Effects of landuse intensification on stream basal resources and invertebrate communities

Liliana García[1,4], **Wyatt F. Cross**[2,5], **Isabel Pardo**[1,6], **and John S. Richardson**[3,7]

[1]Department of Ecology and Animal Biology, Universidade de Vigo, Vigo, Spain 36310
[2]Department of Ecology, Montana State University, Bozeman, Montana, USA 59717
[3]Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

Abstract: Human population growth and development have degraded freshwater ecosystems through direct negative effects on basal resources and higher trophic levels. Knowledge of how basal resources are influenced by anthropogenic activities is needed to examine foodweb responses and to evaluate negative effects of human disturbance. We combined quantitative sampling of all putative resources and consumers and naturally occurring stable isotopes of resource C and N to investigate how land use influences characteristics of basal resources (leaf litter, fine particulate organic matter [FPOM] suspended in water, FPOM deposited in pools, and epilithon) and the invertebrate communities in 9 streams of British Columbia (Canada) on a seasonal basis. Study streams were grouped as forest, cropland, and urban, based on percentages of land use in their catchments. We tested for seasonal and spatial differences in biomass, isotopic variability, and overlap of different basal resources and their relationships with invertebrate communities. Our results show that landuse intensification promotes wholesale degradation, which includes deterioration of water quality, changes to the quantity and quality of basal resources, and shifts in community structure of benthic invertebrates. Stream basal resources showed large variations in isotopic signatures caused by landuse changes, with the largest isotopic variability observed in cropland streams and the smallest in urban streams. Invertebrate communities had fewer taxa and reduced functional diversity in impaired streams (i.e., cropland and urban) via simplification of feeding styles of consumers, probably because of bottom-up controls. Our study highlights the importance of quantifying the isotopic variability of basal resources to estimate effects on food webs over time and along landuse intensification gradients.
Key words: degradation, ecosystem simplification, land-use intensification, stable isotopes, trophic niche

Landuse intensification, i.e., land-cover change and pollution associated with anthropogenic activities (e.g., agriculture, urbanization), is a major factor altering the structure and function of Earth's terrestrial and aquatic ecosystems (Vitousek et al. 1997, MEA 2005). Important responses to landuse intensification, such as habitat homogenization and water pollution, can reduce biodiversity, simplify trophic networks, and alter ecosystem processes and services (e.g., Estes et al. 2011, Hladyz et al. 2011, Cardinale et al. 2012). As a consequence, ecosystems are experiencing wholesale degradation via simplification of habitat, resources, and organisms. Stream ecosystems, in particular, are highly vulnerable because of their low-lying position in the catchment (Allan 2004). Changes in riparian vegetation cover (Findlay et al. 2001, Hladyz et al. 2011) and allochthonous subsidies (Richardson et al. 2010), nutrient enrichment (Niyogi et al. 2003), contaminant pollution (Singer and Battin 2007), in-

creased sediment inputs and turbidity (Wood and Armitage 1997, Quinn 2000), and hydrologic alteration (Wang et al. 2001) all contribute to stream ecosystem degradation.

Effects of landuse intensification on freshwater ecosystems are of particular interest because freshwater ecosystems have conservation, economic, and cultural importance (Dudgeon et al. 2006, Vörösmarty et al. 2010). Understanding the effects of land cover on streams is an important goal for stream management and conservation. A growing body of literature is focused on assessment of changes in streams promoted by landuse conversion to urbanized areas (Paul and Meyer 2001, Meyer et al. 2005, Walsh et al. 2005). This field of understanding led to the basic knowledge of mechanisms and responses to urbanization (Roy et al. 2016). Because the human population will keep increasing in the coming years, a better understanding of the consequences of landuse change is needed to develop more effective man-

E-mail addresses: [4]lilizar@uvigo.es; [5]wyatt.cross@montana.edu; [6]ipardo@uvigo.es; [7]john.richardson@ubc.ca

agement strategies for maintaining freshwater ecosystem services.

Stream ecosystem integrity often is assessed in response to current water legislation, such as the Clean Water Act (CWA; formally the 1972 Federal Water Pollution Control Act) in the USA or the Water Framework Directive (WFD; European Commission 2000) in Europe. In addition to assessments based on these policy frameworks, tools such as ecological stoichiometry (Singer and Battin 2007, O'Brien and Wehr 2010), measures of functional structure, and stable-isotope analysis (Layman et al. 2012) have been used to examine ecosystem integrity and the effect of land-cover change on stream ecosystems. The responses of foodweb structure to perturbations provide an integrated measure of stream integrity by considering interactions among trophic levels and ecological processes that control basal resources and nutrient cycling (e.g., Layman et al. 2007, 2012, Thompson et al. 2012).

Stable-isotope analysis has emerged as one of the primary means to analyze the trophic structure and energy flow in ecological communities (Post 2002, Layman et al. 2012). The isotopic signatures, expressed in δ notation, reflect the ratios of heavy-to-light isotopes (e.g., $^{13}C : ^{12}C$ or $^{15}N : ^{14}N$) in a sample in relation to an international standard so that data collected from across the globe are comparable. The $δ^{13}C$ values represent a measure of diversity of basal resources available and, the $δ^{15}N$ values represent changes in trophic position and can be used to infer diet, so they are useful for quantifying the existence of nutrient enrichment. However, an appropriate measure of trophic structure can be interpreted only relative to the isotopic variation of basal resources (Peipoch et al. 2012). Alteration or removal of basal resources or increase of nutrient inputs through landuse intensification may induce shifts in C and N flows and can lead to bottom-up effects on higher-order consumers and emergent ecosystem properties (Kominoski and Rosemond 2012). The composition, biomass, and isotopic variability of food resources (i.e., dietary variation) influence isotopic niche space (Layman et al. 2007, Newsome et al. 2007, Jackson et al. 2011), energy and elemental pathways within food webs (Cabana and Rasmussen 1996, Pingram et al. 2012), and patterns of biodiversity and ecosystem functioning (Thébault and Loreau 2003). Shifts in basal resources have important ecological consequences for individual specialization and resilience to natural or anthropogenic perturbation (Bolnick et al. 2003). Understanding the variability of basal resources is crucial for addressing large-scale changes in freshwater ecosystems that derive from anthropogenic activities. In spite of this awareness, studies tend to focus on specific consumers (i.e., invertebrates, fish) without considering the variation of all resources within the system.

We designed a comprehensive field study to investigate the effects of landuse intensification on stream food webs considering all putative basal resources on a seasonal basis. We asked whether landuse intensification alters the base of the food web by shifting basal resource composition, biomass, and isotopic variability and promotes bottom-up effects on species or functional composition of stream macroinvertebrates. We hypothesized that: 1) Basal resource characteristics, in terms of quantity and quality, will vary seasonally as a result of natural abiotic variation, but differences among landuse categories also will reflect gradients of catchment degradation. 2) Isotopic variability at the base of the food web will vary because of the alteration of riparian–terrestrial subsidies. Impaired streams could exhibit greater isotopic variability if changes are mostly caused by nutrient enrichment. As an alternative hypothesis, impaired streams could exhibit lower isotopic variability because of homogenization of food resources if the magnitude of the human disturbance is strong enough to simplify resources in the system. 3) Changes in the abiotic environment and basal resources will influence the structure of higher trophic levels by reducing consumer diversity and by shifting the composition of functional feeding groups (FFGs) toward generalists, probably because of the presence of bottom-up controls.

METHODS
Study sites and landuse categories

Our study sites were situated in the Coastal Trough physiogeographic region of British Columbia within the Georgia Depression (Holland 1976). This area stretches from the urban core of the City of Vancouver to its rural/suburban fringe. Study sites consisted of 100-m reaches of nine 2nd-order streams draining catchments of similar bedrock and surface geology and having well-established riparian tree canopies that create shade and cover for aquatic communities.

We selected the streams to represent a gradient of landuse intensification, including some in minimally disturbed catchments and others impaired by different anthropogenic activities, such as crop agriculture, livestock, and urbanization (Table 1). We designated 3 categories (forest, cropland, and urban) a priori based on the relative proportions of different land uses. The forest category included different types of forests (e.g., temperate, coniferous, mixed) and shrub lands. The cropland category included grasslands and croplands that are arable or have pastoral uses. The urban category included land with a larger number of artificial barriers like houses and roads/m² than other categories. These 3 categories of land use reflect a range of degradation in the terrestrial landscape and, thus, a gradient of overall loss of linkages between terrestrial and aquatic ecosystems.

Forest cover at sites in the 1st category ranged from ~65 to 100% (Table 1). The category included 2 sites in regional parks and 1 uphill site in the outskirts of the city of Coquit-

Table 1. Percentages of land uses and shade at each stream, grouped by landuse category: forest, cropland, and urban. Percentages of land cover were exported from the 2013 Land Cover of North America at 250 m (Commission for Environmental Cooperation). Forests and shrublands (%) include different types of forest (i.e., temperate or subpolar needleleaf forests, broadleaf deciduous forests, mixed forests) and shrublands. Grasslands and croplands (%) includes wetlands. Only 2 sites had wetlands in their catchments (Anderson Creek: 10%, Nathan Creek: 2%). * Indicates study sites in regional parks.

