^{13}C$ and $\delta^{15}N$ values for various consumers and basal food resources at forest sites (F1–F2) and agricultural land sites (M1–M2). Colored rectangles denote putative basal food resources, and the dimensions represent mean $\delta^{13}C$ and $\delta^{15}N$ values (± SD). Species codes are shown by numbers in Supplementary Table S8 and are listed in Supplementary Tables S6 and S7. The groups of taxa (dotted, blue circles) were based on the hierarchical cluster analysis (see Supplementary Fig. S3).

compositions of consumers differed significantly between the forest stream sites (F1–F2) and the agricultural stream (M1–M2) sites ($P=0.001$). Although the significance was marginal ($P=0.046$), there was a difference between sites F1 and F2 within the forest streams. This isotopic difference in consumers across the forest and agricultural streams was attributed to both the $\delta^{13}C$ and $\delta^{15}N$ values (1-way univariate PERMANOVA, Pseudo-$F_{3,90}=182$ and 158, $P=0.001$ for both; Table 2). The difference between sites F1 and F2 was attributed to the $\delta^{13}C$ values ($t=2.73$, $P=0.003$) but this difference was extremely small, approximately 1‰ of mean values. The overall ranges of their $\delta^{13}C$ and $\delta^{15}N$ values shifted from the forest streams (−31.8‰ to −23.5‰ and −2.8‰ to 6.7‰, respectively) to the agricultural streams (−23.7‰ to −17.1‰ and 7.1‰ to 14.1‰, respectively).

Collected consumers were clustered into two main groups using $\delta^{13}C$ and $\delta^{15}N$ values (Supplementary Fig. S3, Table S8; Fig. 3). The grouping of consumers was primarily related to the stream (forest and agricultural channel) reach. Within each site type, predators (as well as omnivores) had higher $\delta^{15}N$ values than other feeding guilds (i.e., grazer, scraper, shredder, collector-gatherer, and herbivore), assigning their higher trophic positions. Consumer groups occupying respective trophic levels were then differentiated by different $\delta^{13}C$ ranges, indicating their reliance on different mixes of terrestrial vs. instream organic matter.

Consumer $\delta^{15}N$ and $\delta^{13}C$ combinations on the biplot plane indicated trophic pathways of organic matter from terrestrial and instream resources within food webs (Fig. 3). In the forest streams, one compartment, including cluster groups A2, A3, and A4 (ranging from primary to tertiary consumers), had $\delta^{13}C$ values between −27.6‰ and −23.5‰. The Chinese minnow (*Rhynchocypris oxycephalus*), assigned to B5, was also included to this compartment. This indicated high levels of autochthony, with these consumers (both invertebrates and fish) relying predominantly (median 68–76%) on instream biofilms for their nutrition (Fig. 4). The other compartment, comprising cluster groups A1, A5, and A6, exhibited lower $\delta^{13}C$ values (between −29.1‰ and −26.3‰), indicating an increased dependence (median 36–53%) on terrestrial organic matter sources for their nutrition. The distinct $\delta^{13}C$ ranges and increasing $\delta^{15}N$ values across trophic groups within each compartment indicated strong trophic linkages. In the agricultural streams, consumer $\delta^{13}C$ values of cluster groups B1, B2, and B3 (mainly comprising predatory invertebrates and fish) ranged from −21.2‰ to −17.1‰, indicating nutritional contributions of 48–70% from instream biofilms. These three groups included 40 of 45 taxa analyzed. For group B4 (only two predatory invertebrates and fish), the $\delta^{13}C$ range of −22.2‰ to −21.3‰ indicated equal contributions of instream biofilms (22–24%) and riparian leaf litter (20–21%) to their nutrition, with additional contributions of forested channel biofilms (19–20%), and terrestrial leaf litter (17–18%). This contrasted with the high levels of autochthony observed in most consumers. The Korean brown frog (*Rana amurensis coreana*) of group B5 showed contributions of 35% and 41% from biofilms and riparian leaf litter, respectively.

Longitudinal patterns of food web structure

No significant differences were observed in the community-wide isotope niche metrics [$\delta^{15}N$ and $\delta^{13}C$ ranges (NR and CR), the convex hull-shaped total area (TA), and standard ellipse area (SEAc) in $\delta^{13}C$–$\delta^{15}N$ space] between forest and agricultural streams nor between pre- and post-monsoon seasons (Table 3). The NR and CR were consistent across locations (2-way ANOVA, $P=0.363$ and 0.064, respectively) and seasons ($P=0.238$ and 0.429,

Source	df	SS	MS	Pseudo-F	P (perm)
PERMANOVA					
Site	3	2877	959	166	**0.001**
Season	1	3.84	3.84	0.67	0.470
Site × Season	3	31.1	10.4	1.80	0.113
Residual	86	495	5.76		

Pairwise “site”		t	P (perm)
Site	F1 vs. F2	1.91	**0.046**
	vs. M1	14.1	**0.001**
	vs. M2	13.4	**0.001**
	F2 vs. M1	18.2	**0.001**
	vs. M2	17.3	**0.001**
	M1 vs. M2	0.73	0.550

		$\delta^{13}C$			$\delta^{15}N$		
Source	df	MS	Pseudo-F	P (perm)	MS	Pseudo-F	P (perm)
Univariate PERMANOVA							
Resource group	3	330	182	**0.001**	645	158	**0.001**
Residuals	90	1.81			4.08		

Pairwise “site”	$\delta^{13}C$ t	$\delta^{13}C$ P	$\delta^{15}N$ t	$\delta^{15}N$ P
F1 vs. F2	2.73	**0.003**	1.45	0.148
vs. M1	15.5	**0.001**	13.9	**0.001**
vs. M2	14.7	**0.001**	13.1	**0.001**
F2 vs. M1	18.7	**0.001**	17.3	**0.001**
vs. M2	17.7	**0.001**	16.3	**0.001**
M1 vs. M2	1.21	0.206	0.31	0.751

