A mechanistic understanding of ecological responses to land-use change in headwater streams

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Abstract. Anthropogenic activities, such as oil and natural gas development (ONGD), have significantly altered the landscape. It is often challenging to identify the mechanistic processes underlying ecological responses to land-use change (LUC). In aquatic ecosystems, alterations to habitat and food availability and water quality associated with increased LUC are key mechanistic pathways that deserve management consideration. We used structural equation modeling to evaluate how LUC associated with ONGD could influence macroinvertebrate and fish across 40 sites in six headwater streams in the Wyoming Range of the Upper Green River Basin, Wyoming. The most important mechanistic pathway varied, but responses were frequently driven by a direct effect of LUC or related to changes in food availability and water quality. Habitat complexity was the least important mechanistic pathway in our models. Our results also highlight that responses may reflect an organism's degree of habitat or resource specialization and/or sensitivity to changes in water quality. Habitat pathways were more important for habitat specialists (e.g., Mottled Sculpin, *Cottus bairdii*), food pathways were more important for food specialists (e.g., Colorado River Cutthroat Trout, *Oncorhynchus clarki pleuriticus*; Mountain Sucker, *Catostomus platyrhynchus*), and sensitivity to increased salinity was important for intolerant species (e.g., *O. clarki*, *C. bairdii*, and predatory macroinvertebrates). Continued identification of the specific mechanisms underlying species' responses to increased LUC will aid in the conservation of ecologically and economically important species.

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INTRODUCTION

Management of anthropogenic stressors requires an understanding of the underlying mechanisms that produce observed ecological patterns (e.g., declines in species abundance and diversity; Shea et al. 2004, Loreau and de Mazancourt 2008). But multiple stressors often challenge our ability to identify the management and conservation actions needed to maintain ecological integrity (Townsend et al. 2008, Craig et al. 2017).

For instance, stressors associated with anthropogenic land-use change (LUC) frequently include increased contaminants and nutrients, decreased vegetative cover, and increased soil erosion, which can significantly change the landscape and modify important factors maintaining ecological integrity (i.e., habitat complexity, water quality, and food availability; Wootton 1994, Shea et al. 2004). Therefore, identifying important mechanistic pathways will be necessary for targeted management actions that reduce negative

effects of emerging anthropogenic stressors. Furthermore, quantifying the relative strength of those pathways will give ecologists and resource managers improved predictive power regarding future stressor effects (Shea et al. 2004).

Anthropogenic LUC is the principal avenue of environmental degradation (Paul and Meyer 2001, Allan 2004, Song et al. 2018). Agriculture, mining, and urbanization are anthropogenic activities that have received considerable attention from researchers due to their high level of associated LUC (Ripley et al. 1996, Allan et al. 1997, Vitousek et al. 1997, Palmer et al. 2010). More recently, the rapid expansion of oil and natural gas development (ONGD) is of increasing human health and environmental concern around the globe (Sutherland et al. 2011, Olmstead et al. 2013), as this activity can also significantly modify the landscape's surface (Williams et al. 2008, Entrekin et al. 2011). The important mechanisms underlying responses to ONGD will likely vary by species, being dependent on how specialized a species is to food and habitat (Gray et al. 2007, Devictor et al. 2008) and its sensitivity to water quality changes (Posthuma et al. 2001). For example, ONGD has altered critical habitat along mule deer migration routes, resulting in behavioral changes in habitat selection to avoid developed areas (Sawyer et al. 2006, 2009). In addition, sagebrush-obligate songbirds (Hethcoat and Chalfoun 2015) and sage grouse (Walker et al. 2007) populations have precipitously declined near ONGD fields because of increased nest predation and deterioration of high-quality lekking habitat, respectively. Recent studies have begun linking the responses of many different aquatic species in relation to increased ONGD (Johnson et al. 2015, Entrekin et al. 2018, Walters et al. 2019). Yet, our understanding of how this emergent land-use could affect the different mechanistic pathways and the relative strengths of those pathways in aquatic ecosystems remains incomplete.

In aquatic ecosystems, alterations in habitat and water quality and food availability associated with increased LUC are key mechanistic pathways that deserve consideration (Fig. 1). Specifically, the installation of roads, well pads, pipelines, wastewater storage ponds, and refining facilities associated with ONGD can significantly alter forest and riparian habitats, resulting
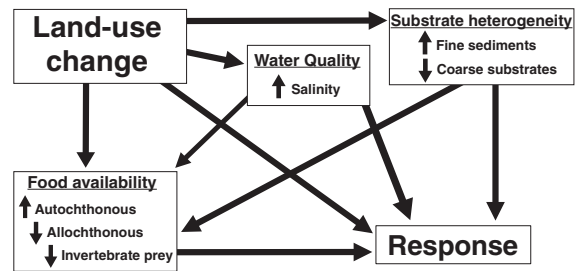

Fig. 1. Conceptual diagram showing the hypothesized pathways and predictions for how land-use change associated with oil and natural gas development could affect aquatic organisms.