Landuse categories	Stream name	Forests and shrublands (%)	Grasslands and croplands (%)	Urban (%)	Shade (%)
Forest	Little Campbell River*	100.0	0.0	0.0	63.0
	Kanaka Creek*	95.8	4.2	0.0	85.0
	Scott Creek	65.0	12.6	22.4	75.0
Cropland	Bertrand Creek	56.6	43.4	0.0	35.0
	West Creek	45.5	54.5	0.0	45.0
	Nathan Creek	44.3	54.1	1.6	50.0
Urban	Anderson Creek	41.7	35.2	23.1	55.0
	Hyland Creek	19.4	0.0	80.6	70.0
	Stoney Creek	0.0	0.0	100.0	60.0

lam that included 22% suburban development in residential areas but retains a high percentage of forest. The percentage of cropland at sites in the 2nd category ranged from ~43 to 55% (Table 1). Urban land use at sites in the 3rd category ranged from ~23 to 100% and included low- and high-intensity urban areas (Table 1).

Water chemistry and physical properties

We collected 3 replicate water samples (50 mL) for analysis of dissolved nutrient concentrations (i.e., PO_4^{3-}-P, NH_4^+-N and NO_3^--N). We filtered water samples through precombusted glass-fiber filters (Whatman GF/C, 47-mm diameter, 1.2-μm pore size; VWR, Ontario, Canada), kept them on ice for transport to the laboratory, and froze them until further analysis. Water samples were analyzed with an automated chemistry analyzer (Alpkem Flow Solution IV; OI-Analytical, College Station, Texas) at the Technical Services Laboratory for the British Columbia Ministry of Environment in Victoria, British Columbia, Canada. We measured streamwater pH, specific conductivity (at 25°C), temperature, and dissolved O_2 in situ with standard meters (YSI 63 and YSI 550A; YSI Environmental, Yellow Springs, Ohio). We recorded wetted channel width and depth along 3 random transects at each 100-m reach, and we estimated discharge at the downstream edge of the reach on each sampling date based on the midsection method (Gore 2007).

We conducted field sampling of foodweb components in autumn 2014 and spring 2015 to capture seasonal differences in environmental variables and biotic assemblages. Environmental variables included percentages of land uses, water chemistry, and physical stream properties.

Basal-resource compartments

Riparian leaf litter   Terrestrial leaf litter was collected, as recently fallen leaves, from the ground of the adjacent riparian area at each stream and sampling time. Streams grouped within the forest category exhibited high tree diversity, but the other stream categories did not. We selected 3 species that were dominant in the forest streams and were present in the adjacent riparian area of other stream types: alder (*Alnus rubra* Bong.), vine maple (*Acer circinatum* Pursh), and black cottonwood (*Populus trichocarpa* Torr. and A. Gray). We randomly collected a total of 10 to 15 recently fallen leaves of these native tree species at each stream reach and season, pooled leaves in 3 samples, and stored them in paper envelopes. Once in the laboratory, leaves were oven-dried at 60°C for 48 h or until constant mass and ground to a fine powder with a coffee grinder or an agate mortar and pestle, depending on the sample size. We stored leaf powder in Eppendorf vials until analysis of stable isotopes (see *Stable isotope analysis*).

Fine particulate organic matter suspended in stream water (FPOM_W)   We collected water samples in 3 different 10-L carboys at each study reach and transported them to the laboratory. Once in the laboratory, we filtered 3 replicates of known volumes of homogenized water samples from each carboy onto precombusted glass-fiber filters (Whatman GF/C 47-mm diameter, 1.2-μm pore size) within a few hours after collection in the field. The resulting filtrates were the samples of $FPOM_W$ collected for quantification of biomass (3 replicates for ash-free dry mass [AFDM], 3 replicates for chlorophyll *a* [Chl *a*]) and stable isotopes (3 replicates for ^{13}C and ^{15}N). Samples for AFDM were oven-dried at 60°C for 48 h to constant mass and weighed. Filters were placed in a muffle furnace at 500°C for 1.5 h, kept in a desiccator until constant mass was attained, and reweighed to determine AFDM. Samples for Chl *a* were extracted in acetone (90%), and pigments were quantified by spectrophotometry (Cary 5000; Agilent Technologies, Ontario, Canada).

We oven-dried samples for analysis of stable isotopes at 60°C for 48 h to constant mass and stored dried filters until analysis (see *Stable Isotope Analysis*).

FPOM deposited in the sediment (FPOM_S)   We used a turkey baster to collect samples of FPOM_S (50 mL) from 3 to 5 randomly selected pools at each study reach by sucking material off the stream bed. Samples of FPOM_S collected for quantification of biomass (3 replicates for AFDM, and 3 replicates for Chl *a*) and stable isotopes (3 replicates for isotopes of ^{13}C and ^{15}N) were filtered and processed as described above for FPOM_W.

Epilithon   We collected 9 replicate epilithon samples from different stones along randomly selected transects at each study reach. We brushed the stones to collect combined samples of the epilithon for quantification of biomass (3 replicates for AFDM and 3 replicates for Chl *a*), and stable isotopes (3 replicates). Samples of epilithon collected for quantification of biomass and stable isotopes were filtered and processed as described above for FPOM_w. The surface area of each stone was estimated from pictures taken in the field, and processed in the laboratory with digital image analysis (ImageJ, version 1.48; https://imagej.nih.gov/ij/).

Elemental concentrations and stable-isotope analysis of basal resources   C and N content and natural abundances of their stable-isotope ratios were measured for all basal resources (i.e., leaf litter, FPOM_W, FPOM_S, epilithon) at central laboratory facilities of the University of A Coruña (https://www.sai.udc.es/es/unidades/UTIA). Approximately 3 mg of homogeneous powder from each preserved sample of leaf litter were weighed into ultraclean 3.3- × 5-mm Sn capsules and analyzed with a FlashEA1112 elemental analyzer (ThermoFinnigan, Bremen, Germany) coupled to a DELTAplus mass spectrometer (ThermoFinnigan) through a ConFlo II interface (ThermoFinnigan). Filtered samples (FPOM_W, FPOM_S, epilithon) were divided into 2 subsamples: one for %C and δ^{13}C and the other for %N and δ^{15}N determination. Subsamples used for C analyses were first acidified with vaporous HCl to remove carbonates and re-dried before analysis following the method of Komada et al. (2008). All subsamples were weighed into 9- × 5-mm Sn capsules and analyzed with an EA1108 elemental analyzer (Carlo Erba Instruments, Milan, Italy) coupled to a MAT253 isotope ratio mass spectrometer (ThermoFinnigan) through a ConFlo III interface (ThermoFinnigan).

Stable-isotope ratios of C and N are expressed as the ratio of heavy-to-light C and N relative to Vienna Pee Dee Belemnite (^{13}C/^{12}C) and atmospheric air (^{15}N/^{14}N), using conventional δ notation (δ^{13}C, δ^{15}N) in parts per thousand (‰):

$$\delta X \text{‰} = ([R_{sample}/R_{standard}] - 1) \times 1000, \qquad \text{(Eq. 1)}$$

where X = ^{13}C or ^{15}N and R = ^{13}C/^{12}C or ^{15}N/^{14}N.

As part of each analytical batch run, a set of international reference materials for δ^{13}C (NBS 22, IAEA-CH-6, USGS 24) and δ^{15}N (IAEA-N-1, IAEA-N-2, IAEA-NO-3) (International Atomic Energy Agency, Vienna, Austria) was analyzed for calibration. Replicate assays of the laboratory standard acetanilide indicated measurement errors of ±0.2‰ for δ^{13}C and δ^{15}N.

Benthic macroinvertebrates
We quantified taxonomic composition of benthic macroinvertebrates from 3 riffles and 3 pools in dominant stream habitats (n = 6 per season and stream). We used a Surber sampler (0.09 m^2; 250-µm mesh) and disturbed the substratum within the sampler by hand for 3 min. We returned samples to the laboratory on ice and later preserved them in plastic jars with 70% ethanol. We counted and identified invertebrate taxa under a dissecting microscope to the lowest taxonomic level possible (species and genus level), with the exception of Acari (class), Oligochaeta (family), and Diptera (subfamily). We subsampled to obtain a representative fraction of the total community when needed (Wrona et al. 1982). All invertebrates were classified into FFGs following Merritt et al. (2008).

Statistical analysis
All analyses performed included 3 main factors: season (fixed), landuse category (fixed), and stream (nested within landuse category). Prior to other analyses, we examined whether the percentages of land-cover types differed among landuse categories with a nonparametric permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). We calculated a Euclidean distance matrix for $\sqrt{(x)}$-transformed data.

We analyzed the environmental data set (i.e., landuse and physicochemical variables) based on multivariate methods to examine variation in environmental conditions among and within landuse categories. We calculated Euclidean distance matrices for standardized environmental variables and $\log(x + 1)$-transformed all environmental variables except pH. We used principal coordinates analysis (PCoA; Gower 1966, Anderson et al. 2008) to visualize the distribution of streams based on their environmental conditions in unconstrained ordination space and PERMANOVA to test for differences in environmental variables among season, landuse category, and stream. A Monte Carlo test (9999 permutations) was used to analyze the statistical significance. We used canonical analysis of principal coordinates (CAP; Anderson and Robinson 2003) to test for average differences in environmental conditions among landuse categories. CAP retains the axes that best discriminate among groups and supplements the information provided by PCoA because it emphasizes among-group differences in constrained ordination space (landuse category was the constraining factor).