Table 2. Results of two-way permutational multivariate analysis of variance (PERMANOVA, based on Euclidean distance) to test the significance of differences in $\delta^{13}C$ and $\delta^{15}N$ values (‰) of consumers based on main factors of site and season. The pairwise comparisons are provided for factor ‘site’: the forested headwater stream sites F1 and F2; the agricultural-land channel sites M1 and M2. Results of one-way univariate PERMANOVA to test significances of individual isotope ($\delta^{13}C$ and $\delta^{15}N$) values are followed. Bold represents a significance at $P < 0.05$.

respectively). Similarly, the TA and the SEAc of the isotopic niche did not show any significant changes between locations (2-way ANOVA, $P = 0.436$ and 0.670, respectively) or seasons ($P = 0.246$ and 0.485, respectively). While there was a slight shift in the SEAc at site F2 post-monsoon, which reflected a biofilm-dominated resource base, the food webs at each site exhibited a high degree of isotopic niche overlap in $\delta^{13}C$–$\delta^{15}N$ space between pre- and post-monsoon seasons (Fig. 5a–b). Bayesian estimates of standard ellipse area (‰^{2}) variabilities at 95% credibility intervals further revealed an absence of seasonal patterns in trophic diversity of respective watershed channel locations (Fig. 5c–d). The consumer isotopic niches in $\delta^{13}C$–$\delta^{15}N$ space corroborated a significant longitudinal shift with no overlap between the forest streams and agricultural streams in both seasons, reflecting the prevalence of locally derived resources to the food web base at the respective watershed channel locations.

Discussion

Our study found that the isotopic niches of consumers in the forest and agricultural streams of tributaries in the Suyeung River were closely overlapped in $\delta^{13}C$–$\delta^{15}N$ space during both pre- and post-monsoon seasons. However, these niches were ultimately separated between watershed locations in both seasons. This supports our initial hypothesis that upstream-reach food webs are primarily based on local resources before and after monsoon flow pulses. The patterns we identified by our quantitative food web characterization offer insights into the structure and function of food webs in tributaries across temperate forested and agricultural watersheds. Our results suggest that despite noticeable differences in basal resource use between trophic groups of consumers within each watershed channel, food webs at different watershed channel locations are sustained by local resource bases pre- and post-monsoon. In addition, downstream food webs are reliant on nitrogen inputs from agricultural watersheds. Furthermore, although the community-wide trophic niche metrics (specifically, CR and SEAc) responded differently to monsoon rains across various sites, these metrics remained broadly consistent between seasons and locations. Finally, a comparison of consumer $\delta^{13}C$ and $\delta^{15}N$ values between the tributaries and the downstream river channel indicated that the trophic contribution of forest watershed-derived organic matter to downstream channel food webs was minimal.

The $\delta^{13}C$ values of riparian tree and grass leaf litter (i.e. terrestrial producers) and instream biofilms, which are considered to be the primary basal resources in our stream food webs, were notably different from each other, as is typical in stream systems around the world[24,30,38]. This difference in $\delta^{13}C$ values was accompanied by a sharp increase in $\delta^{15}N$ values from forest to agricultural streams. Consequently, the mean $\delta^{13}C$ and $\delta^{15}N$ values

