Mechanisms of trophic niche compression: evidence from landscape disturbance

Francis J. Burdon^{1,2,3,4}, Angus R. McIntosh¹, and Jon S. Harding¹

¹School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

²Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland

³Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden

⁴Corresponding author: francis.burdon@slu.se

Running header: Isotopic niche compression in streams

Abstract

1. Natural and anthropogenic disturbances commonly alter patterns of biodiversity and ecosystem functioning. However, how networks of interacting species respond to these changes remains poorly understood. We described aquatic food webs using invertebrate and fish community composition, functional traits, and stable isotopes from twelve agricultural streams along a landscape disturbance gradient.
2. We predicted that excessive deposition of fine inorganic sediment (sedimentation) associated with agricultural activities would negatively influence aquatic trophic diversity (e.g., reduced vertical and horizontal trophic niche breadths). We hypothesized that multiple mechanisms might cause trophic niche ‘compression’, as indicated by changes in realized trophic roles.
3. Food-web properties based on consumer stable isotope data ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) showed that increasing sediment disturbance was associated with reduced trophic diversity. In particular, the aquatic invertebrate community occupied a smaller area in isotopic niche space along the sedimentation gradient that was best explained by a narrowing of the invertebrate community $\delta^{13}\text{C}$ range.
4. Decreased niche partitioning, driven by increasing habitat homogeneity, environmental filtering, and resource scarcity all seemingly lead to greater trophic equivalency caused by the collapse of the autochthonous food-web channel. Bayesian mixing-model analyses supported this contention with invertebrate consumers increasingly reliant on detritus along the sedimentation gradient, and predatory invertebrates relying more on the prey using these basal resources.

5. The narrowing of the fish community $\delta^{13}\text{C}$ range along the sedimentation gradient contributed to an apparent ‘trophic shift’ towards terrestrial carbon, further indicating the loss of the autochthonous food-web channel. On the vertical trophic niche axis, fish became increasingly separated from aquatic invertebrates with an increase in their estimated trophic position. In combination, these responses were most likely mediated through reduced fish densities and a diminished reliance on aquatic prey.
6. Although species losses remain a major threat to ecosystem integrity, the functional roles of biota that persist dictate how food webs and ecosystem functioning respond to environmental change. Sedimentation was associated with non-linear reductions in trophic diversity which could affect the functioning and stability of aquatic ecosystems. Our study helps explain how multiple mechanisms may radically reshape food-web properties in response to this type of disturbance.

Keywords: food webs; trophic diversity; stable isotopes; isotopic niche; agriculture; fine sediment; sedimentation; stream communities

Introduction

Food webs represent a holistic systems approach to characterizing patterns of biodiversity and energy flow by describing trophic interactions between consumers and resources (Thompson et al., 2012). One major goal in ecology is understanding how vertical (across-trophic level) and horizontal (within-trophic level) diversity contribute to food-web properties such as stability and energy transfer (Duffy et al., 2007, Thompson et al., 2012). Greater horizontal diversity may increase biomass and resource uptake (Duffy et al., 2007), and increased vertical diversity links to theory about food-chain length and omnivory, with implications for trophic cascades (McHugh, McIntosh, & Jellyman, 2010). To investigate trophic interactions in food webs,

increasingly sophisticated methods are being used including stable isotopes, molecular tools, and network analyses (Raso et al., 2014; Wootton & Stouffer, 2016). However, empirical studies of food webs that use underlying environmental gradients remain rare, despite their potential to help disentangle causal relationships between changing habitat conditions and ecosystem functioning (Thompson et al., 2012). We used a landscape disturbance gradient to elucidate potential mechanisms causing changes in aquatic food-web structure and functioning.

Landscape disturbances associated with human activities are profoundly changing the natural dynamics of a wide range of systems (Turner, 2010). In particular, the conversion of land for intensive agriculture has caused unprecedented landscape disturbance and habitat simplification, leading to species extinctions and the loss of important ecosystem services (Tilman et al., 2001). One widespread and pervasive problem often associated with these activities is the degradation of stream habitat through inputs of fine inorganic sediment (Waters, 1995). Excessive deposition of sediment (sedimentation), particularly in hard-bottomed streams, has been associated with species losses and threshold impacts on community composition (Matthaei, Piggott, & Townsend, 2010; Burdon, McIntosh, & Harding, 2013). With increasing sedimentation, reduced biomass and availability of basal resources and invertebrate prey may disrupt ‘bottom-up’ processes, thus affecting energy flow and species distributions in stream ecosystems (Osmundson, Ryel, Lamarra, & Pitlick 2002; Suttle, Power, Levine, & McNeely, 2004). Despite this, there have been few attempts to describe how sedimentation affects aquatic food-web properties, or fit this within a broader theoretical framework regarding trophic diversity and disturbance.

Stable isotope analysis (SIA) has been embraced as one of the main empirical tools for studying the trophic structure and dynamics of food webs (Layman, Arrington, Montana, & Post, 2007a).

Stable isotope ratios (typically carbon and nitrogen) are obtained from an organism's tissues and represent all trophic pathways in the food web leading to that individual. At the individual level, the trophic niche of an organism reflects its consumer-resource interactions (Elton, 1927), and thus can be construed as a trophic role (Leibold, 1995). However, this 'fundamental' trophic niche may seldom be realized because of a variable environment (i.e., the n-dimensional hypervolume), reflecting the broader Hutchinsonian niche (Hutchinson, 1957). Using SIA, the niche concept has been extended to a community-level property characterizing the trophic diversity and complexity of food webs (Layman et al., 2007a). SIA has been widely used in food-web studies, ranging from the influences of habitat fragmentation on estuarine communities to the consequences of hydrodynamic disturbance in streams (Layman, Quattrochi, Peyer, & Allgeier 2007b; McHugh et al., 2010). Despite the promise of isotope-based metrics in describing the trophic structure and functioning of food webs (Layman et al., 2007a), it still remains poorly understood what underlying ecological processes contribute to the patterns these metrics help describe.