in increased sediment deposition and habitat homogenization in streams when proper best management practices are not implemented (Entrekin et al. 2011). Habitat structural complexity can strongly regulate a species' distribution and local abundance (i.e., habitat template hypothesis; Poff and Ward 1990, Townsend and Hildrew 1994, Devictor et al. 2008), with decreased habitat complexity associated with LUC being a primary cause for declines in aquatic diversity (Walters et al. 2003, Violin et al. 2011). Like many other resource extraction activities (Pond et al. 2008, Bernhardt and Palmer 2011), increased ONGD can also alter water quality through augmented ions, nutrients, metals, and other dissolved solids (Entrekin et al. 2011, Austin et al. 2015). These water quality changes have been linked to accidental spills during transport, leaky infrastructure (e.g., pipes and storage ponds), and intentional releases (Patz et al. 2004), potentially exceeding tolerance thresholds for many aquatic organisms (i.e., water quality hypothesis; Clements et al. 2012, Tlili et al. 2016). Food availability can likewise be an important factor regulating a species' response (i.e., food availability hypothesis; Johnson and Sherry 2001), where increased ONGD can alter the availability of basal food resources by removing vegetative cover, reducing allochthonous inputs to streams (Hagen et al. 2010). In addition, increased LUC associated with ONGD could indirectly mediate food availability through changes in habitat and/or water quality (Crowder and Cooper 1982). For example, increased nutrients and solar radiation resulting from decreased riparian cover could

augment in-stream primary production (Austin et al. 2015), benefiting algivorous species and negatively affecting other species. Many of these modifications to habitat, water quality, and basal food availability have been observed in streams surrounded by ONGD in shale plays in the Appalachians (Olmstead et al. 2013), in Arkansas (Johnson et al. 2015, Baker et al. 2018), and in Wyoming (Godwin et al. 2015, Girard and Walters 2018, Walters et al. 2019). But given the diversity of stressors associated with the different land-uses and their variable effects, it is essential that we continue to understand and identify how different land-use activities influence important mechanistic pathways for different species.

The main goal of this study was to evaluate the effects of LUC associated with ONGD on headwater streams and the associated mechanistic pathways (i.e., habitat complexity, water quality, and food availability). Specifically, we used structural equation modeling (SEM) to estimate the effect of ONGD on each mechanistic pathway and compared the relative importance of those pathways at 40 sites in six headwater streams in the Wyoming Range, Wyoming. We hypothesized that the important pathway underlying each response would vary among responses, often being related to the degree of habitat and dietary specialization and sensitivity to changes in water quality. Based on this hypothesis, we tested three predictions to evaluate the effect of increased LUC associated with ONGD on 15 different macroinvertebrate assemblage and fish population responses. First, we predicted that LUC would have an overall negative effect on habitat complexity due to increased fine sediments, which would have the strongest effects on habitat specialists like the Mottled Sculpin (*Cottus bairdii*), Colorado River Cutthroat Trout (*Oncorhynchus clarki pleuriticus*), and many Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa. Second, we predicted that LUC would decrease water quality through increased salinity and other pollutants, with stronger negative effects on species that are more sensitive to alterations in water quality, like *O. clarki* and many intolerant EPT species. Finally, we predicted that LUC associated with ONGD would decrease allochthonous food resources and increase autochthonous food resources, which would strongly

affect food specialists (e.g., decreased shredders, increased scrapers, and Mountain Sucker [*Catostomus platyrhynchus*]).

METHODS

Study sites

This study was conducted during summer 2016 in two headwater stream drainages—Dry Piney and South Beaver—of the Wyoming Range in the Upper Green River Basin, the largest tributary of the Colorado River (Fig. 2). Oil and natural gas development has occurred in this basin since the early 1900s, with proposed expansion in the coming years. Riparian corridors of streams in the area are typically narrow, dominated by willows (*Salix* spp.), and are situated within a sagebrush-steppe landscape.

We randomly selected 40 sites from a list of 150 locations that were evenly distributed every 500 m along a GIS stream network. Selected sites were on one of six headwater streams that originate from springs on the eastern flank of the Wyoming Range and flow eastward to the Green River (Fig. 2). Macroinvertebrate samples were taken at all 40 sites (150 m in length), while fish population assessments were conducted at 39 sites (100 m; Appendix S1: Table S1). Stream flows are characteristic of montane fluvial systems, where snowmelt drives early spring peak flows that transition to spring-fed base flow conditions for the rest of the year (Appendix S1: Fig. S1).