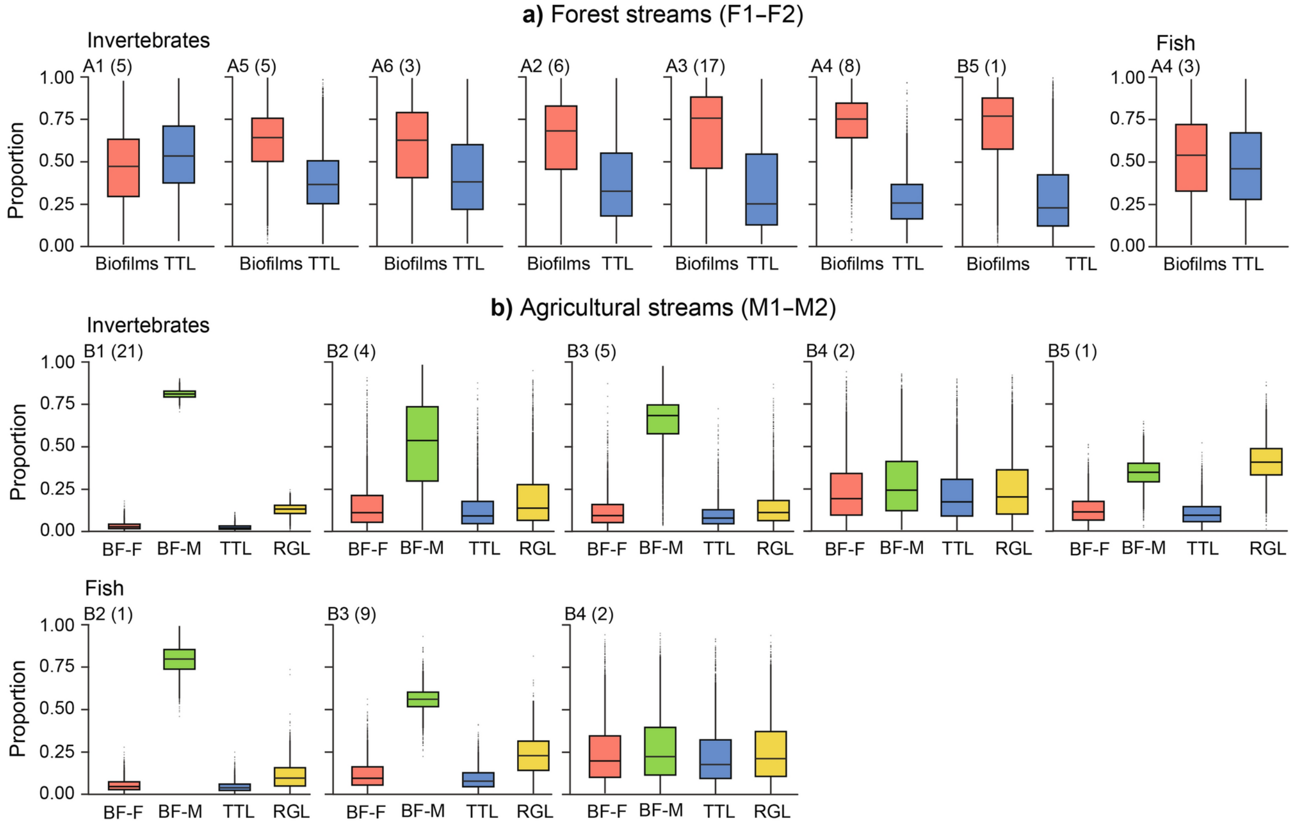

Fig. 4. Contribution (%) of in-stream aquatic and detrital food resources to the nutrition assimilated by different cluster (i.e., trophic) groups of consumers in both forested (**a**) and agricultural (**b**) stream reaches. *N* in parentheses represents the number of species within each group. Abbreviations: TTL = terrestrial tree leaf; BF-F = biofilms of forest streams; BF-M = biofilms of agricultural streams; RGL = riparian grass leaf.

	F1		F2		M1		M2		2-way ANOVA (*P*)		
	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Location	Season	Interaction
NR	5.0	9.6	7.5	6.7	6.1	5.7	5.5	6.1	0.238	0.363	0.408
CR	6.8	4.7	7.6	2.3	6.6	2.6	3.9	4.6	0.429	0.064	0.385
TA	14.0	18.9	31.0	10.3	21.7	5.5	13.1	14.3	0.436	0.246	0.974
SEAc	7.5	11.7	14.6	4.3	10.2	3.4	7.8	10.8	0.670	0.485	0.867

Table 3. Results for the community-wide metrics based on the $\delta^{13}C$ and $\delta^{15}N$ values of whole consumers at channel sites during two seasons, providing information on trophic diversity ($\delta^{15}N$ range, NR; $\delta^{13}C$ range, CR; total area, TA; a standard ellipse area corrected for small sample sizes, SEAc). Results of 2-way ANOVA for the isotopic niche measures. Main factors were locations (the forested- and the agricultural-land channels) and seasons (pre- and post-monsoon). Pre and Post represent pre- and post-monsoon.

of these potential sources were highly site-specific and remained constant between pre- and post-monsoon periods. Consistent with these results, the $\delta^{13}C$ and $\delta^{15}N$ values of consumers did not change with time but rather exhibited a longitudinal trend, increasing in tandem along the continuum of forest and agricultural streams. This suggests that the utilization of different basal resources varies depending on location during both seasons.

Considering that total SPM (i.e., seston) in streams is comprised of a diverse range of particulate matter from various sources[38,39], it could reflect the availability of organic matter from the entire watershed area to consumers at each stream channel location (i.e., forested vs. agricultural channel). Phenological patterns in primary production and riparian vegetation, which influence the availability of allochthonous and autochthonous food resources in streams, are closely linked to the seasonality of rains[40,41]. Nevertheless, our research revealed that both quantitative (chlorophyll *a*, SPM, ash-free dry weight, POC, and PN) and qualitative (C:N, $\delta^{13}C$, and $\delta^{15}N$) measures of organic matter in suspension and biofilm remained relatively consistent within locations in forested and agricultural areas before and after summer monsoon rains. These measures exhibited considerable variation across the tributary continuum. Despite increased water discharge and turbidity in agricultural streams, most quantitative indicators were higher in these channels compared with those in forest streams. This result denies

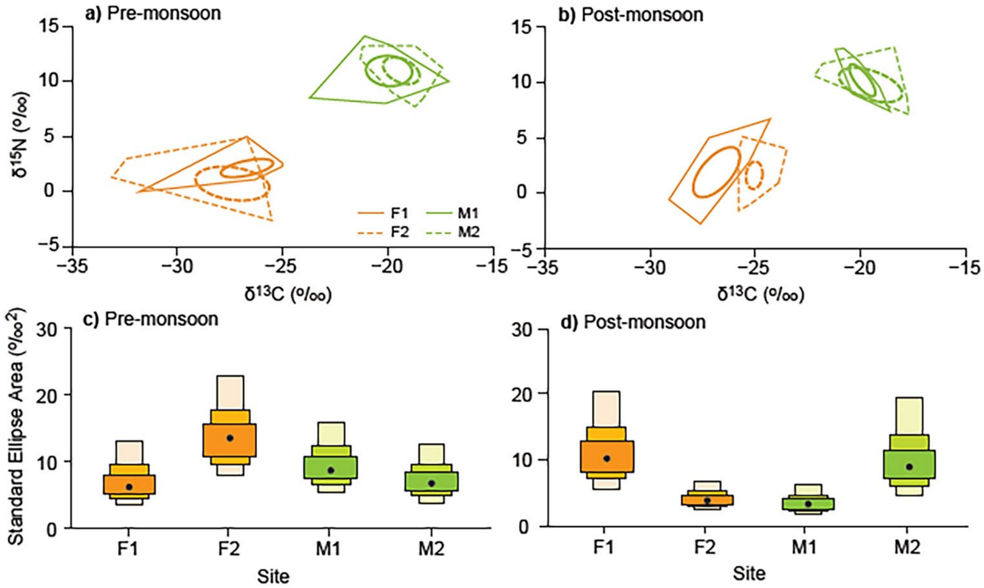

Fig. 5. Standard ellipse areas corrected for small sample size (SEA_C; thick lines) and convex hulls representing total area (TA; thin lines) for each food web at the forested (yellow: F1, solid lines; F2, dashed lines) and the agricultural stream sites (green: M1, solid lines; M2, dashed lines) in the pre-monsoon (**a**) and post-monsoon (**b**) seasons. Density plots showing the credibility intervals of the standard ellipse areas (SEAc). Boxes from wider to thinner indicate the 50%, 75%, and 95% credibility intervals at each site in pre-monsoon (**c**) and post-monsoon (**d**) seasons. Black dots represent the mode.