We predicted a 'compression' of the trophic niche (i.e., a reduction in trophic diversity as indicated by a smaller total area occupied by communities in isotopic niche space) in streams impacted by sedimentation. Sedimentation has wide-ranging impacts on aquatic ecosystems by homogenizing and degrading benthic habitat, thereby negatively affecting consumers and their resources (Waters, 1995; Burdon et al., 2013). Consequently, we expected that the 'realized niche' breadths of stream food webs, shown by the consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges (Layman et al., 2007a), would contract with increasing sedimentation. We hypothesized that four proximate mechanisms could explain changes in trophic diversity and realized niche breadths (Fig.1):

- a) Niche ‘partitioning’ (Fig.1A), resulting from a heterogeneous resource base with specialists that consume different food sources (Schoener, 1974), thus contributing to greater trophic diversity (i.e., niche differentiation). We expected that sites with low sediment would show the greatest trophic diversity owing to greater habitat and resource heterogeneity (Beisel, Usseglio-Polatera, & Moreteau, 2000);
- b) Niche ‘elimination’ (Fig.1B), through habitat loss and degradation (i.e., environmental filtering) causing the non-random loss of specialist consumers (Woodward, 2009). Here we expected to see reduced abundances of invertebrate ‘predator’, ‘shredder’, and ‘grazer’ functional-feeding groups. For example, sedimentation has been associated with declines in grazing invertebrates reliant on hard substrates to consume diatoms (Rabení, Doisy, & Zweig, 2005);
- c) Niche ‘generalists’ (Fig.1C), where food scarcity leads to dietary convergence (e.g., increased omnivory), because all consumers become trophic generalists in accordance with optimal foraging theory (Pyke, Pulliam, & Charnov, 1977). We expected to see 1) little or no change in abundances of consumer functional feeding groups, but changes in realized trophic niches, and 2) an overall reduction in basal resources and invertebrate prey abundances consistent with sedimentation-induced resource scarcity; and
- d) Niche ‘homogeneity’ (Fig.1D), where resource homogenization means consumers rely on a narrower range of food items, because resources that are ‘hyper-abundant’ should be highly favored (Schoener, 1974). Thus, we expected to see a numerical increase in invertebrate ‘collectors’ correlated with an increase in detritus associated with sedimentation.

Niche processes (Fig. 1A–D) are non-exclusive and could occur simultaneously. We were interested in elucidating evidence for their relative contribution to changes in trophic diversity associated with sedimentation in stream ecosystems.

Materials and Methods

Study sites

We studied twelve 1st–3rd order wadeable and perennially-flowing agricultural streams located on the Canterbury Plains, an eastern region of New Zealand’s South Island. Following Burdon et al. (2013), our study design aimed for orthogonality along two dominant stressor gradients. To achieve this, sites with differing levels of sedimentation (i.e., ‘low’, 1–19%; ‘medium’, 13–42%; and ‘high’, 76–100% streambed cover) and nutrient concentrations (i.e., ‘low’, 0.14–1.76 mg/L NO₃-N, 2.6–36.1 µg/L PO₄⁻³; and ‘medium-high’, 0.43–5.46 mg/L NO₃-N, 9.5–18 µg/L PO₄⁻³) were crossed in a three × two factorial design. Our aim was to avoid confounding the stressor gradients and the data is analysed as continuous variables. Following Thompson and Townsend (2005), each independent 30-m long stream reach was dominated by run-riffle sequences. Reaches were sampled twice during base-flow conditions (habitat, resources, and invertebrates were sampled first, followed by fish communities) in the austral summer (6th December 2009 to 5th March 2010). For more information on study sites and site selection, see Appendix A.

Data collection

To associate sedimentation impacts on benthic habitat with agricultural-related landscape disturbance, riparian habitat characteristics were recorded following Burdon et al. (2013). Briefly, riparian habitat quality was estimated over a 100-m stream segment using 13 subjective attributes graded from poor (1) to excellent (5) on each bank; bank scores were averaged and

summed to provide an index of riparian condition (Harding et al., 2009). Canopy cover was also assessed using ocular estimation with a systematic approach (i.e., ten transects across the stream channel) to reduce variation and observer bias (Harding et al., 2009).

Deposited fine inorganic sediment (<2 mm grain size) was characterized using two subjective (visual) and two quantitative (physical) measurements following Burdon et al. (2013). To quantify sediment cover within each 30-m 'reach', ten 0.09-m² gridded quadrats were stratified-randomly selected and substrate composition visually assessed at 25 grid intersections within each quadrat. Using the same methodology, substrate composition at the 'patch' scale was assessed in the five Surber samples collected for invertebrates (see below). Sediment depth was recorded at ten stratified-randomly selected points in each reach. Suspendable inorganic sediment (SIS; g/m²) was similarly estimated using the Quorer method (Burdon et al. 2013).

Water samples at each site were collected on both sampling occasions for chemical analysis. Filtered (LabServ[®] GF/F, 25-mm Ø; Thermo Fisher Scientific New Zealand Ltd, North Shore City, NZ) stream water collected in acid-washed bottles (100 mL) was placed on ice, then frozen prior to analysis for nitrate (nitrate and nitrite nitrogen; mg/L) and DRP (dissolved reactive phosphorus; µg/L) using a SYSTEA Easychem discrete colorimetric auto-analyser (SYSTEA S.p.A., Anagni, Italy; Appendix B.1). A further 1-L water sample was collected for estimation of total suspended solids (TSS; g/L) following Burdon et al. (2013).

Basal resources were collected for estimation of resource availability and stable isotope analyses. Fine benthic and coarse particulate organic matter (FBOM and CPOM respectively; g/m²) collected in Surber samples was elutriated and separated using a 2-mm Endecott sieve. Organic matter samples were dried (48-hrs, 50 °C), weighed, ashed (4-hrs, 550 °C), and re-weighed. To estimate periphyton/biofilm availability (chlorophyll-*a* µg/cm²), five cobbles or sediment

samples were randomly collected from study reaches. Where fine sediment occurred in large deposits, a glass petri dish (45-mm Ø) was used to remove a circular section of sediment from the stream bed to 7.5-mm deep (Biggs & Kilroy, 2000). Cobble/sediment samples were immersed in 90% ethanol for 24-hrs (in the dark) at 10 °C for pigment extraction. Analysis of stone surface area and spectrophotometric chlorophyll-*a* followed Biggs and Kilroy (2000).

For stable isotope analysis (SIA) of basal resources, we retained sub-samples of organic matter (fine benthic organic matter, FBOM; and coarse particulate organic matter, CPOM). Algae and macrophyte samples were collected in the field, and biofilm samples were scraped from additional cobbles ($n = 10$). Suspended fine particulate matter (SFPM) was collected using a plankton net (45-µm mesh) suspended in the channel thalweg for ten minutes. We also collected terrestrial vegetation samples (e.g., grasses, shrubs, and trees) from the riparian zone. All samples were dried (48-hrs, 50 °C) prior to preparation for SIA.