Land-use change

We calculated percent LUC (%LUC) as the proportion of the landscape that was disturbed by all infrastructure (e.g., roads, well pads, pipelines, holding ponds, refining facilities) associated with ONGD within the contributing catchment and at the site scale within a 1 km circular buffer of each site. Following Girard and Walters (2018), we estimated %LUC by combining well location data with hand-digitized roads, pipelines, holding ponds, and refining facilities using polylines and polygons from GIS Basemap imagery in ArcMap. We used %LUC associated with ONGD because it is the main infrastructure-related LUC in the study area (Girard and Walters 2018). Models using site-level and catchment-level %LUC yielded consistent results. In
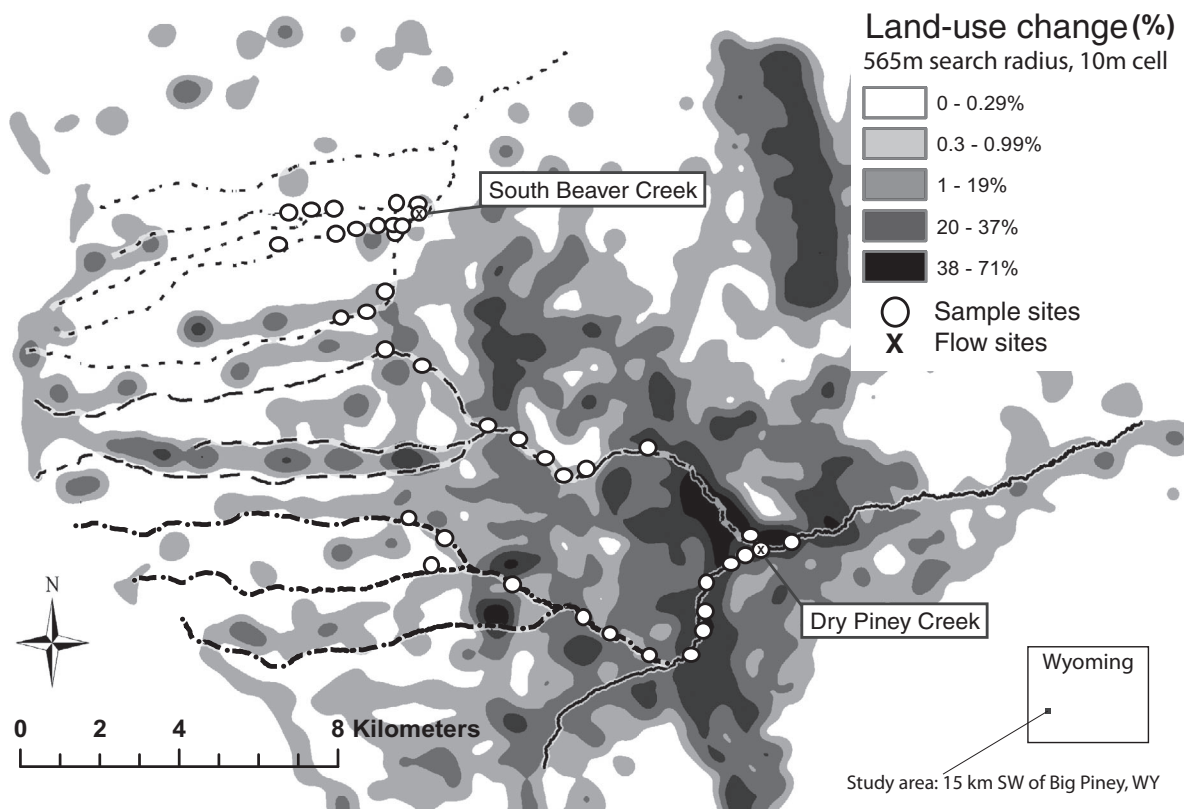
Fig. 2. Map of study area in the Upper Green River Basin's Wyoming Range depicting land-use change (LUC; %) associated with oil and natural gas development and the 40 sample locations. See Appendix S1: Table S1 for detailed locations and LUC for each site.

addition, site-level and catchment-level %LUC were highly correlated ($r = 0.82$), so we used catchment-level %LUC as our disturbance metric in all models.

Abiotic characteristics

We measured several water quality and habitat variables to evaluate the potential pathways through which LUC associated with ONGD could affect our response variables. We measured in situ water temperature (°C), pH, dissolved oxygen (%), and specific conductivity ($\mu S_{25°C}/cm^2$) at each site using a YSI Professional Plus meter (YSI, Yellow Springs, Ohio, USA). All in situ measurements were taken once in June and once in August of 2016 at each site. Dissolved oxygen (>80%), temperature, and pH measurements were all outside ranges deemed stressful to most freshwater organisms (Table 1); therefore, we used specific conductivity as the

water quality metric in our analyses to represent changes in water quality potentially associated with ONGD. In addition, a recent study found that ONGD was related to increased salinity in these streams (Walters et al. 2019).

We quantified in-stream habitat at each site during base flow conditions in August 2016 using a cross-sectional transect method (Barbour et al. 1999). We focused on substrate type and heterogeneity to provide a metric of substrate heterogeneity relevant to benthic macroinvertebrate (Burdon et al. 2013) and fish feeding and spawning. At each transect—established every 10 m for a total of 16 transects per site—substrate type and fine sediment depth were recorded along five points at 5%, 25%, 50%, 75%, and 95% of the wetted channel width (80 points total). Sediment depth was measured at each transect point by inserting a meter stick into soft sediments until a coarser substrate underneath was

Table 1. Summary of physicochemical and biotic characteristics of sites surveyed in Dry Piney and South Beaver drainages (Upper Green River Basin, Wyoming Range) during August 2016 (n = 40 sites).

Variable	Method/Replication	Units	Median	Minimum	Maximum
Water Quality					
Temperature	Direct measurement†	°C	11	6	19
pH	Direct measurement†		8.3	8.0	8.7
Specific conductivity	Direct measurement†	µS$_{25°C}$/cm	474	383	846
Disturbance/Habitat					
Catchment land-use change	GIS mapping	%	4	0.7	9
Substrate heterogeneity‡	16-transects/80-points	H‡	1.1	0.6	1.6
Mean sediment depth	16-transects/80-points	cm	35	10	261
Coarse substrates	16-transects/80-points	%	65	4	87
Biological					
Invertebrate metrics					
Diversity‡	Hess sampler/6 SMPs	H‡	1.9	1.4	2.3
Dominant percent	Hess sampler/6 SMPs	%	40	12	64
Total density	Hess sampler/6 SMPs	no./m^2	8083	1973	57,413
Taxa richness	Hess sampler/6 SMPs	no. sp.	15	11	22
EPT richness	Hess sampler/6 SMPs	no. sp.	12	8	16
EPT density	Hess sampler/6 SMPs	no./m^2	753	94	23,536
%EPT	Hess sampler/6 SMPs	%	10	2	60
Shredder density (SH)	Hess sampler/6 SMPs	no./m^2	222	16	7448
Collector–filterer density (CF)	Hess sampler/6 SMPs	no./m^2	565	55	4547
Collector–gatherer density (CG)	Hess sampler/6 SMPs	no./m^2	11	0	67
Scraper density (SC)	Hess sampler/6 SMPs	no./m^2	745	31	4323
Predator density (PR)	Hess sampler/6 SMPs	no./m^2	1154	273	4461
Fish metrics					
Cutthroat Trout (*O. clarki*)	Electrofishing	no. 100/m^2	0	0	7
Mottled Sculpin (*Cottus bairdii*)	Electrofishing	no. 100/m^2	0	0	95
Mountain Sucker (*Catostomus platyrhynchus*)	Electrofishing	no. 100/m^2	1	0	75
Basal food resources					
CBOM	Hess sampler/6 SMPs	mg/m^2	21,199	5359	113,964
FBOM	Bottomless bucket/6 SMPs	mg/m^2	9	0.3	58
SPOM	Grab sample/1 SMP	mg/L	0.5	0.4	0.6
Algae	Stone/sediment/6 SMPs	mg/m^2	414	142	9127