the influence of water depth, flow velocity, and turbidity on primary production in shallow tributaries, which differs from larger river systems[24,38,42]. Furthermore, the C:N molar ratios of SPOM were similar to those of biofilm (7.0–8.2 vs. 6.1–7.2) in agricultural streams, yet significantly different from biofilm (16.4–21.6 vs. 12.1–14.2) and somewhat like terrestrial plants adjacent to forest streams (18.1–45.2)[30]. This suggests a reduction in the relative accessibility of terrestrial carbon as the tributaries transitioned from forested to agricultural landscapes[43], supporting the observed longitudinal shifts in $\delta^{13}C$ and $\delta^{15}N$ values of SPOM and consumers.

During both seasons, consumers at the respective tributary locations relied mainly on locally available and produced basal resources for their nutrition. The $\delta^{13}C$ values of consumers either overlapped with or were slightly higher than those of the available food sources sampled in forest streams (F1 and F2) but were intermediate between the available sources in agricultural streams (M1 and M2). This site-dependent difference may be attributed to the varying trophic fractionation effects of dietary isotopic values on the isotopic values of invertebrates and fishes, as accounted for in our isotope mixing-model calculations using diet-dependent fractionation factors[44] (see Table S9 for more details). The $\delta^{13}C$ range between terrestrial leaf litter and forested instream biofilms was lower compared to those between riparian leaf litter and agricultural land instream biofilms. However, two distinct isotopic compartments of consumers, separated by their $\delta^{13}C$ values, can differentiate food web pathways of both food sources, suggesting trophic niche partitioning[45]. The feeding strategy of consumers plays a significant role in determining their resource use[46]. In this study, macroinvertebrate taxa employing the same feeding strategy were arbitrarily partitioned into different cluster (i.e., trophic) groups based on their stable isotope signatures. Therefore, it may be challenging to partition a priori known functional groups to trophic groups occupying trophic positions between litter- and biofilm-based food chains. The reliance of consumers on different organic matter sources may reflect the availability of resources[11,38], accessibility to resources[42], and their food preference or selectivity[7,47], thereby accounting for the process of resource segregation of these generalist feeders, as expected from the absence of shredders. While the importance of terrestrial leaf-litter detritus as an important trophic base has been commonly accepted for temperate forest headwaters[25,48], the role of instream biofilm as the primary basal resource assimilated by macroinvertebrates has been demonstrated in diverse forested streams, even where its availability is limited[7,46,49,50].

In the tributaries within agricultural landscapes, consumers were classified into trophic groups with a narrower $\delta^{13}C$ range compared with the broader range between leaf litter and biofilm, enabling more accurate tracking of dietary contributions. Both macroinvertebrate and fish groups relied mainly on locally produced biofilms in both seasons, with a few exceptions (four taxa in the cluster group B4 of 45 taxa). Minimal use of forest stream-derived litter and biofilm was detected in the agricultural streams, likely due to rapid transport. Macroinvertebrate taxa with diverse feeding strategies were clustered into a trophic group, resulting in trophic niche (i.e., resource use and trophic position) homogeneity[44], primarily relying on abundant autochthonous biofilms. This finding supports that autochthonous biofilm contributes significantly to the available basal resource pools, like some temperate open canopy streams[30,50,51]. The $\delta^{13}C$ ranges of predatory invertebrate and fish taxa groups were aligned well with those of the former macroinvertebrate group. Active movement of fish between instream and riparian cover habitats and their ability to consume a variety of prey in diverse foraging spaces depending on their feeding strategy[52,53] support the observed groupings based on stable isotope signatures. Along with the $\delta^{13}C$ ranges, their increased $\delta^{15}N$ values suggest active feeding on invertebrate prey, which have limited mobility and a small foraging range, further indicating trophic transfer of autochthonous basal resources.

Despite the increased water flow following the monsoon season, the impact of resource pulses from forested montane streams on the trophic base of food webs in agricultural reaches is unlikely. Instead, higher water flows associated with monsoonal rains may decrease the accumulation of wood and litter debris on the stream bed[54]. Agricultural reaches, characterized by shallow water, low shading, turbidity, and a lack of retentive mechanisms like woody debris dams, may facilitate the use of biofilms and periphyton by consumers, with resource availability stimulated by nutrient inputs from adjacent watersheds[28,55]. The $\delta^{15}N$ values of consumers reflected longitudinal changes in the values of producers across tributaries in both seasons. However, although we consider the varying trophic fractionation effects of dietary $\delta^{15}N$ values on invertebrate and fish $\delta^{15}N$ values (mean 2.02‰ to 6.84‰, Table S9), as shown earlier for the distribution $\delta^{13}C$ values, the trophic fractionation factor is unlikely to explain the ~ 10‰ $\delta^{15}N$ difference within nearly identical NRs between forested and agricultural stream food webs.