To quantitatively sample invertebrate communities, five Surber samples (0.0625 m², 250-µm mesh) were collected from channel thalwegs at stratified (evenly-spaced) randomly-selected locations. Additional composite qualitative kicknet samples (250-µm mesh) were collected to encompass all microhabitats (e.g., riffles, macrophytes, marginal vegetation, wood, and leaf litter) present in the reach; invertebrate samples were placed on ice before being frozen. Kicknet samples were also used to obtain invertebrate specimens for SIA (see below). In the laboratory, thawed benthic samples were passed through a 500-µm Endecott sieve (Endecotts Limited, London, UK) and all invertebrates removed, identified, and counted to the lowest practicable level (usually genus) using identification guides (e.g., Winterbourn, Gregson, & Dolphin, 2006). Data from kick-net and Surber samples were combined to estimate invertebrate taxonomic richness.

We used traits (i.e., functional-feeding groups, FFGs) to describe changes to aquatic invertebrate communities. FFGs are a well-established method to describe the functional roles of stream invertebrates (Cummins, 1973). Using invertebrate trait data from the New Zealand Freshwater Biodata Information System (FBIS), we assigned trait affinity scores using “fuzzy-coding” (Chevenet, Dolédec, & Chessel, 1994) to five FFGs: “predators”, “omnivores”, “shredders”, “grazers” and “collectors”. For more information, see Appendix B.1.

Fishes and decapod crustaceans were sampled using quantitative electro-fishing techniques (Appendix B.1) for species identification and SIA samples. Qualitative data was used for fish community analyses because sediment-induced turbidity reduced the effectiveness of quantitative methods.

Stable isotope analysis (SIA)

Although there are well-documented limitations of SIA, it remains one of the main tools to empirically describe food webs (Layman et al., 2007a). SIA using carbon and nitrogen was performed on consumers and basal resources to assess changes to food-web properties along the sedimentation gradient (Fig.2). Thawed kicknet samples were passed through a 500- μ m sieve and retained stream invertebrates removed for isotopic analysis according to two criteria: highly abundant taxa (i.e., ≥ 100 individuals present in samples) and/or large bodied (i.e., > 5 -mm body length); thus potentially contributing disproportionately to overall biomass. All fish taxa recorded from study streams were sampled for SIA, and where possible, three specimens of each species were collected to adequately characterize the range of sizes present at sites; dorsal muscle tissue was removed from thawed individuals for SIA.

Samples of basal resources, invertebrates, and fish were dried (60 °C, 48 hours) and homogenized prior to encapsulation. We pooled multiple individuals for small-bodied

invertebrates (e.g., a minimum of 50 chironomid individuals) to get sufficient biomass for a sample, and where possible, enough for technical replication (i.e., >1 pooled samples per taxa). For larger-bodied taxa we attempted to sample multiple specimens individually (i.e., ≥ 3 and a maximum of 10 individuals). Stomach contents of predatory aquatic invertebrates were removed prior to drying (Jardine, Curry, Heard, & Cunjak, 2005). Animal samples (~1.0-mg) and basal resources (~2.0-mg) were encapsulated into 8 x 5-mm tin capsules (OEA Laboratories Ltd., Cornwall, UK) and sent to the Stable Isotope Facility (University of California, Davis, CA, USA) where they were analysed on a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). For more details, see Appendix B.2.

To evaluate trophic diversity (TD), we used three ‘community-wide’ isotope-based metrics. The carbon and nitrogen range (CR and NR) measure the total realized niche breadth in the horizontal and vertical dimensions within the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plot space, thus representing community-wide measures of trophic diversity (Layman et al. 2007a). The third TD metric summarizes the first two metrics using the sample-size corrected standard ellipse area (SEAc); an approach less susceptible to sample size and extreme values (Jackson, Inger, Parnell, & Bearhop, 2011). We predicted that the CR and NR would contract along the sedimentation gradient, leading to a smaller area described by SEAc in the isotopic niche space.

Firstly, to avoid the potential bias generated by differences in the ranges of values between the stable isotopes, we used the correction recommended by Cucherousset and Villger (2015). Each TD metric was calculated in a standardized multidimensional space where each axis was scaled to have the same range (see Appendix B.2). TD metrics were calculated for individual communities (fish and invertebrates), and ‘whole’ communities (fish and invertebrates combined) using the “siber” package in R (Jackson et al., 2011). There was no correlation

between SIA invertebrate taxa richness and the dominant stressor gradients: sedimentation (Pearson's correlation, $r = -0.38$, $t_8 = -1.16$, $P = 0.28$) and nitrate-nitrogen ($r = -0.14$, $t_8 = -0.41$, $P = 0.69$). In addition, we used baselines of mean invertebrate $\delta^{15}\text{N}$ and mean terrestrial vegetation $\delta^{13}\text{C}$ to further assess changes in the niche breadth consumers (Post, 2002). Because % canopy cover was confounded with terrestrial vegetation $\delta^{13}\text{C}$, we corrected values using residuals from linear regressions of $\delta^{13}\text{C}$ and canopy cover (Appendix B.2). To test the hypothesized 'compression' of the trophic niche envelope we used linear regressions of maximum, mean, minimum $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ for invertebrates and fish.

Bayesian stable isotope mixing models

We used the Bayesian mixing-model R package "simmr" to estimate changes in resource flows through stream food webs (Parnell et al., 2013). For each site, mixing models using default "simmr" settings for the number of iterations, 'burn' in, and Markov chain Monte Carlo (MCMC) chains used to estimate mean dietary contributions of basal resources to primary consumers and prey to predators. FFG-specific trophic enrichment factors (TEF) values were calculated from our data following Caut, Angulo, and Courchamp (2009). For primary consumer mixing-models we used mean TEF values of primary consumer FFGs: $1.51 \pm 0.47\text{‰}$ ($\delta^{13}\text{C}$) and $1.91 \pm 0.74\text{‰}$ ($\delta^{15}\text{N}$); for predators: $1.59 \pm 0.42\text{‰}$ ($\delta^{13}\text{C}$) and $1.41 \pm 0.69\text{‰}$ ($\delta^{15}\text{N}$). Putative food resources were pooled into ecologically meaningful groups to improve model performance (Nielsen, Clare, Hayden, Brett, & Kratina, 2018). Basal resources were pooled into four groups: phototrophs (macrophytes, bryophytes, filamentous algae), biofilms, FPOM (FBOM, SFPM), and terrestrial resources (CPOM, terrestrial vegetation). Potential prey taxa were classified into three FFGs: "grazers", "collectors", and "shredders". Prey groups (Wilks' $\lambda = 0.106$, $P < 0.001$)

and resource groups (Wilks' $\lambda = 0.054$, $P < 0.001$) differed in their isotopic signatures (tested using the “manova” R function).