Note: Abbreviations: CBOM, coarse benthic organic matter; EPT, Ephemeroptera, Plecoptera, Trichoptera;FBOM, fine benthic organic matter; SMPs, samples; SPOM, suspended particulate organic matter.

† YSI Professional Plus.

‡ Shannon's diversity index.

reached and averaged for each site. We calculated percent coarse substrate as the proportion of transect points covered by coarse substrate at each site. Coarse substrates were defined as all substrate >2 mm using the Wentworth scale (Wentworth 1922). We used Shannon's diversity index to estimate substrate diversity (McClain and Barry 2010).

We used a principal component analysis (PCA) to reduce substrate diversity, mean sediment depth, and percent coarse substrate into a single substrate heterogeneity index (habitat PCA-1, 56% of total variance; Appendix S1: Table S2, Fig. S2). This habitat index revealed a

gradient from deeper, finer substrate to coarser substrate and was used to represent habitat complexity in all SEMs.

Food resource availability

We selected six sample locations for basal food availability and benthic macroinvertebrates at each site in August 2016 using a random number generator, where every stream meter within each site (i.e., 0–150 m) had an equal chance of being selected. All sample locations were required to have at least 10 m between them—if sample locations were within 10 m of each other, an additional random number was generated until

all sample locations met the 10 m requirement. For each random sampling location, the exact location for each food type and macroinvertebrate sample was adjusted according to specifics below.

We considered coarse benthic organic matter (CBOM; >1 mm), fine benthic organic matter (FBOM; >47 μm and <1 mm), suspended particulate organic matter (SPOM; >47 μm and <1 mm), and algae as basal food resources in our analyses. We collected one SPOM sample from each site by submerging a 500-mL Nalgene bottle from the water's surface to the substrate. Fine benthic organic matter samples were collected within 1 m of each randomly selected sample location by vigorously disturbing the substrate inside a bottomless bucket by hand and taking a subsample in a 500-mL Nalgene bottle. We filtered all FBOM and SPOM samples through pre-weighed, pre-ashed filters (GF/F, 47-mm, Pall) and dried them at 60°C for at least 48 h. Coarse benthic organic matter was measured from processed macroinvertebrate Hess samples (described in *Benthic macroinvertebrates*). Once separated from the benthic macroinvertebrate, we placed all CBOM materials in pre-weighed aluminum tins to dry at 60°C for at least 48 h. We quantified ash-free dry mass (AFDM) for all CBOM, FBOM, and SPOM samples following Steinman and Lamberti (2017).

To estimate algal availability, coarse substrate or fine sediment samples were collected within 1 m of each random sampling location. We collected and rinsed all coarse substrates with filtered stream water to remove any entrained CBOM and FBOM from the filamentous algae. We then placed coarse substrates in labeled containers, stored them in a dark cooler on ice, and transported to the laboratory for further processing within 48 h. In the laboratory, we scrubbed attached algae from coarse substrates using a hard-bristled toothbrush to create an algal slurry. Fine sediment samples were only used to quantify algal availability when no coarse substrate was available within 1 m of the random sample location. Where fine sediment samples were collected, a glass petri dish (90 mm diameter) was inserted approximately 10 mm into the streambed to remove a circular section of sediment (Biggs and Kilroy 2000, Burdon et al. 2013). Fine sediment samples were mixed with 100 mL

of filtered stream water to create algal slurries. Subsamples of the homogenized algal slurries were filtered through a pre-ashed, pre-weighed filter (Pall GF/F, 47 mm diameter), and algal AFDM was quantified following Steinman and Lamberti (2017).

We used a PCA to reduce CBOM, FBOM, SPOM, and algal biomass into a single food availability index (food PCA-1, 55% of total variance; Appendix S1: Table S2, Fig. S2), which revealed a gradient of less food to more food. We used this food availability index in all macroinvertebrate assemblage SEMs (i.e., diversity, taxa density, taxa richness, and %EPT; Table 2). We

Table 2. Food availability variables used for each macroinvertebrate assemblage, FFG, and fish density metrics.