To address our 1st and 2nd hypotheses, we studied the spatial and temporal variability of food resources. We used

analysis of variance (ANOVA), followed by Tukey's post hoc pairwise comparisons to test all response variables (biomass, stoichiometry, and stable isotopes) for each basal resource (leaf litter, $FPOM_w$, $FPOM_s$, and epilithon) for differences among streams, seasons, and landuse categories. ANOVAs were performed on Box–Cox-transformed data to meet normality assumptions. We used isotope biplots of the basal resources to characterize variation and evaluate effects of season and landuse intensification. We applied quantitative metrics based on a Bayesian approach (Jackson et al. 2011) to estimate the isotopic δ-space occupied by each basal resource. This approach allowed us to compute the Layman metrics and the standard ellipse area accounting for variability among groups (for details, see Jackson et al. 2011). Layman metrics are useful for quantifying trophic structure metrics and examining responses of community- or population-level trophic structure to natural and anthropogenic sources of environmental variation (Layman et al. 2007, 2012). The basic metrics used in our study were the N range (NR) and the C range (CR), which represent the diversity of basal resources in the δ-space, and the standard ellipse area (SEA; ‰^{2}). SEA is a measure of isotopic niche width, frequently applied to consumers because it reflects what an animal assimilates from its diet and the habitat in which it resides (Bearhop et al. 2004, Newsome et al. 2007). Standard ellipse areas are derived from the variance and covariance matrix of δ^{13}C and δ^{15}N values, which encompass ~40% of the data (Jackson et al. 2011). We analyzed only food resources and, thus, assumed that the SEA represents the core of isotopic variability of basal resources within and among landuse categories. It reflects both variation in basal resource identity and what primary producers assimilate from the environment. We used a version of the SEA corrected for small sample size (SEAc) to improve accuracy. For leaves, we pooled data from both seasons because the ANOVAs showed no significant differences of δ^{13}C and δ^{15}N values. We ran the analysis for each season separately for in-stream basal resources ($FPOM_w$, $FPOM_s$, and epilithon). We fitted Bayesian multivariate normal distributions to each group to compare isotopic variability among basal resources and landuse categories (Jackson et al. 2011). To facilitate comparisons, we resampled all metrics (n = 10,000 iterations), and we calculated and plotted modes and 95% credible intervals of standard ellipses to quantify differences.

To test our 3rd hypothesis, we analyzed the invertebrate data by multivariate methods to examine variation in invertebrate assemblage composition among and within landuse categories. We used nonmetric multidimensional scaling (NMDS) based on a Bray–Curtis dissimilarity matrix computed from relative taxon abundances and from FFGs for ordination of streams. We also used PERMANOVA of the Bray–Curtis dissimilarity matrix to test for effects of main factors on the macroinvertebrate assemblages. We used a similarity percentage analysis (SIMPER) to identify taxa separating different landuse categories in multivariate space and to quantify the contribution of individual taxa in each category. Taxa with a high average % contribution to dissimilarity and a high ratio of the average % contribution to its standard deviation discriminate consistently between groups. SIMPER is a pairwise analysis and was limited to the main fixed-factor levels (season and land use). We used the BIOENV procedure (Clarke and Ainsworth 1993, Clarke and Gorley 2006) to examine which environmental variables were best correlated with the invertebrate assemblages, including a permutation test (999 permutations) to evaluate the significance of the results.

We estimated densities (number of individuals/m^2) for each sample and used the macroinvertebrate matrix to calculate richness (number of species/sample), diversity (Shannon–Weaver's diversity index), and evenness (Pielou evenness index) for each sample. We used ANOVA followed by Tukey's post hoc pairwise comparisons to test all invertebrate metrics for differences between seasons and among streams and landuse categories. We ran ANOVAs on Box–Cox-transformed data to meet normality assumptions. To test whether landuse changes promote reduced functional diversity, we used ANOVA to evaluate the Shannon diversity of FFGs for each of the 3 streams in each category.

We used a principal component analysis (PCA) to explore the relationships among landuse changes, water quality, and basal resources. We removed all variables that were highly correlated and used a total of 9 variables in the PCA (shade, dissolved O_2, PO_4^{3-}-P, dissolved inorganic N [DIN], % forest, % cropland, % urban, epilithon-Chl a, and epilithon-δ^{15}N). The PCA reduced the information of all environmental variables to stressor gradients (PCA axes). We used linear regressions and scores along PCA axes to explore relationships between stressor gradients and invertebrate metrics.

We performed multivariate analyses with PERMANOVA+ for PRIMER (version 6; PRIMER-E, Plymouth, UK; Clarke and Gorley 2006, Anderson et al. 2008). All the other analyses were run in R (version 2.15.2; R Project for Statistical Computing, Vienna, Austria). We calculated isotopic metrics with the *SIBER* package (see Jackson et al. 2011 for detailed methods and Layman et al. 2007 for original descriptions of the metrics; at https://cran.r-project.org/web/packages/SIBER/vignettes/Introduction-to-SIBER.html). The significance level was set at α = 0.05 for all analyses.

RESULTS
Environmental variables
Percentages of land use differed among landuse categories (PERMANOVA, Pseudo-F = 8.88, p = 0.003; all pairwise comparisons, $p < 0.05$; Table 1). Temperature differed between seasons, and nutrient (PO_4^{3-}-P and NO_3^--N) concentrations differed between seasons and among landuse categories (Table 2). On average, urban and cropland

Table 2. Mean (±SD) physicochemical variables measured at each study stream grouped into 3 landuse categories ($n = 9$). N : P ratios were estimated as molar ratios from %N and %P data. Values with the same letters within rows are not significantly different ($p > 0.05$). EC = specific conductance, DIN = dissolved inorganic N.

Environmental variable	Autumn			Spring		
	Forest	Cropland	Urban	Forest	Cropland	Urban
pH	7.14 ± 0.07^a	7.46 ± 0.03^b	7.51 ± 0.07^b	7.39 ± 0.10^{ab}	7.44 ± 0.04^b	7.31 ± 0.14^{ab}
EC (mS/cm)	0.05 ± 0.02^a	0.10 ± 0.01^b	0.12 ± 0.01^{bc}	0.09 ± 0.02^c	0.16 ± 0.02^b	0.13 ± 0.02^b
Temperature (°C)	7.57 ± 0.28^a	6.23 ± 0.06^a	8.40 ± 0.38^a	13.63 ± 0.46^b	13.98 ± 0.68^b	13.03 ± 0.56^b
O_2 (mg/L)	11.23 ± 0.14^a	12.48 ± 0.06^b	11.14 ± 0.11^a	10.10 ± 0.21^c	10.24 ± 0.14^c	10.06 ± 0.07^c
Discharge (m^3/s)	0.11 ± 0.02^a	0.06 ± 0.01^b	0.09 ± 0.02^{ab}	0.03 ± 0.01^c	0.01 ± 0.00^c	0.02 ± 0.01^c
PO_4^{3-}-P (µg/L)	8.04 ± 3.17^a	45.83 ± 11.51^b	17.08 ± 3.12^c	21.52 ± 5.77^c	49.33 ± 8.85^b	20.55 ± 1.90^c
NO_3^--N (µg/L)	517.01 ± 47.39^a	1929.31 ± 240.08^b	2353.84 ± 261.56^b	225.34 ± 111.33^c	427.54 ± 105.03^{ac}	1338.02 ± 664.65^a
NH_4^+-N (µg/L)	42.13 ± 11.22^a	67.76 ± 10.37^{ab}	57.10 ± 5.92^{ad}	101.59 ± 45.02^a	20.11 ± 4.43^{ac}	20.13 ± 1.09^{acd}
DIN (µg/L)	559.13 ± 58.53^a	1997.07 ± 244.74^b	2410.95 ± 259.49^b	326.92 ± 97.49^a	447.66 ± 107.53^a	1358.14 ± 665.68^a
N : P ratio	436.76 ± 101.81^a	131.25 ± 17.81^{ab}	376.36 ± 50.51^a	37.00 ± 13.15^c	39.38 ± 14.80^c	111.81 ± 54.14^{bc}

streams had 5 and $3.2\times$ higher NO_3^--N and DIN concentrations, respectively, than forest streams (Table 2). Cropland streams had $3.2\times$ higher PO_4^{3-}-P concentrations than forest streams and the lowest N : P ratios (Table 2).

Environmental variables differed among and within landuse categories, and season had a strong effect on the distribution of sites (PCoA; Fig. 1A). Environmental variables differed significantly between seasons (PERMANOVA, Pseudo-$F = 7.94$, $p = 0.002$), and among landuse categories (Pseudo-$F = 3.17$, $p = 0.01$), and streams (Pseudo-$F = 140.5$, $p < 0.001$). Despite this variation, streams were distinctly grouped within landuse categories established a priori based on CAP (Fig. 1B), and pairwise comparisons showed that each landuse category was significantly different from the others (P[perm] < 0.001) independent of season (no significant season × land use interaction, Pseudo-$F = 1.04$, $p = 0.44$).

Quantity and quality of basal resources

Differences in basal resource quantity and quality were associated with landuse intensification, and these patterns were influenced by season (Table 3). In general, the quantity and quality of resources varied among basal foodweb components, but were more autotrophic during spring than autumn (Fig. 2A–I). Epilithon had the highest autotrophic biomass and the lowest C : N ratio, reflecting their potential importance as a food source, in terms of quantity and quality, relative to other basal compartments (Fig. 2C, I).