We estimated the trophic position (TP) of predators (invertebrates and fish) using the “OneBaseline” model in the Bayesian mixing-model R package “tRophicPosition” (Quezada-Romegialli et al., 2018). This approach includes isotopic variation in the baseline indicator, the consumer, and the TEFs to provide robust estimates of consumer TP. The same TEFs were used for invertebrate predators as described above. For omnivorous crustaceans we used published values of $2.04 \pm 0.11\text{‰}$ ($\delta^{13}\text{C}$) and $4.24 \pm 0.99\text{‰}$ ($\delta^{15}\text{N}$) following Grey and Jackson (2012). Fish TEFs for muscle tissue were calculated from our data following Caut et al. (2009): $1.51 \pm 0.47\text{‰}$ ($\delta^{13}\text{C}$) and $1.91 \pm 0.74\text{‰}$ ($\delta^{15}\text{N}$). We used the mode for TP estimates. All primary consumer invertebrates were included for the baseline to enable comparisons among predator groups. We also estimated the median % contribution of allochthonous carbon (α) to predator groups using the “TwoBaselinesFull” model in “tRophicPosition”. Results from the “simmr” mixing-model analyses were used to classify prey taxa into two baseline groups: autochthonous (‘grazers’) and allochthonous (‘collectors’ and ‘shredders’).

Data analysis

Following Burdon et al. (2013), principal components analysis (PCA) was used to decompose four measures of deposited fine sediment (“reach” and “patch” cover, sediment depth, SIS) into a single sediment index (PC1) explaining 85% variation (Appendix B.3, Table B3). A constant (3) was added to aid interpretability.

Community composition data were analysed to better explain proximate changes influencing SIA metrics. Invertebrate taxa richness was rarefied to standardize richness estimates for 1000 individuals using the R function “rarefy”. Fish community occupancy data (presence-absence)

and relative abundances, invertebrate densities (individuals/m²), and total and SIA invertebrate occupancy data were analysed with non-metric multi-dimensional scaling (NMDS). Variation partitioning of community composition with sediment and nutrients was assessed using partial redundancy analyses (pRDA; Appendix B.3). All community analyses used the R package “vegan” (Oksanen et al., 2019).

The significance and shape of bivariate relationships between sedimentation (PC1) and stream responses were evaluated with linear and generalized additive model (GAM) regressions. GAMs were fitted with the “gam” function in the “mgcv” R package (Appendix B.3). We used hierarchical partitioning (HP) to explore the influence of sedimentation after accounting for potentially confounding factors (i.e., concentrations of nitrate-nitrogen and DRP, % canopy cover, and stream widths). Statistical significance was based on the upper 95% confidence limit (Z-score > 1.65) following 999 randomizations; HP analyses were conducted using the “hier.part” R package (Walsh & Mac Nally, 2007).

Results from SIA mixing models were analysed using linear mixed-effects models (LMM) with the “lmer” R function in the “lme4” R package. The fixed effects were sedimentation (PC1), concentrations of nitrate-nitrogen and DRP, % canopy cover, and stream widths. The random effects were consumer taxa identity and site. LMMs testing the contribution of basal resources to invertebrate primary consumers included three FFGs (‘grazers’, ‘collectors’, and ‘shredders’) and their interaction with sedimentation as fixed effects. Non-significant predictors were removed using likelihood ratio tests, but sediment, nitrate, and canopy were retained in all models testing α to ensure consistency across predator groups. Visual assessment of residual plots and BIC scores were used to identify outliers. Post-hoc contrasts were performed using the “testInteractions” function in the “phia” R package. Residual data after partialing out the

influence of nitrate concentrations and canopy cover was used to visualize dietary contributions of allochthonous resources to stream consumers.

For HP and LMM analyses, response and predictor variables were transformed (log or logit) to help meet assumptions of heteroscedasticity and linearity. Two sites identified as outliers were excluded from subsequent analyses. One site (Courtenay) seemingly had a novel carbon source (e.g., methanotrophy), and the other (Cridges) had an apparent nutrient disturbance prior to sampling, leading to disequilibria in consumer isotopic signatures. An additional site (Waihikuawa) was excluded from the fish community TD regressions due to low taxa richness (<3). For more information on data analysis, see Appendix B. All analyses were conducted in R (R Core Team, 2017).

Results

Landscape disturbance gradient

Stream sedimentation was more likely to occur with upstream riparian habitat degradation, evidenced by the correlation of deposited sediment (PC1) with decreasing riparian condition (Pearson's correlation, $r = -0.749$, $t_{10} = -3.58$, $P < 0.01$). Nutrient concentrations and canopy cover were not associated with sediment (Table B3, SI).

Basal resources

The biomass of fine benthic organic matter (FBOM) increased with sedimentation (Fig.C1A, SI); a result confirmed by hierarchical partitioning (HP) analysis ($Z = 2.71$, $P < 0.05$). Standing primary production (benthic chlorophyll-*a*, mg/cm²) and terrestrial detritus (coarse particulate organic matter, CPOM, AFDM g/m²) did not change with any environmental predictor tested.

Invertebrate community responses

Sedimentation was associated with changes in aquatic invertebrate communities. Invertebrate β -diversity was influenced by sedimentation (PC1), with this stressor independently explaining 27% variation in community structure (e.g., abundances; pRDA, $F_{1,9} = 4.57$, $P < 0.01$). Nutrients had no significant influence (Table C2, SI). However, HP analysis indicated that α -diversity (i.e., rarefied invertebrate taxa richness) did not change with sediment, but was instead negatively influenced by nitrate concentrations ($Z = 2.5$, $P < 0.05$).