Previous studies reported that the $\delta^{15}N$ values of dissolved nitrate in the Han and Yeongsan Rivers, which are adjacent to the Suyeung River, showed a wide range of 3–16‰ along the river channels[56,57]. These values were higher in channels located in drainage basins with agriculture and livestock farms and (sub)urban areas than in those in pristine montane areas with small farms. The $\delta^{15}N$ values of the main nitrate sources in the river basins—precipitation (− 7.2‰ to 0.2‰), soil N (− 0.1‰ to 0.6‰), fertilizer (− 2.6‰ to 10.1‰), sewage (2.2‰ to 21.9‰), and manure (12.5‰ to 21.6‰)[56]—fell within their typical worldwide ranges[58,59]. Based on these measurements, it can be concluded that manure and sewage are the main sources of nitrate in the river channels of agricultural watershed, whereas precipitation and soil N are the main sources in the channels of montane areas. Additionally, the application of ^{15}N-depleted fertilizers to a field can cause significant increases (up to 11‰) in the $\delta^{15}N$ values of terrestrial grass[60]. The observed increase in the $\delta^{15}N$ values of basal resources and aquatic consumers from montane forest to agricultural streams is indicative of the incorporation of allochthonous nitrogen of agriculture-watershed origin into downstream food webs[61,62].

At the community level, forest and agricultural streams occupied distinctly separate isotopic niche spaces, with seasonal overlaps in their respective locations. This result can be interpreted through two different mechanisms. During the pre-monsoon season, niche segregation between contrasting upstream locations may reflect limited hydrological connectivity, which restricts the transfer of matter and resources through tributaries. In contrast, despite their proximity and increased hydrological connectivity during the heavy monsoon rains, the spatial change in basal resource use associated with nitrogen inputs within tributaries supports the rapid downstream transport of materials originating from forests and riparian zones[17,18]. This transport results in low availability of these materials in the agricultural stream reaches[24,30]. Furthermore, community-wide niche metrics (CR, NR, and SEAc) were broadly consistent across locations and seasons, indicating that monsoon rains do not influence trophic diversity (i.e., vertical and horizontal niche breadths, and entire niche area). However, this consistency observed in trophic diversity measures may require further investigation, as discussed below.

Consumer CRs (horizontal niche breadths) corresponded to the overall $\delta^{13}C$ range of organic matter sources in forested channel reaches but were significantly narrower in agricultural reaches. These CRs appeared consistent across different locations and seasons. Although the seasonal effect on CR was statistically marginal ($P = 0.064$), CRs tended to be reduced following monsoon rains across the tributary continuum, reflecting lower variability within sites after the monsoons. The narrower CRs (i.e., reduced $\delta^{13}C$ variability) following monsoon rains mirrored changes in community assemblages, which shifted from diverse feeding guilds to more abundant omnivorous-predatory consumers (Tables S7–S8). More importantly, this lowered $\delta^{13}C$ variability within respective communities suggests a homogenization in basal resources due to heavy rains. Regardless of the seasonal CR pattern, consumers in forested channels utilized all basal resources with narrow $\delta^{13}C$ ranges, while those in agricultural streams relied exclusively on a hyperabundant biofilm between broad $\delta^{13}C$-value resources, which may be attractive to all consumers[45]. Despite slight deviations in resource use by fish, greater isotopic redundancy in consumers suggests niche homogeneity during both seasons, with no disturbance by flow pulses[45]. The consumer NRs (vertical niche breadths) were identical temporally and spatially, further indicating that trophic interactions persist in local food webs without disruption[42]. High consumer omnivory, as evidenced by the observed continuous rather than discrete trophic positions[7], may be responsible for such interactions.

The observed consistency in community-wide SEAc across contrasting upstream locations was attributed to different patterns of seasonal variabilities between individual sites. Indeed, SEAc showed a reduction at F2 and M1, but an opposite trend at F1 and M2 following monsoon rains. The SEAc reduction at the former sites after monsoon can be explained by the decreased CRs, while the SEAc expansion at the latter sites by the increased NRs (Table 3). This result further suggest that niche changes are based on site-specific species composition, as well as the predictable homogenization of basal resources, rather than resource addition (i.e., increase in resource diversity) by increased hydrological connectivity. The diverging patterns in SEAc between sites indicate no directional reshaping of food web properties across channel reaches (i.e., forest and agricultural land) following monsoon rains. Consequently, the absence of directional reshaping as well as distinct separation in isotopic niche spaces in contrasting channel reach communities highlight that the effects of monsoon rains on trophic niches of upstream tributary food webs are insignificant[30,43,63].

During the summer season on the Korean peninsula, heavy rains (50–60% of the annual precipitation)[64], including monsoonal rains from late June to late July and tropical storm-associated rains in August, can increase the flow of water in streams and bring woody debris and litter from forested, agricultural, and riparian watersheds. However, our results suggest that although heavy rains may increase the hydrological connectivity, the short-term monsoonal pulses of rains, which typically occur within a period of days or weeks[65], do not lead to changes in the longitudinal trend of food web structure or trophic niche across channels within agricultural systems, as observed in other streams in temperate, glacial, and floodplain areas[42,43,63]. This is likely due to huge volumes of fast flowing water promoting transport downstream with little retention of allochthonous debris during the short period[17,18], reducing consumer accessibility to resources and further processing. Furthermore, highly elevated δ^{15}N values of the downstream SPOM indicate an indirect effect of nitrogen inputs from agricultural watersheds on biofilm biomasses after monsoon rains.