In spring, the $FPOM_w$ compartment had the highest values of Chl a in cropland streams and the highest AFDM values in urban streams (Fig. 2A, D). Biomass of $FPOM_s$ differed significantly between seasons but not among land uses, with higher Chl a and lower AFDM in spring than in autumn (Table 3, Fig. 2B, E). In spring, epilithon biomass was lower (~$7.7\times$ less Chl a) in urban than in cropland and forest streams (Fig. 2C).

Regarding the quality of basal resources, the epilithon had the lowest C : N ratios, suggesting its higher food quality relative to other basal resources (Fig. 2G–I). $FPOM_s$ C : N was affected by a season × landuse interaction. Seasonal differences were apparent in forest and cropland, but not in urban streams (Fig. 2H).

Isotopic variability of basal resources

Natural abundance of stable isotopes was variable and overlapped among basal resources (Table S1). However, large and significant effects of land use and season on mean values were apparent (Table 3), and isotopic variability was greater in cropland and urban streams than in forest streams and was greater in spring than autumn (Table S1, Fig. 3A–I).

On average, all basal resources (i.e., terrestrial and in-stream) showed a pattern of increasing ^{15}N enrichment from forest to urban (~$1.6\times$ more enriched than forest streams) to cropland streams (~$2.6\times$ more enriched; Table S1). A season × landuse interaction affected epilithon-δ^{15}N (Table 3). Cropland streams had higher epilithon δ^{15}N in autumn than in spring, but this difference was not apparent in the other streams (Table 1). δ^{15}N values of $FPOM_s$ were higher in spring than in autumn.

The more heterotrophic compartments ($FPOM_w$ and $FPOM_s$) showed less isotopic variability in ^{13}C than did epilithon (Table S1). $FPOM_w$ δ^{13}C and epilithon δ^{13}C varied significantly between seasons and among land uses (Table 3). Cropland streams had lower δ^{13}C values than did forest and urban streams, and δ^{13}C values were lower in spring than in autumn (Table S1). $FPOM_s$ δ^{13}C did not differ between seasons or among land uses (Table 3).

The SEAs of basal resources overlapped across seasons and land uses, but differences were evident among landuse categories (Fig. 3A–I, Table S1). Cropland streams showed, on average, greater isotopic variation than urban and forest
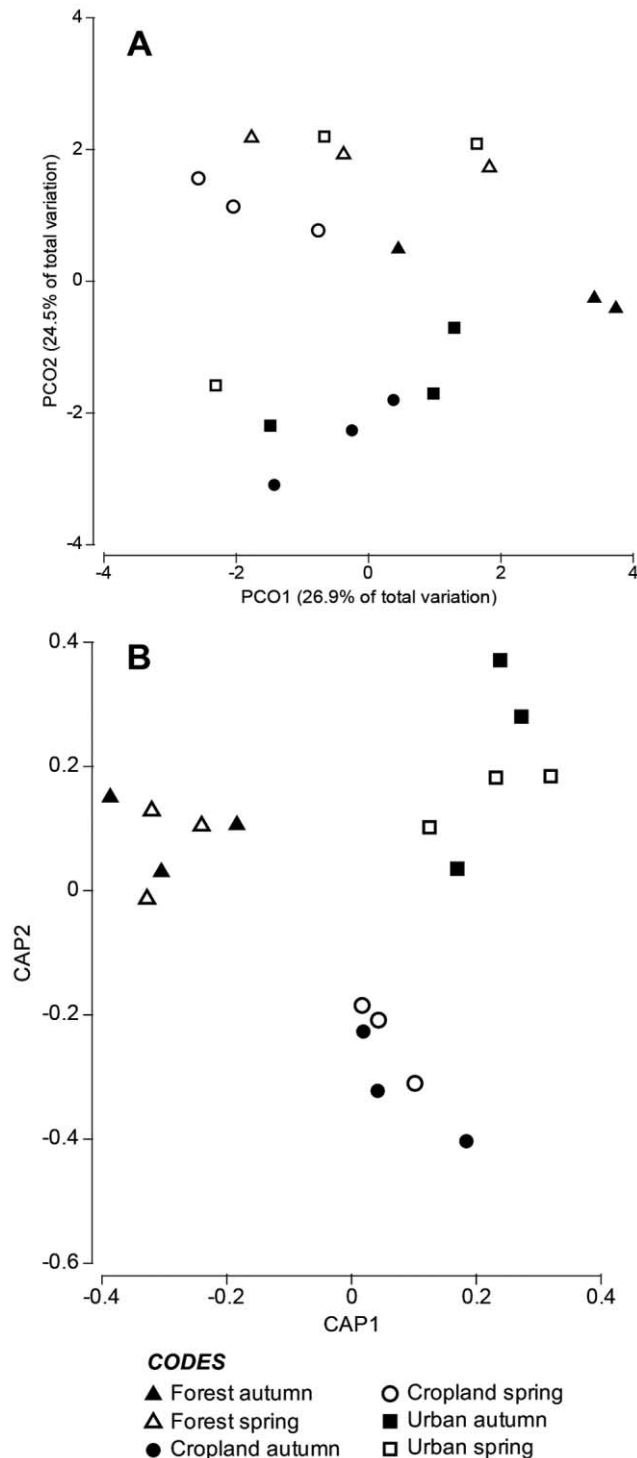
ability, primarily in NR, than alder leaves (7- and 5× more variable, respectively) with strong differences among land uses (Fig. 3B, C, Table S1). Isotopic variation in these leaf types was greater in cropland and urban than in forest streams (Fig. 3A–C). Among in-stream basal resources, epilithon showed the greatest isotopic variation, independent of season (Fig. 3F, I). Epilithon was much more isotopically variable in cropland streams than in other landuse categories (Fig. 3F, I). The $FPOM_w$ compartment of urban streams showed the lowest and least variable values, independent of season (Fig. 3D, G). The $FPOM_s$ compartment showed a contrasting pattern with greatest variation in urban streams in autumn, rather than in spring as found in other landuse categories (Fig. 3E, H).

Invertebrate assemblages

Invertebrate composition differed among streams (Pseudo-F = 8.63, p < 0.001), independent of landuse category. However, dissimilarity percentages showed that the invertebrate composition also differed by ~68% among land uses (Table 4). One urban stream (Hyland Creek) had the highest similarity percentage, which reflects a homogeneous community, whereas the most diverse community was in a forested stream (Kanaka Creek) in a regional park (SIMPER; Table 4). The subset of environmental variables that best explained the variability of the invertebrate assemblages included %urban, specific conductance, discharge, and N : P (BIOENV, R^2 = 0.435, p < 0.001).

Invertebrate communities were influenced by temporal variability (i.e., seasonal effects). Significant community compositional differences existed among seasons and streams (PERMANOVA, season × stream interaction, Pseudo-F = 4.35, p < 0.001), and season affected invertebrate assemblages (Pseudo-F = 3.03, p = 0.004), but the NMDS plot based on invertebrate abundances showed high dispersion (Fig. 4A). FFGs showed similar results (PERMANOVA, Pseudo-F = 2.66, p = 0.05), and the NMDS plot showed a slightly different distribution of sites, with urban streams more dispersed than and different from the other stream groups (Fig. 4B). Invertebrate composition did not differ among land uses, but invertebrate metrics differed significantly between seasons and among land uses (Table 5, Fig. 5A–F). On average, total invertebrate density was ~2× greater in spring than autumn, and density was ~1.8 and ~4.2× greater in cropland than in forest and urban streams, respectively (Fig. 5A). Ephemeroptera, Plecoptera, Trichoptera (EPT) density was affected by a season × land use interaction (Table 5, Fig. 5B). Invertebrate density (total and EPT) was lowest in urban streams, followed by cropland and forest streams, but this difference was observed only in autumn. Taxon richness (total and EPT) was highest in forest streams, followed by cropland and urban streams (Fig. 5C, D). Cropland and urban streams had the lowest diversity (Fig. 5E), and evenness was lowest in cropland streams in spring (Fig. 5F).

Figure 1. Distribution of sites in the environmental principal coordinates analysis (PCoA) (A) and canonical analysis of principal coordinates (CAP) (B) ordination plots across seasons and landuse categories.

streams. For example, the magnitude of these changes differed within and among basal resources (Fig. 3A–I). Among terrestrial basal resources, alder leaves showed little variation in the δ-space (CR = 0.7, NR = 0.4; Fig. 3A), whereas maple and cottonwood leaves showed higher isotopic vari-

Table 3. Results of analysis of variance to examine whether chlorophyll a (Chl a), ash-free dry mass (AFDM), and the C : N ratio of basal resources differed significantly between seasons, and among streams and land uses (forest, $n = 3$; cropland, $n = 3$; urban, $n = 3$). Basal resources include fine particulate organic matter suspended in stream water ($FPOM_w$), fine particulate organic matter deposited in sediments in pools ($FPOM_s$), and epilithon scrubbed from rocks. Bold F-ratio values are significant at $p < 0.001$ (**) and at $p < 0.05$ (*).