Sedimentation was associated with changes in invertebrate functional-feeding groups (FFGs). Despite the increase in FBOM, the frequency of collectors did not significantly change with sedimentation. However, the trait affinity (mean trait score per individual) for collectors increased asymptotically along the sediment gradient (Fig.C1B, SI); a result confirmed by HP analysis ($Z = 8.79$, $P < 0.05$). In contrast, the frequency of grazers ($Z = 4.51$, $P < 0.05$, Fig.C1C, SI), shredders ($Z = 4.82$, $P < 0.05$, Fig.C1D, SI), and predators ($Z = 1.79$, $P < 0.05$) all decreased with sedimentation.

Invertebrate community SIA metrics also responded to the sediment gradient, with communities occupying a smaller area in isotopic niche space with increasing sedimentation (Fig.2).

Invertebrate trophic diversity (TD) measured by the standard ellipse area (SEAc) decreased along the sediment gradient (Fig.3A). This reflected changes in the horizontal niche axis, where sedimentation had a strong, negative non-linear influence on invertebrate $\delta^{13}\text{C}$ carbon range (CR; Fig.3B). TD and CR were negatively influenced by sediment in the HP analyses ($Z = 5.4$, $P < 0.05$ and $Z = 4.34$, $P < 0.05$, respectively). There was no significant influence of any environmental predictor tested on the invertebrate $\delta^{15}\text{N}$ nitrogen range (NR; Fig.3C).

Fish community responses

Fish β -diversity was not influenced by sediment or nutrients (Table C2, SI). Fish community richness indicated a weak unimodal relationship with sediment (Fig.C2, SI), but richness was generally lower at high levels of sedimentation; a result confirmed by HP analysis ($Z = 1.66$, $P < 0.05$).

Fish community SIA metrics were influenced by sedimentation. Fish community TD (SEAc) using species means had a 'U-shaped' relationship with increasing sediment (Fig.3D), but did not significantly respond to any environmental predictor in the HP models. Fish CR similarly declined non-linearly with sedimentation (Fig.3E); but the reduction was confirmed by HP analysis ($Z = 2.54$, $P < 0.05$). No environmental predictor had a significant influence on fish NR (Fig.3F).

Food-web responses

The TD (SEAc) of invertebrates and fish combined showed a strong, non-linear negative response to deposited sediment (Fig.C3, SI); a decrease supported by HP ($Z = 4.02$, $P < 0.05$). The reduction in whole community TD was strongly linked to a narrowing CR with increasing sediment ($Z = 4.19$, $P < 0.05$; Fig.C3, SI). No environmental predictor was associated with whole community NR (Fig.C3, SI).

The minimum and mean invertebrate $\Delta\delta^{13}\text{C}$ values relative to the terrestrial vegetation baseline increased along the sediment gradient (Fig.4A, $Z = 2.14$, $P < 0.05$; and $Z = 4.19$, $P < 0.05$, respectively), whereas the maximum invertebrate $\Delta\delta^{13}\text{C}$ did not change with any environmental predictor tested. Stream fish tracked invertebrates, with the mean $\Delta\delta^{13}\text{C}$ of salmonids and anguillids also increasing with sedimentation ($Z = 2.51$, $P < 0.05$). There were vertical changes

in the trophic niche, with a significant reduction in the maximum invertebrate $\Delta\delta^{15}\text{N}$ along the sedimentation gradient ($Z = 2.14$, $P < 0.05$). Stream fish contrasted this invertebrate response, with the mean $\Delta\delta^{15}\text{N}$ of salmonids and anguillids (Fig.4B; $Z = 2.15$, $P < 0.05$) and eleotrids ($Z = 4.41$, $P < 0.05$) *increasing* with sedimentation.

The stable isotope mixing-model analyses indicated that detritus (fine particulate and terrestrial organic matter combined) contributed more to the diets of invertebrate primary consumers with increasing sedimentation (Fig.5A; Table 1). The invertebrate primary consumer FFGs mostly conformed to expectations with grazers relying more on phototrophs and less on biofilms, FPOM, and detritus in general (Table 1; Fig.C4, SI). Although collector and shredder diets were similar, collectors relied more on biofilms ($X^2 = 7.95$, $P < 0.01$; Fig.C4, SI). There were other dietary changes along the sediment gradient, with the contribution of biofilms decreasing whilst FPOM increased (Table 1; Fig.C4, SI). Grazers consumed less phototrophs and more terrestrial resources along the sedimentation gradient (Table 1; Fig.C4, SI). Grazers also consumed less phototrophs with increasing nitrate concentrations, and the detrital contribution to invertebrate primary consumers increased with canopy cover (Table 1).

Invertebrate collectors contributed more to the diets of predatory invertebrates with increased sedimentation (Fig.5B, Table 2). The dietary contribution of grazers decreased with canopy cover (Table 2). The contribution of allochthonous carbon to invertebrate predators increased along the sedimentation gradient, but their estimated trophic position (TP) did not change with any environmental predictor (Table 2). The contribution of allochthonous carbon to stream fish also increased along the sedimentation gradient (Fig.5C; Table 2), with an approximate shift from 40% to 60%. The TP of fish *increased* along the sedimentation gradient, approximately rising from 3.8 to 4.4 (Fig.5D; Table 2).

Discussion

Our results suggest a radical reshaping of food-web properties along the landscape disturbance gradient. Sedimentation associated with degraded riparian habitat appeared to ‘compress’ stream communities in isotopic niche space, leading to a drastic reduction in the trophic diversity of stream food webs (Fig.6). This was likely driven by the loss of the autochthonous food-web channel and an increased reliance on allochthonous inputs. Four consumer-resource mechanisms may have contributed to changes in realized niche breadths (Fig.1A-D). Greater niche partitioning at low sediment levels leading to wider consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges (Fig.1A) appeared to be replaced by three non-exclusive mechanisms (i.e., niche ‘elimination’, ‘generalists’, and ‘homogeneity’) driving narrower consumer ranges in isotopic niche space (Fig.1B-D). Paradoxically, this trophic simplification led to an *increase* in food-chain length, evidenced by the realized trophic position of stream fish along the sedimentation gradient.

Niche ‘partitioning’ and ‘elimination’ mechanisms

Niche ‘partitioning’ (Fig.1A) reflects theories about niche differentiation and is intimately linked to the relationship between habitat and species diversity (Cardinale, 2011). Substrate heterogeneity frequently has a strong positive correlation with stream invertebrate diversity; a relationship attributed to the “greater number of niches” in more heterogeneous habitat (Beisel et al., 2000). In contrast, sedimentation typically results in more homogenous instream habitat dominated by fine particles (Waters, 1995; Burdon et al., 2013). This may have functional consequences, because larger substrate particles typically exhibit greater stability during high flows, accumulate more basal resources, and provide spatial refuge, thus generally resulting in greater abundances and diversity of biota (Quinn & Hickey, 1990). These factors help explain

the greater trophic diversity observed in more heterogeneous sites with low levels of sedimentation.