Conclusions

Our stable isotope evidence suggests that the impact of summer monsoon rains on food web properties in tributaries within temperate forested and agricultural watersheds is equivocal. The limited effects observed may be attributed to rapid changes in stream flow regimes, particularly short-term flow pulses, that quickly recede allowing for communities to recover. In contrast, the longitudinal pattern in the trophic niches of tributary food webs remained mostly consistent before and after the summer monsoon. Previous studies on downstream reaches in the Korean peninsula, unlike our focus on headwater tributary food webs, have shown that the δ^{13}C values of SPOM and many consumers decreased toward terrestrial litter after the monsoon in a dam with a short water residence time (5 days)[22] and in a flowing river[23]. However, these values were consistent with microalgae blooming during pre- and post-monsoon periods in a dam with a stagnant water body (residence time of months to years)[30]. These findings suggest that flow regime may play a crucial role in shaping the food web base in downstream river channels. The corresponding increase in δ^{15}N values in SPOM and consumers toward riparian grass litter further indicates the significant role of agricultural watershed-derived inputs (litter and nitrate for basal resource production) and a lesser influence of low-δ^{15}N matter from forest watersheds in downstream food webs. Overall, our findings contribute to the understanding of how tributary processes may impact changes in downstream food webs during monsoon rains.

Methods

Study location

The Suyeung River is located at the southeast end of the Korean peninsula (Fig. 1). The river flows for 28.6 km with a catchment area of 200 km^2, which is dissected by parallel mountain ranges and contains 83% forested land, 14% agricultural land, and 3% urban area[66]. The study was conducted in the two main tributaries, the Cheolma and Beopgi streams which flow into the Hoedong Reservoir upstream of the main Suyeung River (Fig. 1). The stream substrate is dominated by schist bedrock, with boulders and cobbles throughout the stream corridors. The mean flow ranges from ≤ 0.1 m^3 s^{-1} in the forested headwater streams to 1.3–2.2 m^3 s^{-1} in the agricultural streams (Table 1). The forested headwater stream flows are naturally intermittent due to a dry winter season, a wet spring and autumn, and flash flooding during the summer monsoon. The agricultural streams are well lined by levees and thus have a limited connection with the watershed catchment[30]. These agricultural streams have a riparian littoral zone covered by dense vegetation that is subject to flooding during episodic heavy rain. Although there are relatively few fish species in these channels, there is a diversified aquatic macroinvertebrate community dominated by chironomid larvae[67,68].

We selected four sampling sites for longitudinal comparisons of aquatic food web attributes (Fig. 1). Two forested headwater stream sites (F1 and F2), located approximately 12.3 km upstream of the Hoedong Reservoir, are covered by dense canopies. In contrast, two agricultural stream sites (M1 and M2) are situated about 3.5 km upstream of the reservoir, with a distance of approximately 9 km separating the forested sites from the agricultural sites. In the forested headwater streams, the stream width at base flow was about 0.4–2.1 m over substrates of boulders and stones. The forest plants forming the overhead canopies are dominated by several deciduous tree species (mostly hornbeam, Mongolian oak, purple beautyberry, Japanese spicebush, and Japanese cedar) as well as bracken. These sites are characterized by abundant leaf litter detritus, low biofilm biomass, and low turbidity compared with the agricultural stream sites (Table 1). In the agricultural streams, the wetted width at base flow was 5.5–17.0 m with a substrate mainly comprising boulders and equal proportions of cobbles, pebbles, gravel, and sand. These sites lacked riparian trees. The riparian vegetation was dominated by dense grass, consisting of Amur silver grass (*Miscanthus sacchariflorus*), sedge grass (*Carex dispalata*), shortawn foxtail (*Alopecurus aequalis*) and *Persicaria thunbergia*. Compared with sites F1 and F2, sites M1 and M2 were characterized by a relatively constant flow, low input of terrestrial leaf litter detritus, thick biofilms, and high turbidity.

Hydrological characterization

Samples were collected on May 7–8 (late spring) and September 4–5 (late summer) 2021 (Supplementary Fig. S1). Given that annual precipitation is concentrated during the summer monsoon period (473 mm in the dry season from October to May versus 1125 mm in the monsoon season from June to August), we anticipated that the inputs of terrestrial and riparian materials to the streams would vary by season. As described in the Introduction, stable isotope values of animals can be used to integrate information of assimilated-nutrient history over days and months. The late spring sampling was chosen to obtain information on consumer nutrient sources at low base flow during the dry winter and early spring periods (i.e., pre-monsoon), whereas the late summer sampling (i.e., post-onsoon) followed elevated flow during the summer monsoon.

The elevation of individual sites was determined based on contour lines on a 1:50,000 topographic map. The levee gap width (m) and the wetted width (m, portion of the channel covered in water) of the channel sites were calculated by averaging measurements at five locations in the field. The water depth (m) in the wetted channel was measured at five points located at equal distances across the wetted width. The cross-section (m^2) at a location was calculated by multiplying the mean depth by the wetted width. The velocity of water (m s^{-1}) was measured using a flow meter (Electronic Flow Meter, General Oceanics Inc., Miami, FL). The water flow (m^3 s^{-1}) at each site was calculated by multiplying the mean water velocity by the average width and the mean water depth. Water temperature and turbidity were measured using a YSI ProDSS Water Quality Meter (Yellow Springs, OH).

Sample collection

Base resources available to primary consumers (terrestrial leaf litter, riparian leaf litter, CBOM, SPOM, and biofilm] were collected from the stream channels and within 5 m zones from the stream boundary. For terrestrial sources of organic matter, leaf litter of the 3–7 dominant tree species was collected by hand at the forested headwater stream sites F1 and F2. CBOM was collected by sieving surface sediment deposits through a 200 µm Nitex nylon mesh screen at the forested sites. Standing dead riparian grass leaf litter was taken by clipping above the root at the agricultural stream sites M1 and M2. For biofilm measurements, five small stones (diameter, 10–15 cm) with biofilm patches were randomly collected at each site. Biofilms were scraped off with a toothbrush to represent a final area of 120–220 cm^2, pooled, and divided into two subsamples, one for stable isotope analysis and the other for quantification of mass and chlorophyll *a*. Although the biofilms may contain both autotrophic and heterotrophic components rather than terrestrial organic matter[38], the liquid samples were sieved through a 200 µm Nitex nylon mesh to remove large plant debris. Three replicates for respective measurements were taken, stored in acid-washed polypropylene bottles, and held over dry ice in the dark for return to the laboratory. For measurements of suspended particulate matter (SPM), three10 L water samples were collected from the running water surface at each site, immediately filtered through a 250 µm nylon mesh to remove large particles, and stored in the dark in polypropylene bottles.