Response variable	Basal resource compartment	Season		Land use		Stream		Season × land use	
		F-ratio$_{(df)}$	p	F-ratio$_{(df)}$	p	F-ratio$_{(df)}$	p	F-ratio$_{(df)}$	p
Chl a	$FPOM_w$	**21.74**$_{(1,42)}$	**	**9.86**$_{(2,42)}$	**	**4.24**$_{(6,42)}$	**	**10.37**$_{(2,42)}$	**
	$FPOM_s$	**74.34**$_{(1,42)}$	**	2.39$_{(2,42)}$	0.10	1.72$_{(6,42)}$	0.14	0.77$_{(2,42)}$	0.47
	Epilithon	**70.02**$_{(1,42)}$	**	**11.35**$_{(2,42)}$	**	**7.08**$_{(6,42)}$	**	**5.95**$_{(2,42)}$	**
AFDM	$FPOM_w$	**8.17**$_{(1,42)}$	**	1.87$_{(2,42)}$	0.17	**6.34**$_{(6,42)}$	**	**4.12**$_{(2,42)}$	*
	$FPOM_s$	**19.69**$_{(1,42)}$	**	0.10$_{(2,42)}$	0.91	**7.56**$_{(6,42)}$	**	0.21$_{(2,42)}$	0.82
	Epilithon	**19.23**$_{(1,42)}$	**	2.90$_{(2,42)}$	0.07	**4.94**$_{(6,42)}$	**	**8.55**$_{(2,42)}$	**
C : N ratio	Leaf litter	**6.30**$_{(1,114)}$	*	1.15$_{(2,114)}$	0.32	**2.82**$_{(6,114)}$	*	0.59$_{(2,114)}$	0.56
	$FPOM_w$	**40.08**$_{(1,42)}$	**	**19.18**$_{(2,42)}$	**	**5.87**$_{(6,42)}$	**	0.56$_{(2,42)}$	0.58
	$FPOM_s$	**4.62**$_{(1,42)}$	*	0.12$_{(2,42)}$	0.88	**2.70**$_{(6,42)}$	*	**4.24**$_{(2,42)}$	*
	Epilithon	**14.48**$_{(1,42)}$	**	**21.70**$_{(2,42)}$	**	**2.49**$_{(6,42)}$	*	2.34$_{(2,42)}$	0.11
$\delta^{13}C$	Leaf litter	1.58$_{(1,114)}$	0.22	**3.36**$_{(2,114)}$	*	1.21$_{(6,114)}$	0.30	2.26$_{(2,114)}$	0.11
	$FPOM_w$	**17.20**$_{(1,42)}$	**	**19.96**$_{(2,42)}$	**	**18.71**$_{(6,42)}$	**	2.40$_{(2,42)}$	0.11
	$FPOM_s$	0.52$_{(1,42)}$	0.47	1.43$_{(2,42)}$	0.25	**4.32**$_{(6,42)}$	**	0.36$_{(2,42)}$	0.70
	Epilithon	**6.89**$_{(1,42)}$	*	**19.21**$_{(2,42)}$	**	**10.45**$_{(6,42)}$	**	0.55$_{(2,42)}$	0.58
$\delta^{15}N$	Leaf litter	0.87$_{(1,114)}$	0.35	**13.22**$_{(2,114)}$	**	**4.65**$_{(6,114)}$	**	0.70$_{(2,114)}$	0.50
	$FPOM_w$	0.47$_{(1,42)}$	0.50	**86.03**$_{(2,42)}$	**	**19.77**$_{(6,42)}$	**	1.13$_{(2,42)}$	0.33
	$FPOM_s$	**12.78**$_{(1,42)}$	**	**18.46**$_{(2,42)}$	**	**17.20**$_{(6,42)}$	**	2.03$_{(2,42)}$	0.15
	Epilithon	1.32$_{(1,42)}$	0.26	**75.84**$_{(2,42)}$	**	**25.13**$_{(6,42)}$	**	**13.63**$_{(2,42)}$	**

The functional feeding structure of invertebrates varied with land use. Shannon diversity of FFGs differed significantly among landuse categories (Fig. 6). The distribution of FFGs was more even in forest than in cropland or urban streams, and impaired streams had fewer taxa and reduced functional diversity relative to forest streams. Cropland streams had fewer shredders and more collector–filterers relative to forest streams. Urban streams showed the most uneven distribution of FFGs, with collector-gatherers and shredders as the most dominant taxa.

Relationships among land use, water quality, basal resources, and invertebrate metrics

The PCA yielded 5 principal components (PCs) explaining 90.3% of total variance. The first 3 components accounted for 35.4, 21.5, and 17.7% of the variance, respectively. Variables with strong loadings on PC1 included epilithon $\delta^{15}N$, PO_4^{3-}-P, and % cover. A cover gradient existed from cropland streams with low riparian cover to forest streams (Fig. 7). Cropland streams generally had a high proportion of the catchment occupied by agriculture and grasslands and were associated with high PO_4^{3-}-P concentrations and epilithon ^{15}N-enrichment (Fig. 7). PC2 separated streams on the basis of periphyton Chl a in opposi- tion to urban cover and DIN, indicative of a gradient from urban to forest streams. PC3 identified the seasonal dynamic marked by O_2 concentrations, with higher values in autumn (Fig. 7). PC1 was directly related to total, collector–filterer, and collector–gatherer densities ($R^2 = 0.250$, 0.371, 0.263, all $p < 0.05$), indicating that cropland streams had higher densities of invertebrates, dominated by collector–filterer and collector–gatherer species. PC2 was directly related to densities of scrapers and predators ($R^2 = 0.249$, 0.296, $p < 0.05$), suggesting higher values of epilithon Chl a and higher densities of scrapers and predators in forest than in urban streams.

DISCUSSION

We showed the existence of large spatial and temporal variation in food resources across a series of landuse types. This variation must be acknowledged in foodweb studies. Epilithon was the most important food resource in terms of quantity and quality, especially during spring. This result demonstrates the importance of the 'green' pathway in stream food webs. As hypothesized, isotopic signatures at the base of the food web varied depending on the magnitude of landuse differences. Resources showed higher isotopic variability in cropland than in forest streams prob-
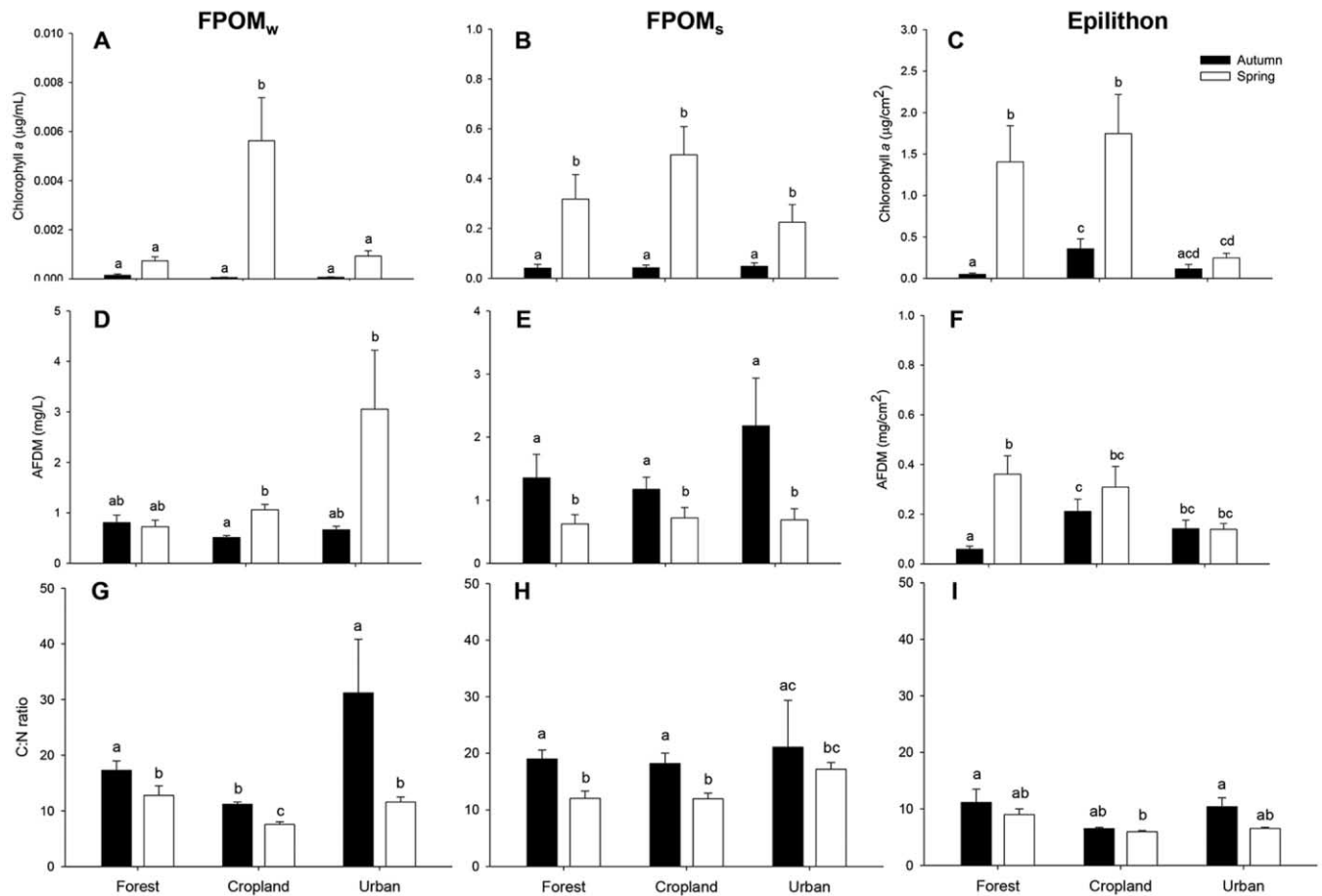
Figure 2. Mean (+SE) chlorophyll *a* (A–C), ash-free dry mass (AFDM) (D–F), and C : N ratio (G–I) for fine particulate organic matter suspended in stream water (FPOM$_w$) (A, D, G), fine particulate organic matter deposited in sediments in pools (FPOM$_s$) (B, E, H), and epilithon scrubbed from surface rocks (C, F, I) collected from streams by season and landuse category. Bars within panels with the same letter are not significantly different ($p = 0.05$). Note different scales and units in the *y*-axes.

ably because of higher nutrient inputs. Meanwhile, urban streams showed a higher dominance of 'brown' resources and lower isotopic variability probably because of homogenization of food resources. Consumer diversity (invertebrate richness and evenness of FFGs) decreased along the landuse intensification gradient confirming the potential importance of bottom-up controls on stream ecosystem structure arising from negative effects of landuse intensification on basal resources and changes in other stream properties, such as water quality and habitat quality.