Sedimentation may have led to environmental filtering of sensitive taxa, thus supporting the niche ‘elimination’ hypothesis (Figs.1B). Perturbations such as landscape disturbance can drive non-random (i.e., trait-mediated) losses in biodiversity that have functional consequences for food webs (Woodward, 2009). Isotopic niche ‘compression’ due to species extinctions has been observed in fragmented estuarine communities (Layman et al., 2007b) and primate communities facing multiple anthropogenic pressures (Crowley et al., 2012). In our example, we saw substantial reductions in the trait frequencies of more specialized invertebrate consumers (i.e., ‘grazers’ and ‘shredders’) along the sedimentation gradient; results similar to other published studies (Rabeni et al., 2005; Yule et al., 2010). Sedimentation likely exerted stresses on stream invertebrates through dislodgement by ‘saltating’ fine sediment particles and habitat degradation (Waters, 1995; Burdon et al., 2013). In particular, reduced abundances of invertebrates that consume diatoms and periphyton, such as the leptophlebiid mayfly *Deleatidium* spp., may have strongly contributed to sedimentation-induced food-web changes.

The reduced horizontal trophic niche envelope for aquatic invertebrates (Fig.6A) was seemingly driven by the loss of the autochthonous food-web channel (Figs.4A,5A). This contributed to the non-linear reduction in trophic diversity (Fig.3A), and could be attributable to habitat loss (i.e., loss of complex and stable benthic habitat). Models based on percolation theory suggest that as habitat loss escalates, patch size decreases and isolation increases in a non-linear fashion, potentially explaining non-linearity in the relationship between sedimentation and biotic responses (Burdon et al., 2013).

Niche ‘generalists’ and ‘homogeneity’ mechanisms

Alternatively, species turnover along environmental gradients may help to regulate trophic structure (Leibold, Chase, Shurin, & Downing, 1997), but the ecological roles of generalist species persisting in disturbed habitats can be altered (Layman et al., 2007b; Lindo, Whiteley, & Gonzalez, 2012). Many stream consumers are polyphagous (Cummins, 1973), and Yule, Boyero, and Marchant (2010) found that several invertebrate taxa which were ‘grazers’ at sites unaffected by sediment became facultative ‘collectors’ at impacted sites in a tropical river. Thus, increasing sedimentation may cause changes in the availability of resources, therefore inducing shifts in consumer diets as demonstrated by our isotopic mixing-model analyses.

Optimal foraging theory predicts that food scarcity should lead to dietary convergence, because all species become generalists (Pyke et al., 1977). This mechanism underpins the most likely scenario for the niche ‘generalists’ hypothesis (Fig.1C). For example, limited food sources in a glacier-fed stream led to high levels of feeding plasticity by the invertebrate community (Zah, Burgherr, Bernasconi, & Uehlinger, 2001). In our study, resource abundances associated with grazing (chlorophyll-a) and shredding (CPOM) did not change along the sedimentation gradient. However, standing stocks of biomass alone may be misleading because we observed strong shifts in the dietary contribution of different resources to stream invertebrates, and other studies have indicated impaired transfers of energy through decreased resource quality and accessibility (Waters, 1995; Burdon et al., 2013).

Changes in consumer access to resources (i.e., scarcity) also includes reduced prey abundances for higher predators, thereby further contributing to the reduced trophic diversity along the disturbance gradient. We observed a reduction in the upper margin of the vertical trophic niche envelope for stream invertebrates along the sediment gradient (Fig.6B). However, the estimated

trophic position of predatory invertebrates did not change, casting doubt on the importance of the vertical trophic niche axis in driving isotopic niche compression in our example. Nonetheless, Yule et al. (2010) found that increasing sedimentation generally led to simpler food webs with increased connectance, suggesting more generalized trophic roles with greater omnivory.

In contrast to the food scarcity scenario invoked by the niche ‘generalists’ hypothesis, where a resource is ‘hyper-abundant’, it should be particularly attractive to all consumers by virtue of its abundance (Schoener, 1974). This is the most likely scenario for the niche ‘homogeneity’ hypothesis (Figs.1D). For example, in seagrass ecosystems, trophic diversity decreased as vegetation cover increased, owing to greater isotopic redundancy in consumers and an increased reliance on epiphytic carbon derived from leaves (Calizza et al., 2013). We observed increases in fine benthic organic matter with sedimentation, both in absolute terms and relative to other resources. Moreover, mixing models indicated increasing consumption of FPOM by invertebrate primary consumers along the sedimentation gradient. However, invertebrate collectors did not increase numerically to this increased resource base, suggesting that the niche ‘homogeneity’ mechanism was not solely responsible for the changes observed in our study.

Importantly, the niche ‘elimination’, ‘generalists’ and ‘homogeneity’ mechanisms proposed are non-exclusive (Fig.1), and may interact across trophic levels. This scenario is highly likely in our example, where the contribution of basal resources and prey to invertebrates changed in response to sedimentation. Layman et al. (2007b) found that coastal creek fragmentation led to reduced niche breadth of a resilient generalist top predator, a result they attributed to reductions in the diversity of potential prey (i.e., meaning all predator individuals had to exploit the same resources *sensu* niche ‘homogeneity’ as a result of prey niche ‘elimination’). Although it was not clear if resource scarcity (i.e., total energy availability) was a feature of their systems, this

example and our study potentially reflect a general ecological principle, where increased dietary specialization and reduced trophic omnivory should occur where habitat conditions allow for an increase in prey and resources that are preferred or optimal (Post, Pace, & Hairston, 2000). In that regard, favorable habitat conditions should cause community interactions to be more niche-driven than neutral (*sensu* niche ‘generalists’ and ‘homogeneity’), with implications for competition and coexistence (Leibold & McPeck, 2006). However, whilst increased polyphagy and omnivory may be important food-web responses to reduced resource availabilities caused by disturbances (Wootton, 2017), the determinants of food-chain length still remain controversial (Takimoto, Post, Spiller, & Holt, 2012).