For consumer sampling, as many genera as possible of macroinvertebrates were randomly collected at each site using a Surber net (200 µm mesh). To obtain more taxa, samples of snails, annelids, leeches and other epiphytic invertebrates were collected by hand. Fish were sampled using a bamboo net (110 cm × 140 cm; mesh hole size, 4 mm) and a hand-thrown nylon cast net (1.2 m radius; mesh hole size, 4 mm). All animal samples were transported to the laboratory on ice.

Laboratory processing and environmental measurements

Immediately after transport to the laboratory, flora and fauna specimens were sorted and identified to the lowest taxonomic level possible. Invertebrates were kept alive overnight in filtered water from the sampling site to allow evacuation of the gut contents.

For quantification of SPM, 1 L of water per analysis was filtered onto previously combusted (450 °C, 2 h) and weighed Whatman grade GF/F glass microfiber filters (diameter 47 mm; nominal pore size, 0.7 µm) under gentle vacuum (150–200 mm Hg). The filters were ignited at 450 °C for 4 h and weighed again after cooling to room temperature (25 °C) in a vacuum desiccator. Then SPOM concentration was computed by the weight loss after ignition of the filters. For determination of POC and PN, 0.5 L of water was filtered through Whatman GF/F filters (diameter 25 mm; pore size, 0.7 µm). After shocking with several drops of 10% HCl, POC and PN concentrations were determined using an elemental analyzer (Vario Micro Cube, Elementar, Langenselbold, Germany).

For quantification of chlorophyll *a* concentration of SPM, 1 L of water per analysis was filtered onto Whatman grade GF/F glass microfiber filters (diameter 47 mm; nominal pore size, 0.7 µm) under gentle vacuum (150–200 mm Hg). Chlorophyll *a* concentration of biofilms was measured following the same procedure as for SPM samples. Biofilms were concentrated by centrifugation at 3,000 × *g* for 10 min, lyophilized at − 80 °C, and weighed to quantify total mass and chlorophyll *a*. For quantification of ash-free dry weight, a known weight of biofilms was combusted at 450 °C for 4 h and reweighed after cooling to ambient temperature in a vacuum desiccator. Chlorophyll *a* from the SPM and the known weights of biofilm was extracted with acetone:water (90:10 v/v) for 24 h in the dark at − 20 °C, its fluorescence was measured (Turner Designs, Sunnyvale, CA), and its concentration calculated[69].

For isotopic and elemental measurements, litter and CBOM samples were cleaned with deionized water to remove epibionts or any contaminants, and then cut into small pieces. The floral samples were frozen to − 80 °C, lyophilized, and pulverized to a fine powder using a ball mill (Retsch MM200 Mixer Mill, Hyland Scientific, WA). Approximately 7 L of water was filtered through combusted Whatman GF/F filters (diameter 25 mm; pore size, 0.7 µm). The filtered samples were decarbonated by fuming with HCl overnight in a desiccator and then oven-dried at 60 °C for 72 h. Individual biofilm samples were divided into two subsamples. The one for $\delta^{13}C$ was shocked with several drops of 10% HCl to remove inorganic carbonates. The other for $\delta^{15}N$ was not acid-treated because of acid treatment effects on nitrogen isotope ratios[70].

All invertebrates were dissected and removed from their exoskeletons or shells. If possible, their viscera were extracted by dissection and the remaining whole bodies were collected. Tissues from several individuals were often pooled to provide sufficient material for isotope analysis. Tissue samples were lyophilized and pulverized to a fine powder using the ball mill. One half of the now powdered invertebrate tissues was treated with 1 M HCl to remove carbonates prior to $\delta^{13}C$ measurement; the other half was untreated to avoid the acid effects on $\delta^{15}N$ values[71]. Fish samples were dissected to recover the dorsal white muscle tissues. These were washed in a mixed solution (2:1:0.8 v/v) of methanol, chloroform, and water[72] for three 10-min intervals to remove lipids that may be more depleted in ^{13}C than proteins and carbohydrates[73]. The extracts were oven-dried at 60 °C for 24 h and stored in a vacuum desiccator until later analysis. Tissues of individual consumer taxa were pooled to calculate a weighted mean value for $\delta^{13}C$ and $\delta^{15}N$. All isotope measurements were conducted twice and the results are presented as mean values. Feeding guilds of the consumer taxa were identified from the literature (see Supplementary Information).

Stable isotope analysis

Powdered matter was weighed and packed into tin cups, between 0.5 and 1.5 mg for animal tissues and about 5 mg for plant material. Filters containing SPM were wrapped with tin plates. $\delta^{13}C$ and $\delta^{15}N$ values were determined using a continuous flow isotope-ratio mass spectrometer (CF-IRMS; Isoprime, GV Instruments, Manchester, UK) coupled with an elemental analyzer (Vario Micro Cube, Elementar, Langenselbold, Germany). Thus, isotope ratios and C and N elemental concentrations were measured simultaneously. Two packs of the internal reference urea were analyzed after every 5–10 samples. Isotope ratios were expressed as the relative per mil (‰) difference between samples and conventional standard reference materials (Pee Dee Belemnite carbonate and N_2 in air) using the following equation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3$,

where X is the ^{13}C or ^{15}N and R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Measurement precision based on the standard deviation of 20 urea determinations was within 0.2‰ for both isotopes.