Response variable	Basil food resource
Macroinvertebrate assemblage	
Diversity	Food PCA-1: CPOM, FBOM, SPOM, Algae
% Dominant	FBOM availability
Total density	Food PCA-1: CPOM, FBOM, SPOM, Algae
Taxa richness	Food PCA-1: CPOM, FBOM, SPOM, Algae
EPT richness	Food PCA-1: CPOM, FBOM, SPOM, Algae
EPT density	Food PCA-1: CPOM, FBOM, SPOM, Algae
%EPT	Food PCA-1: CPOM, FBOM, SPOM, Algae
Macroinvertebrate FFG	
Shredder density	CBOM availability
Collector–filterer density	SPOM availability
Collector–gatherer density	FBOM availability
Scraper density	Algal availability
Predator density	Total macroinvertebrate density
Fish	
Cutthroat Trout (*O. clarki*)	Total macroinvertebrate density
Mottled Sculpin (*Cottus bairdii*)	Total macroinvertebrate density
Mountain Sucker (*Catostomus platyrhynchus*)	Algal availability

Notes: Food availability PCA-1 results can be found in Appendix S1: Table S2, Fig. S2. Abbreviations: % dominant, non-predacious Chironomidae and Baetidae; CBOM, coarse benthic organic matter; EPT, Ephemeroptera, Plecoptera, Trichoptera; FBOM, fine benthic organic matter; FFG, functional feeding guild; PCA, principal component analysis; SPOM, suspended particulate organic matter.

also used the availability of individual food type for each corresponding macroinvertebrate functional feeding guild (FFG; e.g., CBOM for shredders and algae for scrapers; Table 2). One major assumption of our models is that each FFG strictly depends on their respective food type, as research finds mixed results when relying on FFG classifications without dietary analysis (Palmer et al. 1993, Tomanova et al. 2006). We were unable to conduct dietary analyses for individual taxa in this study; therefore, we ran additional SEMs for each FFG to evaluate the potential for different food types to influence the FFG results. These additional SEMs revealed that different food types had little influence on our FFG results.

Benthic macroinvertebrates

We collected benthic macroinvertebrates from riffle or run habitats within 5 m of each random sampling location using a modified Hess sampler (335 μm mesh; 0.02 m^2). To reduce the potential effect of microhabitat differences on macroinvertebrate assemblages, we targeted the thalweg of riffle and run habitats within a narrow range of depths (10–21 cm) and usually represented the dominant habitat type within each 150 m site. These habitats tended to be a mixture of riffle and run habitats at less disturbed sites and mostly run habitats at more disturbed sites. All samples were preserved in 70% ethanol. In the laboratory, macroinvertebrates were separated from all other organic and inorganic matter, identified to genus where possible and enumerated. For Chironomidae (Diptera), individuals were identified as being non-predaceous (i.e., non-Tanypodinae) and predaceous (i.e., Tanypodinae). All individuals of Nemouridae and Chloroperlidae were grouped by family. Finally, all macroinvertebrates were grouped by FFG based on Merritt et al. (2008).

To characterize macroinvertebrate responses associated with LUC, we calculated total macroinvertebrate diversity, richness, density, percent of the two dominant macroinvertebrate taxa (i.e., Baetidae and non-predatory Chironomidae made up 43% of the samples), percent of macroinvertebrates in the families Ephemeroptera, Plecoptera, and Trichoptera (%EPT), EPT richness, EPT density, and density of each FFG (Table 1; Appendix S1: Table S3). We used Shannon's diversity index to calculate diversity of benthic macroinvertebrates for each sample. Taxa richness and EPT richness were measured as the number of unique macroinvertebrate and EPT taxa collected at each site, respectively. Densities were calculated as the number m^{-2} for each corresponding response variable. All macroinvertebrate responses were averaged across the six replicate samples at each site to represent the overall macroinvertebrate assemblage at each site.

Fishes

We collected fish from 39 100-m sites on one occasion using three-pass depletion with a backpack electrofisher (Smith-Root; model LR-24; Vancouver, Washington, USA) between June and July of 2016. We sampled fish in association with long-term population surveys that have been conducted annually at these sites since 2012 (Girard and Walters 2018). We placed block nets (3.18 mm mesh) at the upstream and downstream margins of each site to limit escapement and colonization during sampling. Captured fish were enumerated and released back to their original site of capture. We collected individuals of the three dominant fish species: *O. clarki* (9%), *C. bairdii* (67%), and *C. platyrhynchus* (22%). The only other fish species collected during population surveys between 2012 and 2018 made up <5% of captured fish across all years at 64 sites and included native Speckled Dace (*Rhinichthys osculus*), and non-native Fathead Minnow (*Pimephales promelas*), White Sucker (*Catostomus commersonii*), and Brook Trout (*Salvelinus fontinalis*). We estimated abundance of each species at each site separately using multiple-pass depletion methods (Seber and Le Cren 1967, Carle and Strub 1978). We converted fish abundance estimates to density (no. 100 m^{-2}; Appendix S1: Table S4), which was used in each corresponding fish SEM that is described in detail below.

Statistical analysis

We used SEM to evaluate the hypothesized pathways driving population and assemblage responses for different stream organisms. The techniques and usefulness of SEMs in ecology have been exhaustively described elsewhere (Grace 2006). Briefly, SEM is a multivariate statistical technique that combines factor analysis and multiple regressions to evaluate structural

relationships between different endogenous (i.e., dependent) and exogenous (i.e., independent) variables in a single model (Grace 2006). SEMs provide a useful approach for understanding the causal pathways and mechanisms underlying relationships in complex systems. Each pathway within a given SEM can be viewed as a different hypothesis and used to simultaneously test the different causal relationships between all variables. SEMs are also useful in that they have the flexibility to represent the modeling situation that best matches the data and are largely used as confirmatory rather than exploratory analyses (Grace 2006).