Effects of land use on water chemistry

Effects of landuse intensification on water chemistry were fairly consistent between seasons. Higher N and P concentrations were measured in cropland and urban streams than in forest streams. NO_3^--N enrichment was 5× greater in urban and 3× greater in cropland than in forest streams, and PO_4^{3-}-P enrichment was 3× greater in cropland than in forest streams. Greater dissolved nutrient concentrations are typical of streams in agricultural

and urbanized areas because of runoff from nonpoint sources and from urban sewage and wastewater (Paul and Meyer 2001, Walsh et al. 2005). Unmeasured physicochemical variables, such as higher metals, pesticides, and other organic contaminants seem to be characteristic of urban streams (Paul and Meyer 2001, Walsh et al. 2005), even at low levels of catchment urbanization (Hatt et al. 2004). These substances contribute to the deterioration of water quality and impair the ecological integrity of the streams, influence invertebrate composition, and decrease biodiversity.

Characteristics of basal resources and importance to the food web

Landuse changes directly influence the input of nutrients, allochthonous resources, autochthonous production, and the quantity and quality of available food resources (Richardson et al. 2010), and may simplify trophic structure and reduce biological diversity (Allan 2004, Hladyz et al. 2011). Studies addressing the effects of changes in
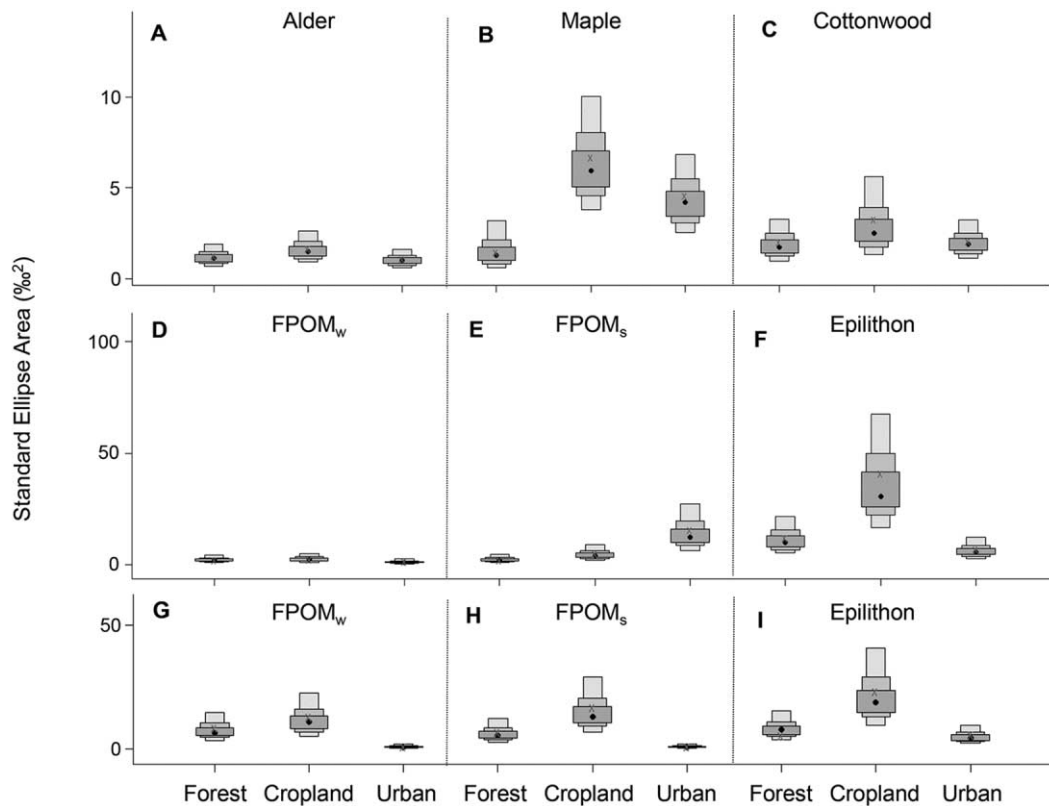
Figure 3. Variability of basal resources in the δ-space of leaf litter of alder (A), maple (B), and cottonwood (C) (pooled across seasons), fine particulate organic matter suspended in stream water (FPOM$_w$) (D, G), fine particulate organic matter deposited in sediments in pools (FPOM$_s$) (E, H), and epilithon scrubbed from surface rocks (F, I) collected in autumn (D–F), and spring (G–I) from streams in 3 landuse categories. Isotopic variability is represented by the standard ellipse areas (SEA$_c$; ‰^{2}) derived from the variance and covariance matrix of the natural stable isotopes (^{13}C and ^{15}N) (Jackson et al. 2011). Black dots represent their mode, light gray crosses represent the maximum likelihood estimated standard ellipses, and shaded boxes represent the 50, 75 and 95% credible intervals from dark to light gray.

vegetation cover on the energy flow and trophic relations in aquatic environments are essential to understand the mechanisms that regulate their ecological integrity. We did not quantify allochthonous inputs to streams, but we used the percentages of landuse cover as a proxy of the alteration in each catchment. Organic matter subsidies from riparian vegetation are a significant portion of the energy input to some freshwater ecosystems (Fisher and Likens 1973, Richardson et al. 2010). These subsidies strongly influence invertebrate consumers, and this influence could have a particularly large effect on invertebrate functional composition. Streams in catchments with ~50% grasslands and croplands had the lowest percentages of shredding invertebrates.

Much research on in-stream basal resources has been focused on the spatial and temporal variability of algal populations and periphyton biomass (see Rosemond et al. 2000), whereas in-stream FPOM has been less studied (but see Sakamaki and Richardson 2011). Primary production by algae is a prominent component of most benthic systems and provides a key basal resource to stream food

webs (Minshall 1978), but FPOM is a key longitudinal link in stream food webs and is the predominant food source for filter- and deposit-feeding invertebrates (Bundschuh and McKie 2016). The presence and dominance of some feeding types over others among land uses can be explained in part by the availability of different food resources in each landuse category (see discussion below).

The range of biomass values we observed for various basal resources is comparable to values reported by other researchers in the same geographical area (e.g., Kiffney et al. 2003, Sakamaki and Richardson 2011). Nutrients and light are important constraints on primary producers and, thus, for energy and nutrient transfer through food webs (Dickman et al. 2008, Malzahn et al. 2010). In coastal streams of western North America, light, temperature, and nutrients can limit algal biomass (Kiffney and Bull 2000, Warren et al. 2016, Kaylor et al. 2017). We observed that more favorable abiotic conditions (e.g., light, temperature, and discharge) promoted higher autotrophic biomass and higher quality of all basal resources during spring, suggesting the potential for higher primary productivity at this

Table 4. Average similarity percentages among the study streams based on SIMPER analysis. Values along the diagonal represent similarity percentages within each stream across seasons. Bold = highest and lowest similarity percentages of within-stream comparisons.

Landuse categories	Stream name	Little Campbell	Kanaka	Scott	Bertrand	West	Nathan	Anderson	Hyland	Stoney
Forest	Little Campbell River*	56.22								
	Kanaka Creek*	68.52	**45.69**							
	Scott Creek	70.61	68.61	50.12						
Cropland	Bertrand Creek	68.70	79.96	68.06	53.92					
	West Creek	53.58	65.00	65.78	70.67	55.71				
	Nathan Creek	68.86	74.01	61.32	63.43	65.57	58.76			
Urban	Anderson Creek	61.57	75.24	67.34	66.71	64.23	64.60	47.56		
	Hyland Creek	77.26	76.62	58.74	66.00	75.24	62.64	68.44	**58.40**	
	Stoney Creek	69.99	74.64	61.03	66.61	67.22	62.98	67.17	54.86	55.67

season. We hypothesized that increased nutrient loading promoted by anthropogenic activities would stimulate the nutritional quality and the palatability of food resources, and our results agreed with that hypothesis. Our research shows that both season and land use influenced the availability of all studied basal resources. Thus, both light and nutrients may limit autotrophic and heterotrophic compartments. The differences in the quality of basal resources we observed are comparable to those reported by others examining the effects of urbanization (Singer and Battin 2007) and landuse gradients on stream food webs (O'Brien and Wehr 2010, Milanovich et al. 2014). Such combined effects (higher food availability and better abiotic conditions) may have important consequences for higher trophic levels, with potential important effects through the food web (Antón et al. 2011).