Statistical analysis

A permutational multivariate analysis of variance (PERMANOVA, based on Euclidean distance) was employed to test the significance of distributions of the $\delta^{13}C$ and $\delta^{15}N$ values among putative basal resources (i.e., terrestrial leaf litter, riparian grass leaf litter, CBOM, SPOM, and biofilms). The PERMANOVA does not necessarily need to meet normality. Our PERMANOVA design was based on three factors: resource, fixed with five basal resource groups; site, fixed with four sites (F1, F2, M1, and M2); and season, fixed with pre-monsoon (May) and post-monsoon (September). When differences were significant, subsequent pairwise comparisons for individual isotope ($\delta^{13}C$ and $\delta^{15}N$) values were performed between factor groups (i.e., basal resources and sites) by 1-way univariate PERMANOVA.

A PERMANOVA was performed to test for significant differences in seasonal and spatial distributions of isotope values of the entire consumer community. This PERMANOVA design was based on two factors: site, fixed with two locations (F1 and F2, forested headwater streams versus M1 and M2, agricultural streams) and season, fixed with pre-monsoon and post-monsoon seasons. When significant differences were detected, a 1-way univariate PERMANOVA was performed separately on $\delta^{13}C$ and $\delta^{15}N$ values, followed by a pairwise comparison. Because both $\delta^{13}C$ and $\delta^{15}N$ values included negative values, we transformed the isotopic data to positive values by adding constant values. For $\delta^{13}C$, we added 35 for resources and 34 for consumers. For $\delta^{15}N$, we added 7 for resources and 3 for consumers. The significance level set at $P < 0.05$ was obtained using 999 permutations of residuals with unrestricted permutation of raw data. PERMANOVA was performed using PRIMER version 6 combined with the PERMANOVA + PRIMER add-on[74].

Mixing model and trophic diversity

A hierarchical cluster analysis (Euclidean distance, group average method) was conducted on the $\delta^{13}C$ and $\delta^{15}N$ values of individual consumer taxa to identify trophic groups and interspecific patterns in resource use. Prior to clustering, isotope data were transformed to positive values by adding constant values of 34 and 3 for $\delta^{13}C$ and $\delta^{15}N$ values, respectively.

We assessed the contribution of autochthonous (aquatic) and allochthonous (terrestrial) resources to the nutrition of trophic groups (as identified by the abovementioned cluster analysis) using a Bayesian mixing model, Stable Isotope-Mixing Models in R with SIMMR (versions 0.5.1.216 and R 4.3.2). This isotope modeling technique incorporates the uncertainty in source proportions, trophic enrichment, and diet data. Because CBOM and SPOM represent a mixture of aquatic and terrestrial sources and isotope values were close to those of biofilms, they were not used as end members. Because there were no temporal changes in isotope signatures of basal resources, we used mean $\delta^{13}C$ and $\delta^{15}N$ values of terrestrial tree leaf litter and biofilm as end members of autochthonous and allochthonous resources to the forest stream food webs. Given the expected contribution of forest stream-derived resource due to the stream connectivity during monsoon rains, we ran a four-source mixing model based on riparian leaf litter, biofilms from both reaches, and tree leaf litter in this estimation for the agricultural stream food webs. We calculated trophic fractionation factors for invertebrates and fishes based on data on diet isotope ratios, as proposed by the 'Diet-Dependent Discrimination Factor'[44], and used trophic fractionation factor in the mixing model (Table S9). Prior to model estimation, the consumer isotope values were adjusted with these trophic enrichment factor values to consider the multiple trophic steps from primary consumers. The model was fitted via Markov chain Monte Carlo, and model convergence was examined via Gelman–Rubin and Geweke diagnostics. The estimated median source proportions (%) and associated 95% credible intervals are reported.

We further tested the effect of the summer monsoon on trophic diversity at entire community levels using community-wide isotopic metrics[37]. To do this, we quantified and compared the $\delta^{15}N$ range (NR, a proxy of trophic lengths as a vertical niche descriptor) and the $\delta^{13}C$ range (CR, a proxy of the breadth of dietary sources as a horizontal niche descriptor) at community levels. We also quantified the area of $\delta^{13}C$–$\delta^{15}N$ space (a convex hull-shaped total area, TA) occupied by all consumers and a standard ellipse area corrected for small sample sizes (SEAc)[75]. Larger isotopic spaces reflect a relatively higher trophic diversity in communities[37]. Comparisons of these measures of trophic diversity between sites and seasons were made by graphical representation of TA and SEAc, and the community overlap that represents the percentage overlap of the surface of the smaller ellipse. These analyses were performed using the Stable Isotope Bayesian Ellipses package in R (SIBER)[75].

Ethics statement

There was no vertebrate or invertebrate species, which of experiment was required for Institutional Animal Care and Use Committees (IACUC) approval. Fishing and delivery of fish to laboratory was conducted by commercial fishermen, all fish were dead in the net when harvested, and there was no protected vertebrate or invertebrate species in our sample; IACUC approval for this sampling method was not required.

Data availability

All data generated or analysed during this study are provided in supplementary information files.

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Author contributions
H.Y.K. and C.K.K. identified overarching research goals, designed the experiments and drafted the manuscript; B.G.L., and J.K.S. performed data curation and validation; B.G.L. and H.J.P. contributed to materials/analytical tools; H.Y.K., C.K. and H.J.P. performed field investigation and laboratory experiments for isotope analysis; H.Y.K. and J.K.S. designed and prepared figures; All authors analyzed the data and reviewed the manuscript.

Declarations

Competing interests
The authors declare no competing interests.

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Correspondence and requests for materials should be addressed to C.-K.K.