Sediment influences on fish

Our community analyses indicated that overall, sediment had weaker effects on stream fishes than benthic invertebrates. Yule et al. (2010) likewise observed no influence of sedimentation on fish distributions. The absence of a deterministic influence of sediment on stream fish β -diversity highlights how other processes contributing to metacommunity dynamics (e.g., dispersal limitation) may affect the composition of these larger-bodied organisms in freshwaters, because species distributions are typically constrained by network connectivity (Shurin, Cottenie, & Hillebrand, 2009). However, there appeared to be functional consequences for the trophic role of stream fish with sedimentation.

We observed a reduction in the horizontal trophic niche and an increase in the realized trophic position of stream fish along the sedimentation gradient. Tunney, McCann, Lester, and Shuter (2012) suggested that increasing resource accessibility led to a *decrease* in food-chain length (i.e., reduced predator trophic position) and an expansion in habitat coupling (i.e., increasingly coupled macrohabitats). In our study sedimentation acted in reverse, with the loss of the

autochthonous food-web channel and shift towards allochthonous resources potentially ‘compressing’ the horizontal trophic niche and *increasing* food-chain length. Adaptive foraging in predators with changing resource availabilities could enable these changes (Kondoh & Ninomiya, 2009). Sedimentation was associated with the loss of grazers and shredders at the base of the food web, which may have caused stream fish to feed more on higher trophic levels. In particular, reduced abundances of the leptophlebiid mayfly *Deleatidium* spp. likely forced fish to consume alternative prey that included mesopredators. However, when top–down forces are strong enough to exclude intermediate consumers, the movement of prey among habitat patches can facilitate omnivory (Takimoto et al., 2012). Thus, where fish have generalist-feeding behaviors, terrestrial prey subsidies can offset reductions of benthic prey, therefore helping to stabilize stream food webs by enabling predators to persist (Rooney, McCann, Gellner, & Moore, 2006). For example, Kraus et al. (2015) showed that stream fish increased their use of terrestrial prey subsidies due to pollution-induced reductions in benthic invertebrates.

Reduced fish densities may have also enabled stream fish to increase their trophic position relative to aquatic invertebrate prey along the disturbance gradient. Lower fish production and reduced abundances are common responses to stream sedimentation (Waters, 1995). We could only estimate fish abundances at some sites, but declining abundances and species richness at high levels of sedimentation might have weakened intra- and interspecific competition. This may have enabled resident fish to better partition available resources at degraded sites, potentially via larger fish foraging over greater distances and relying more on terrestrial prey subsidies.

Concluding remarks

We have revealed food-web responses that highlight the deleterious consequences of landscape disturbance on ecosystems. Although there is evidence that habitat degradation associated with

sedimentation strongly contributes to non-linear structural changes in invertebrate communities (Burdon et al., 2013), the increasing trophic equivalence of consumers observed here suggests more complex effects on the structural and functional properties of stream food webs. Typically, decreasing diversity across trophic levels can result in lower biomass accrual and resource uptake, thus impairing ecosystem functioning (Duffy et al., 2007). However, it is not only species losses, but the functional roles of persisting biota which dictate how food webs and ecosystem functioning respond to environmental change (Layman et al., 2007b, Lindo et al., 2012). One consequence may be decreased stability, because trophic niche ‘compression’ indicates that energy flow paths are more homogenous, potentially leading to less stable food-web structures (Rooney et al., 2006; Layman et al., 2007b). This may be particularly profound where landscape disturbances alter the stabilising influence of trophic interactions with differing strengths and distributions (Wootton & Stouffer, 2016). Whilst it seems likely that terrestrial resource subsidies help offset changes for higher trophic levels in our streams, trophic simplification may still render top predators more susceptible to population fluctuations and local extinctions (Layman et al., 2007b). With ecosystems facing multiple anthropogenic threats globally, ecologists need to apply novel approaches to better recognise the functional consequences of environmental change and biodiversity loss. Using a food-web perspective enhances our understanding, thus contributing to improved conservation of ecosystems and the successful remediation of degraded habitats.

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Author's contributions

F.J.B. and J.S.H. conceived the study; F.J.B. created the conceptual framework, designed the research, collected the data, conducted analyses, and wrote the paper. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.xgxd254bv> (Burdon, McIntosh, & Harding, 2019).

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Supporting Information

Appendix A

Study sites

Appendix B

Detailed methods descriptions

Appendix C

Additional results

Table 1. Results from linear mixed-models testing environmental influences on the dietary contribution of autochthonous and allochthonous basal resources to invertebrate primary consumers. Grazers are included in the models as the reference level. FPOM, Fine particulate organic matter; Detritus, FPOM + Terrestrial resources.

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

Basal resource	Predictors	Estimates	95% CI	Marginal R^2	Conditional R^2
Phototrophs	(Intercept)	0.734*	0.103 – 1.366	0.631	0.805
	Collector	-2.086***	-2.806 – -1.367		
	Shredder	-2.133***	-3.003 – -1.263		
	Sediment	-0.250**	-0.438 – -0.063		
	logit(Canopy)	-0.194	-0.424 – 0.035		
	log(Nitrate)	-0.350***	-0.501 – -0.199		
	Sediment × Collector	0.236*	0.039 – 0.433		
	Sediment × Shredder	0.282*	0.017 – 0.546		
Biofilm	(Intercept)	-1.453***	-1.878 – -1.028	0.538	0.688
	Collector	0.841***	0.558 – 1.125		
	Shredder	0.366*	0.009 – 0.723		
	Sediment	-0.172*	-0.311 – -0.032		
	logit(Canopy)	0.219**	0.081 – 0.357		
FPOM	(Intercept)	-2.285***	-2.967 – -1.603	0.320	0.514
	Collector	0.661**	0.274 – 1.047		
	Shredder	1.097***	0.603 – 1.590		
	Sediment	0.251*	0.053 – 0.448		
	logit(Canopy)	0.149	-0.123 – 0.420		
	log(Nitrate)	0.230	-0.036 – 0.496		
Terrestrial	(Intercept)	-2.223***	-3.267 – -1.178	0.132	0.393
	Collector	1.133*	0.203 – 2.063		
	Shredder	1.038	-0.103 – 2.178		
	Sediment	0.385*	0.041 – 0.730		
	logit(Canopy)	0.288	-0.057 – 0.632		
	Sediment × Collector	-0.386*	-0.689 – -0.083		
	Sediment × Shredder	-0.466*	-0.914 – -0.019		
Detritus	(Intercept)	-1.117*	-2.115 – -0.118	0.402	0.816
	Collector	0.660**	0.260 – 1.060		
	Shredder	0.750**	0.230 – 1.269		
	Sediment	0.343*	0.052 – 0.634		
	logit(Canopy)	0.486*	0.072 – 0.900		
	log(Nitrate)	0.342	-0.059 – 0.743		