We used SEM to evaluate the relative importance of mechanistic pathways underlying several macroinvertebrate assemblage and FFG responses (13 response variables) and densities of three fish species (Table 1). We evaluated the mechanistic pathways through which LUC could affect our response variables: alterations in substrate heterogeneity, water quality, or food availability. For each response variable, we constructed an SEM that included the direct effect of LUC and the indirect effects of LUC mediated through substrate heterogeneity, water quality, and food availability (Fig. 1). The basal food metric used to represent food availability in each SEM differed with response variable (e.g., food PCA-1 for taxa diversity and CBOM for shredding macroinvertebrates; Table 2). We applied data transformations where appropriate to meet the assumptions of normality and homogeneity of variances, and constants were added to each value to convert negative values to positive values. We visually inspected data (e.g., Cleveland dotplots and boxplots) for outliers, which revealed one site as an outlier. Results of all models were similar with and without this outlier site; therefore, all sites were retained in the SEMs. We also ran SEMs that included other predictor variables (i.e., average width, average depth, and maximum depth) that would reflect differences in habitat, but the inclusion of these variables resulted in inadequate model fit.

We report model fit indices of chi-square (χ^2; >0.05), comparative fit index (>0.90), the standardized root mean square residual (<0.05), Tucker-Lewis index (>0.90), the incremental fit index (>0.90), and the root mean square error of approximation (<0.05) for the SEMs for each response variable (Appendix S1: Table S5). Goodness-of-fit estimates and results for SEMs were run using the sem function in the lavaan package (Rosseel 2012). All analyses were performed in Program R (R Development Core Team 2018).
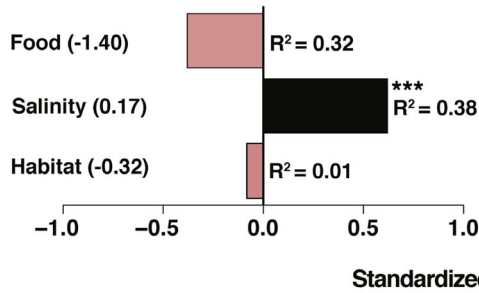
Results

Physicochemical and biological metrics varied across the ONGD gradient (Table 1). Across all 40 sites, catchment-level %LUC averaged 4.21 ± 2.37 and ranged from <1% to 9.2%. Average (±standard deviation) wetted width was 1.27 ± 0.39 m, and average depth was 0.17 ± 0.04 m across sites in 2016. In situ salinity, as measured by specific conductivity, ranged from 383 to 846 $\mu S_{25°C}$/cm and averaged 503 ± 117 $\mu S_{25°C}$/cm. Salinity in the South Beaver reference drainage ranged from 383 to 484 $\mu S_{25°C}$/cm and from 458 to 846 $\mu S_{25°C}$/cm in the more developed Dry Piney drainage, which is consistent with values previously measured at these sites. The availability of basal food resources also varied across sites with CBOM accounting for the greatest proportion of available food (Table 1).

Model fit metrics indicated the SEMs had adequate fit (Appendix S1: Table S5). In all SEMs, water quality (i.e., salinity) was positively related to LUC, while substrate heterogeneity was unrelated to LUC (Figs. 3–5). The effect of LUC on food availability depended on the basal food resource used in each corresponding SEM, either being negative or insignificant (Figs. 3–5).
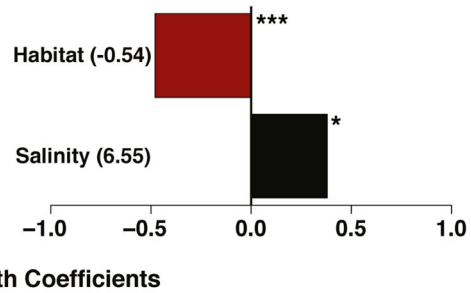
The relative importance of each mechanistic pathway varied with the macroinvertebrate assemblage metric. In all macroinvertebrate assemblage SEMs, water quality was positively related to LUC (Fig. 3ai). Food availability (i.e., food PCA-1) was negatively related to substrate heterogeneity (i.e., habitat PCA-1) and positively related to water quality (Fig. 3aii). Macroinvertebrate diversity was only negatively related to food availability (Fig. 3bi). Taxa density (Fig. 3bii), taxa richness (Fig. 3biii), and EPT density (Fig. 3biv) were negatively related to a direct effect of LUC. Ephemeroptera, Plecoptera, and Trichoptera density was also negatively related to food availability. Percent EPT was negatively related to substrate heterogeneity and food availability (Fig. 3bv). Percent dominant taxa and EPT richness were not related to any SEM pathway.

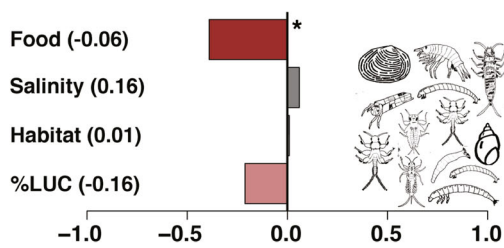## a) General pathways

i. %LUC: endogenous variables

Food (-1.40)   R² = 0.32

Salinity (0.17)   *** R² = 0.38

Habitat (-0.32)   R² = 0.01

−1.0   −0.5   0.0   0.5   1.0

Standardized Path Coefficients

ii. Habitat/Water quality: food availability

Habitat (-0.54)   ***

Salinity (6.55)   *

−1.0   −0.5   0.0   0.5   1.0

b) Response pathways

i. Shannon's diversity (R² = 0.17)

Food (-0.06)   *

Salinity (0.16)

Habitat (0.01)

%LUC (-0.16)

−1.0   −0.5   0.0   0.5   1.0

ii. Total density (R² = 0.29)