Among in-stream resources, epilithon was the compartment that contributed most to autotrophic biomass (i.e., highest Chl a values), confirming its role as an important food resource for invertebrate consumers adapted to graze or scrape materials from mineral and organic substrates. $FPOM_w$ and $FPOM_s$ had high AFDM values, reflecting the high contribution of heterotrophic biomass in these compartments and highlighting their importance as a food resource to consumers with other feeding styles, such as collector–filterers and collector–gatherers. Nevertheless, effects of in-stream resources on consumers should depend on species-specific capacity for nutrient storage, relative growth rate, physiological plasticity, trophic characteristics, and the degree of environmental resource availability relative to organismal demands (Sistla et al. 2015, Warry et al. 2016).

Isotopic variability of basal resources

Variation in isotopic values of basal resources are influenced by landuse changes, climatic region, local scales, and seasonality (Cabana and Rasmussen 1996, Peipoch et al. 2012, Costas and Pardo 2015). We found strong effects

of land use and season on isotopic variability (CR and NR) of all putative basal resources, with values in agreement with other ranges published elsewhere (e.g., Singer
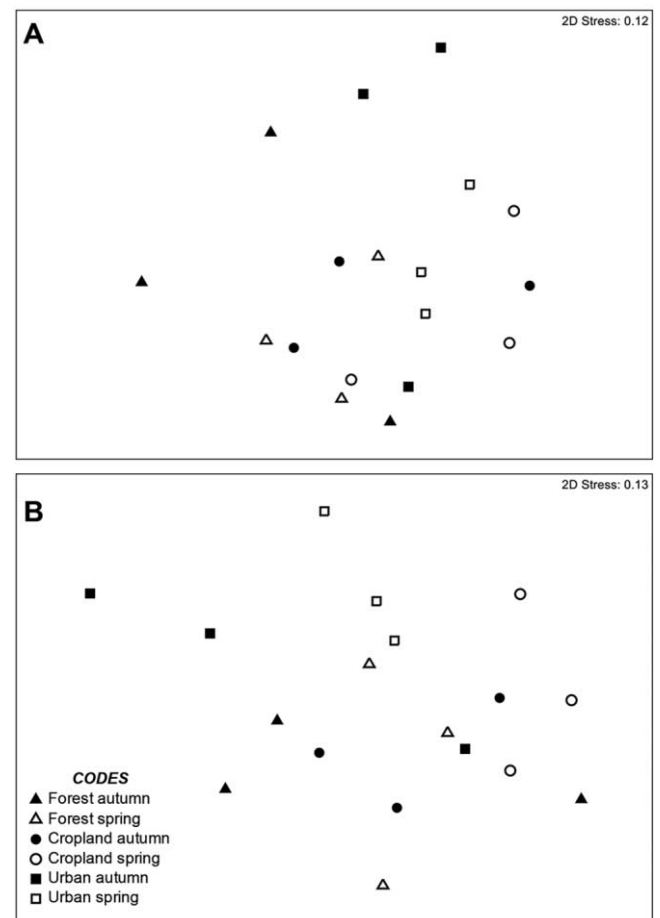

Figure 4. Nonmetric multidimensional scaling (NMDS) ordination plot of the abundance of invertebrate assemblages identified at the lowest taxonomic level (A) and of different functional feeding groups (B) at each study stream.

Table 5. Results of analysis of variance to examine whether invertebrate community metrics differed between seasons or among streams and landuse categories (forest, $n = 3$; cropland, $n = 3$; urban, $n = 3$). EPT = Ephemeroptera, Plecoptera, Trichoptera. Bold F-ratio values are significant at $p < 0.001$ (**) and at $p < 0.05$ (*).

Response variable	Season		Land use		Stream		Season × land use	
	F-ratio$_{(df)}$	p	F-ratio$_{(df)}$	p	F-ratio$_{(df)}$	p	F-ratio$_{(df)}$	p
Total density	**22.39**$_{(1,96)}$	**	**13.06**$_{(2,96)}$	**	**3.91**$_{(6,96)}$	**	2.49$_{(2,96)}$	0.09
EPT density	0.08$_{(1,96)}$	0.78	2.65$_{(2,96)}$	0.08	**5.37**$_{(6,96)}$	**	**6.05**$_{(2,96)}$	**
Total richness	0.06$_{(1,96)}$	0.80	**15.96**$_{(2,96)}$	**	**12.94**$_{(6,96)}$	**	1.21$_{(2,96)}$	0.30
EPT richness	**4.53**$_{(1,96)}$	*	**36.04**$_{(2,96)}$	**	**24.37**$_{(6,96)}$	**	**5.06**$_{(2,96)}$	**
Shannon diversity	**6.55**$_{(1,96)}$	*	**9.62**$_{(2,96)}$	**	**15.15**$_{(6,96)}$	**	**4.70**$_{(2,96)}$	*
Evenness	**12.39**$_{(1,96)}$	**	**3.05**$_{(2,96)}$	0.05	**5.12**$_{(6,96)}$	**	1.68$_{(2,96)}$	0.19

and Battin 2007, O'Brien and Wehr 2010, Peipoch et al. 2012).

Patterns of $\delta^{15}N$ variability in all basal resources were greatest among landuse categories, but also differed among basal compartments. These results are consistent with those of a meta-analysis carried out in >100 streams and rivers (Peipoch et al. 2012), in which land use accounted for the highest proportion of the total variance in ^{15}N. In our study, all basal resources had higher $\delta^{15}N$ values in cropland streams, where chemical fertilizers and livestock manure are the main sources of residues and nutrients, than in urban or forest streams. Fertilizers increase nitrification, leading to soil ^{15}N enrichment. Agricultural residues usually have high $\delta^{15}N$ values (Bateman and Kelly 2007), and most are carried into waterbodies and incorporated into food webs, thereby changing the ^{15}N available in food resources and consumers (Harrington et al. 1998, Broderius 2013).

Patterns of $\delta^{15}N$ variability also differed among basal compartments. Among terrestrial sources, alder leaves showed higher similarity in δ-space and lower NR than maple and cottonwood leaves across landuse categories. These results may be understood by taking into account species-specific differences. Alder trees can fix atmospheric N_2 because of symbiotic root associations with *Frankia alni* (Jackrel and Wootton 2015). Maple and cottonwood trees are non-N_2-fixing plants, which usually have greater $\delta^{15}N$ values than N_2-fixing plants (He et al. 2009). Among in-stream basal resources, the isotopic variability was higher in epilithon than $FPOM_w$ and $FPOM_s$. Cropland streams had autochthonous resources with the widest $\delta^{13}C$ and $\delta^{15}N$ values, mostly during spring. This wide range of values in cropland streams probably is a result of high-nutrient inputs from agricultural practices. This variation also might be a result of higher light inputs or increased temperature because of reduced riparian canopy cover in agricultural streams. Elevated light and temperature promote higher rates of primary production and demand for C during spring and influence the physiological condition of algae and epilithon, thereby affecting isotopic variation, diversity, and abundance. These results are impor-

tant because higher quantities of epilithon and wider isotopic ranges can influence foodweb productivity at its base (Woodland et al. 2012) and can promote changes on higher trophic levels. Similar results were reported by Parreira de Castro et al. (2016) where producers (algae and periphyton) at pasture sites had wider and more dispersed $\delta^{13}C$ and $\delta^{15}N$ values probably because of greater taxonomic diversity.

Invertebrate responses

Season and landuse (individually or combined) strongly influenced all invertebrate metrics quantified in our study (density, richness, diversity, and evenness). Benthic invertebrates may be suitable bioindicators for quantifying responses to multiple stressors, based on their ability to respond to a variety of environmental variables (Hering et al. 2006, Pardo et al. 2014). In our study, cropland streams had, on average, 40% lower EPT richness (i.e., sensitive taxa), and 10% lower diversity relative to forest streams. Urban streams had 50% lower EPT richness, and 20% lower diversity relative to forest streams. Macroinvertebrates respond to the physical and chemical conditions of the ecosystems (e.g., hypoxia or toxic substances in urban streams), and to food availability (Allan 2004). For example, the higher quantity and quality of algal resources caused by NO_3^--N enrichment in cropland streams can be identified as an increase in resource diversity, which, when coupled with increases in light availability during spring, seems to account for the increase of invertebrate densities in these streams (as predicted).