Table 2. Results from linear mixed-models testing environmental influences on the dietary contribution of prey to invertebrate predators, and the allochthonous contribution (α) and trophic position (TP) of stream predators (invertebrates and fish). *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

Predator group	Response	Predictors	Estimates	95% CI	Marginal R^2	Conditional R^2
Invertebrate	Grazer	(Intercept)	-0.370	-1.332 – 0.592	0.234	0.942
		Sediment	-0.205	-0.486 – 0.076		
		logit(Canopy)	-0.564*	-0.917 – -0.211		
	Collector	(Intercept)	-1.652*	-2.970 – -0.335	0.379	0.937
		Sediment	0.603*	0.219 – 0.987		
		logit(Canopy)	0.384	-0.157 – 0.925		
	Shredder	(Intercept)	-1.150*	-1.927 – -0.372	0.316	0.673
		Sediment	-0.096	-0.355 – 0.162		
		logit(Canopy)	0.417	0.042 – 0.793		
	α	(Intercept)	-0.473*	-0.823 – -0.123	0.489	0.837
		Sediment	0.182*	0.077 – 0.288		
		log(Nitrate)	0.115	-0.029 – 0.258		
		logit(Canopy)	0.176	0.025 – 0.327		
	TP	(Intercept)	3.437***	2.795 – 4.078	0.005	0.685
		Sediment	0.024	-0.166 – 0.214		
Fish	α	(Intercept)	-0.753*	-1.359 – -0.146	0.321	0.716
		Sediment	0.263*	0.082 – 0.444		
		log(Nitrate)	0.142	-0.108 – 0.392		
		logit(Canopy)	0.191	-0.072 – 0.455		
	TP	(Intercept)	3.554***	3.269 – 3.838	0.399	0.726
		Sediment	0.160**	0.082 – 0.237

Fig.1 Four consumer-resource interaction motifs potentially influencing community trophic diversity. (A) Consumer (solid circles) specialists focus trophic interactions (black lines) on separate resources (open circles) thus 'partitioning' niche space leading to an expansion of the consumer $\delta^{13}\text{C}$ range (CR). (B) Niche 'elimination' where environmental filtering (i) removes specialist consumers (grey circles), or alternatively, (ii) removes or reduces preferred resources, effectively ceasing interactions. Both pathways lead to a contraction of CR. (C) Niche 'generalists', where resource scarcity leads to consumers equally exploiting limited resources, causing greater trophic equivalence and a contraction of CR. (D) Resource 'homogeneity', where generalist and specialist consumers preferentially exploit an abundant resource (+ indicates increasing resource availability), leading to a contraction of CR. Mechanisms related to sediment disturbance are indicated. Although these examples describe changes in consumer CR, the same principles apply to the consumer $\delta^{15}\text{N}$ range (NR). Key assumptions made: basal resources show isotopic separation with a constant range, and consumer assimilation and fractionation rates are equivalent.

Fig.2 Stable isotope biplots of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) describing food webs from twelve agricultural streams influenced by deposited sediment (PC1). Black ellipse, invertebrate sample-corrected standard ellipse (SEAc); grey ellipse, fish SEAc. Where appropriate, errors bars (± 1 standard deviation) are shown. The ostracod *Herpetocypris pascheri* (grey diamond; plots C, D, G, J, and K) and lamprey *Geotria australis* (open grey circle; plots D and F) were excluded from SIA.

Fig.3 Evidence for trophic niche ‘compression’ using community stable isotope metrics from twelve agricultural streams along a sedimentation gradient (PC1). Invertebrate community responses: (A) trophic diversity (TD), (B) $\delta^{13}\text{C}$ ranges (CR), and (C) $\delta^{15}\text{N}$ ranges (NR) along the sedimentation gradient. Fish community responses: (D) TD, (E) CR, and (F) NR. Generalized additive models (GAMs) fitted smoothing functions to data where appropriate (with the effective degrees of freedom and deviance explained stated, but see Table C3, SI for full results). Grey shading, 95% confidence intervals; outlier sites in grey: square (Cridges); triangle (Courtenay); circle (Waihikuawa).

Fig.4 Evidence of trophic niche ‘compression’ and ‘decoupling’ along the sedimentation gradient (PC1). Panel A show the change in minimum $\delta^{13}\text{C}$ values of aquatic invertebrates relative to the terrestrial vegetation baseline; B shows the change in mean $\delta^{15}\text{N}$ values for larger stream fishes (i.e., salmonids and anguillids) relative to the aquatic invertebrate baseline. Grey shading, 95% confidence interval; outlier sites in grey: square (Cridges); triangle (Courtenay).

Fig.5 Description of food-web changes in agricultural streams along a sedimentation gradient (PC1) using Bayesian stable isotope mixing-model analyses. Panel A shows the increasing contribution of detritus (fine particulate and terrestrial organic matter) to the diets of aquatic invertebrate primary consumers (grouped into functional-feeding guilds), and B shows the increasing % contribution of invertebrate collectors as prey for predatory aquatic invertebrates. Panel C shows an increasing contribution of terrestrially-derived carbon to stream fishes, and D demonstrates the increase in the estimated trophic position of fish. Errors associated with estimated values are reported in Appendix C. Black lines, regression slopes; grey shading, 95% confidence interval. Two outlier sites (Cridges, Courtenay) are excluded from the residual plots (A,C), but are otherwise present as open circles (B,D).

Fig.6 Processes *potentially* contributing to trophic niche 'compression' and other food-web changes associated with landscape disturbance (sedimentation). Panel A describes key changes in $\delta^{13}\text{C}$ values, B describes changes in $\delta^{15}\text{N}$ values, and C indicates how these changes manifest in the isotopic niche space. In panels A-B, colored lines indicate basal resources (green, autochthonous; brown, allochthonous); black, fish; and grey, trophic niche envelopes of aquatic invertebrates. In Panel C, colored symbols indicate basal resources; black-dashed ellipse, the fundamental trophic niche of aquatic invertebrate communities; and in grey, the realized trophic niche under sediment disturbance.