Food (0.02)

Salinity (0.65)

Habitat (0.01)

%LUC (-0.45)   **

−1.0   −0.5   0.0   0.5   1.0

iii. Taxa richness (R² = 0.43)

Food (-0.01)

Salinity (0.11)

Habitat (0.01)

%LUC (-0.17)   ***

−1.0   −0.5   0.0   0.5   1.0

iv. EPT density (R² = 0.29)

Food (-0.11)   *

Salinity (0.41)

Habitat (-0.10)

%LUC (-0.79)   *

−1.0   −0.5   0.0   0.5   1.0

Standardized Path Coefficients

v. %EPT (R² = 0.33)

Food (-0.31)   **

Salinity (-1.50)

Habitat (-0.28)   *

%LUC (-0.67)

−1.0   −0.5   0.0   0.5   1.0
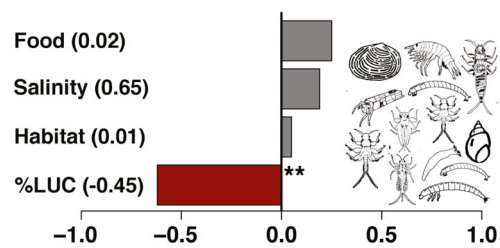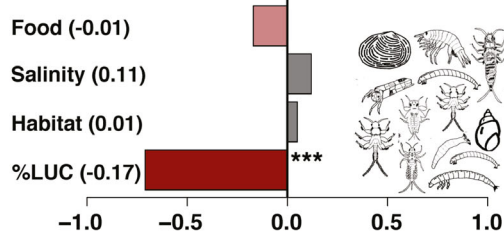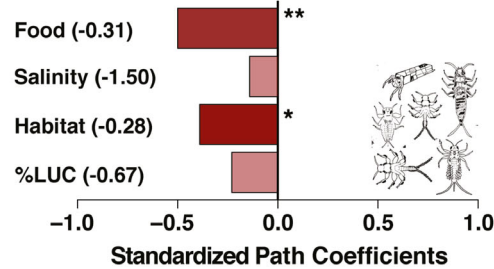
Standardized Path Coefficients
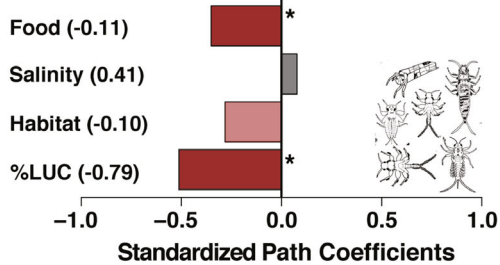
Fig. 3. Final results for macroinvertebrate assemblage structural equation models with standardized and

(Fig. 3. *Continued*)

unstandardized path coefficients reflecting the general pathways for all macroinvertebrate assemblage models (panel a) and for each macroinvertebrate assemblage response (panel b). Values outside parentheses represent standardized path coefficients, while values inside parentheses represent unstandardized path coefficients. Pathway significance is denoted by the following: $^*P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$. Significant positive coefficients are indicated by black boxes, and significant negative coefficients are indicated by red boxes. Nonsignificant path coefficients are indicated by gray (positive) and pink (negative) boxes. The amount of variation explained by all pathways connecting a specific variable is shown by the R^2 values.

Shredder (Fig. 4a), scraper (Fig. 4b), and collector–gatherer (Fig. 4d) densities were negatively related to LUC. Scraper (Fig. 4b) and collector–gatherer (Fig. 4d) densities were also positively related to water quality, with a significant indirect effect of LUC being mediated through water quality for only scraper density. Collector–filterer density was positively related to food availability (i.e., SPOM; Fig. 4c). Predator density was indirectly related to LUC mediated through water quality (negative) and food availability (positive; Fig. 4e).

The relative importance of each mechanistic pathway also varied with each fish species with differences in food availability and water quality frequently being important predictors (Fig. 5). No fish species was directly related to LUC, suggesting that we modeled the important mechanistic pathways underlying fish densities in this system. Density of *O. clarki* was negatively related to LUC through a significant indirect effect of water quality (i.e., salinity) and positively mediated through a significant indirect effect of food availability (i.e., macroinvertebrate density; Fig. 5a). Density of *C. bairdii* was also driven by a negative, indirect effect of LUC mediated through water quality and a positive effect of substrate heterogeneity (i.e., coarser substrates; Fig. 5b). *Catostomus platyrhynchus* density was positively related to algae availability, which was unrelated to LUC (Fig. 5c).

Discussion

The mechanistic pathway through which species were affected was highly variable and not always linked to LUC associated with ONGD. Direct effects of LUC were negatively associated with six of the 15 response variables, all being related to declines in lower macroinvertebrate trophic levels. In four cases, the effect of LUC was indirectly mediated through water quality and/or food availability, sometimes in unpredicted ways. Surprisingly, substrate heterogeneity was unrelated to LUC and was a significant mechanistic pathway in only two instances (i.e., %EPT and *C. bairdii* density). While not always driven by LUC, food availability and water quality were important pathways driving relationships for seven and five response variables, respectively. We found several examples where food and habitat specialization and sensitivity to changes in water quality were represented in our models. Our results indicate that the important mechanistic pathways through which LUC associated with ONGD can affect different species are numerous, complex, and not always straightforward or predictable.