Landuse changes and their consequent shifts in the availability of food resources and abiotic conditions (e.g., nutrients, toxic metals) can alter the proportional contributions of different species or functional feeding groups to invertebrate communities (Dolédec et al. 2011). In our study, forest streams supported a more diverse and even distribution of FFGs than did other stream groups. Representation of shredders was lower and of collector–filterers and collector–gatherer species was higher in cropland than in forest streams. These results agree with the hypothesis that changes in the abiotic environment and basal resources
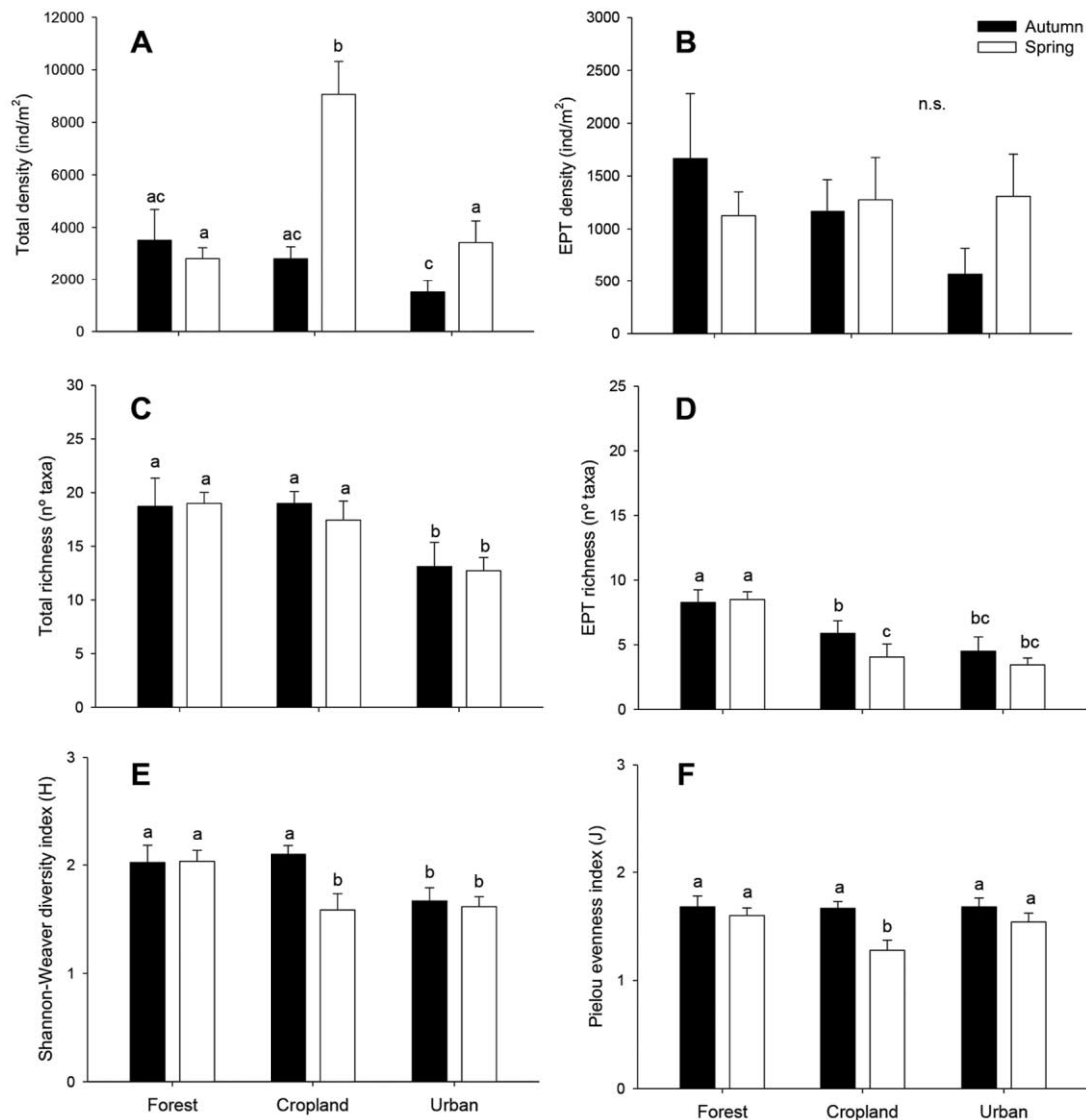
Figure 5. Mean (+SE) total density (A), Ephemeroptera, Plecoptera, Trichoptera (EPT) density (B), total richness (C), EPT richness (D), Shannon–Weaver diversity (E), and Pielou evenness index (F) for invertebrates in streams in 3 landuse categories in spring and autumn. Bars within panels with the same letters are not significantly different ($p > 0.05$).

promoted by landuse change modify the invertebrate structure and composition of FFGs. Urban streams showed a more uneven contribution of FFGs. Collector–gatherers (mainly Orthocladiinae species) and shredders (mainly the nemourid *Zapada* spp.) were the dominant taxa. Orthocladiinae are abundant worldwide and nemourids are common detritivores inhabiting streams of northern temperate regions around the globe (Richardson 2001). Densities of Orthocladiinae and nemourids were 2 and 3× higher, respectively, in urban than in forest streams. Moreover, other shredders (e.g., *Tipula* spp., Limnoniinae) and collector–gatherers (e.g., *Pericoma* spp.) were present only in urban streams. These results suggest a greater tolerance of these species in contrast to other collector–gatherers, such as *Paraleptophlebia* spp., *Centroptilum* spp., *Serratella* spp., and

shredders, such as *Lepidostoma* spp. and *Micrasema* spp., which were less abundant in urban than in forest streams.

The effect of nutrient enrichment was evident at the base of the food web in cropland streams where all food resources had higher NR values than in urban or forest streams. This higher isotopic variability may promote degradation of the ecosystem by broadening trophic niches (i.e., highest SEA). Broader trophic niches would alter the composition of exploited resources, which may favor more tolerant and generalist invertebrate species. Parreira de Castro et al. (2016) reported that tropical headwater streams altered by pasture or sugar cane plantations had wider and more overlapping trophic niches and more generalist invertebrates than did unaltered streams, as seen for cropland streams in our study. In contrast, the lower isoto-
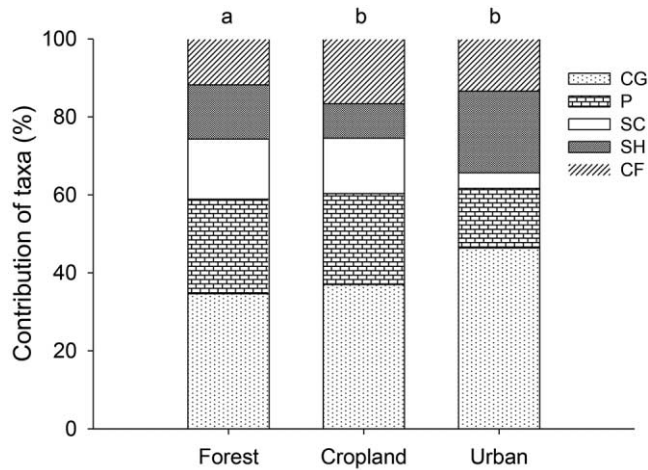
Figure 6. Mean contributions of different macroinvertebrate functional feeding groups (FFGs) in each landuse category based on SIMPER analysis. CG = collector–gatherers, P = predators, SC = scrapers, SH = shredders, and CF = collector–filterers. Bars with the same letters have similar Shannon diversity of FFGs among land uses.

pic variability observed in basal resources of urban streams may lead to ecological simplification through homogenization of functional diversity and loss of invertebrate biodiversity because of environmentally adverse conditions.
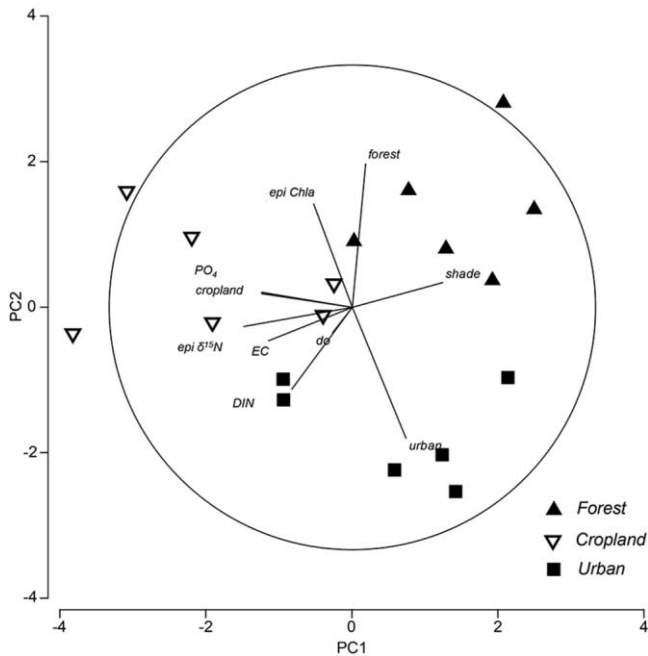
Figure 7. Principal component analysis (PCA) showing the relationships between environmental variables and landuse changes. The circle shows correlations and plot of the loadings of the variables with principal components 1 and 2, epi Chla = epilithon chlorophyll *a* concentration, DIN = dissolved inorganic N, epi δ15N = δ^{15}N of epilithon, EC = specific conductance, do = dissolved O_2.

Conclusions

Quantity, quality, and isotopic variability of basal resources responded strongly to landuse differences and abiotic conditions (i.e., seasonal effects), and these changes had consequences for higher trophic levels. Effects of nutrient loading entering at the base of food webs influenced all basal resources, which form the dietary resource of consumers. These effects may travel through the food web to affect higher trophic levels, demonstrating bottom-up controls of stream food webs. We conclude that landuse intensification, via cropland or urbanization activities, may lead to decreased biodiversity and benthic macroinvertebrate assemblages characterized by taxa with generalist feeding behaviors. Further analysis of consumer isotopic niches would demonstrate the extent to which these responses propagate through the food web along a gradient of landuse intensification.

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