Effect of LUC

The direct effect of LUC only emerged for lower trophic levels, being negatively related to collector–gatherer, shredder, scraper, EPT, and total macroinvertebrate densities, as well as taxa richness. These direct relationships between LUC and response variables suggest that there were unmeasured factors associated with LUC that were important predictors such as additional contaminants (e.g., polycyclic aromatic hydrocarbons, trace metals), legacy effects of land-use, or local-scale stream flows. Thus, additional investigations would be needed if managers were interested in further understanding LUC effects on such responses. In contrast, higher trophic levels (i.e., macroinvertebrate predators and fishes) and many other macroinvertebrate responses were best explained by our mechanistic pathways (i.e., habitat, food, or water quality) and were not always linked to LUC. One possible explanation for the lack of a direct LUC effect on higher trophic levels is the spatial scale at which these trophic levels interact with resources across the
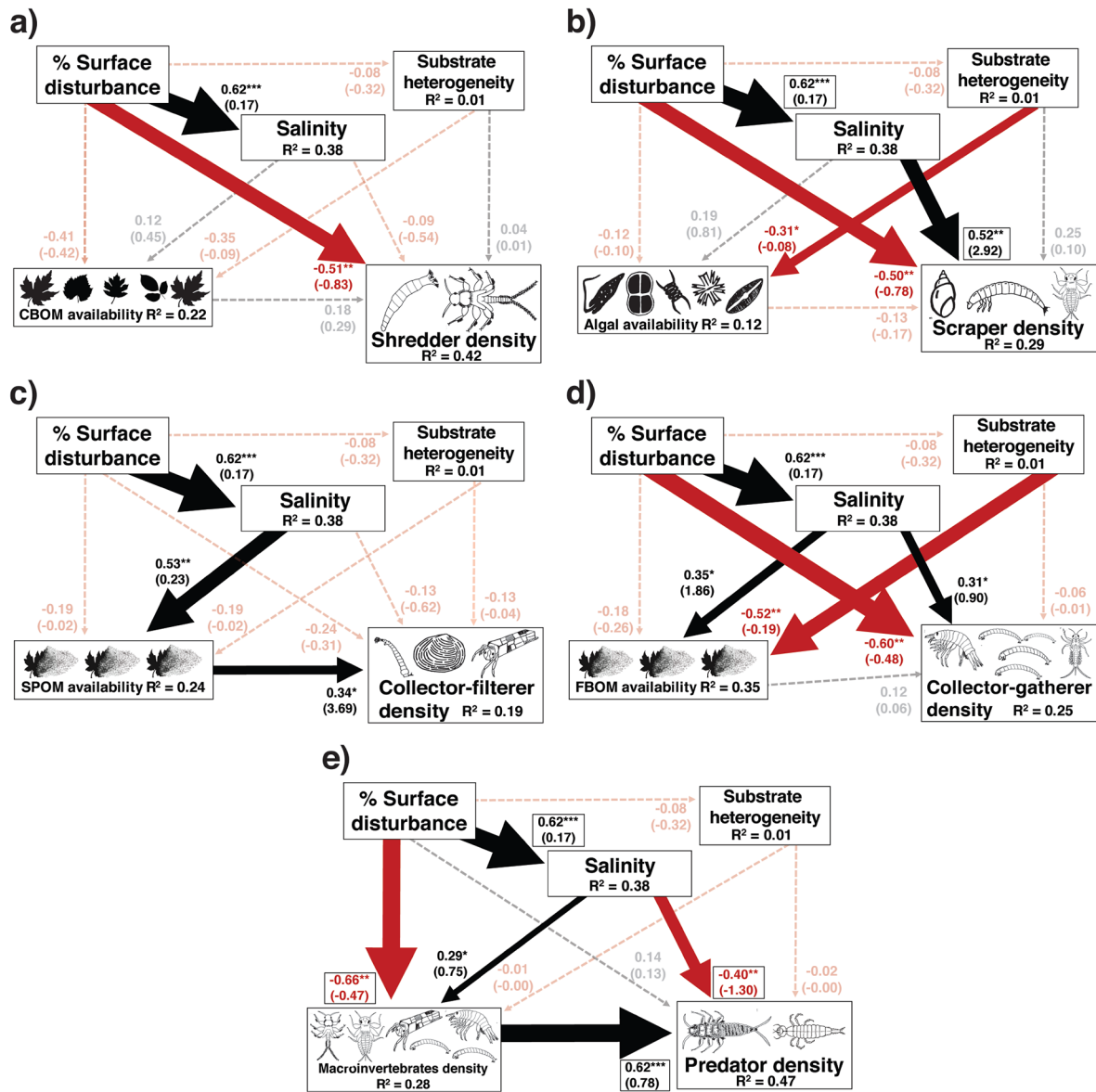
Fig. 4. Final results for each macroinvertebrate functional feeding guild structural equation model with standardized and unstandardized path coefficients. Values outside parentheses represent standardized path coefficients, while values inside parentheses represent unstandardized path coefficients. Pathway significance is denoted by the following: $^*P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$. Significant positive pathways are represented by black arrows, and significant negative pathways are represented by red arrows. Nonsignificant pathways are indicated by dashed, transparent arrows. Outlined path coefficients indicate significant indirect pathways. Arrow thickness reflects the magnitude of the standardized path coefficients. The amount of variation explained by all pathways connecting a specific variable is shown by the R^2 values.

landscape. The great mobility of many fish gives them the opportunity to evaluate the attributes and resources in alternative habitats (Power 1984, Gilliam and Fraser 2001). In fact, ongoing research in these streams (i.e., 2012–2019) indicates that these fish have relatively high dispersal and persistence rates, especially in years with moderate to high flows (Walker et al.,
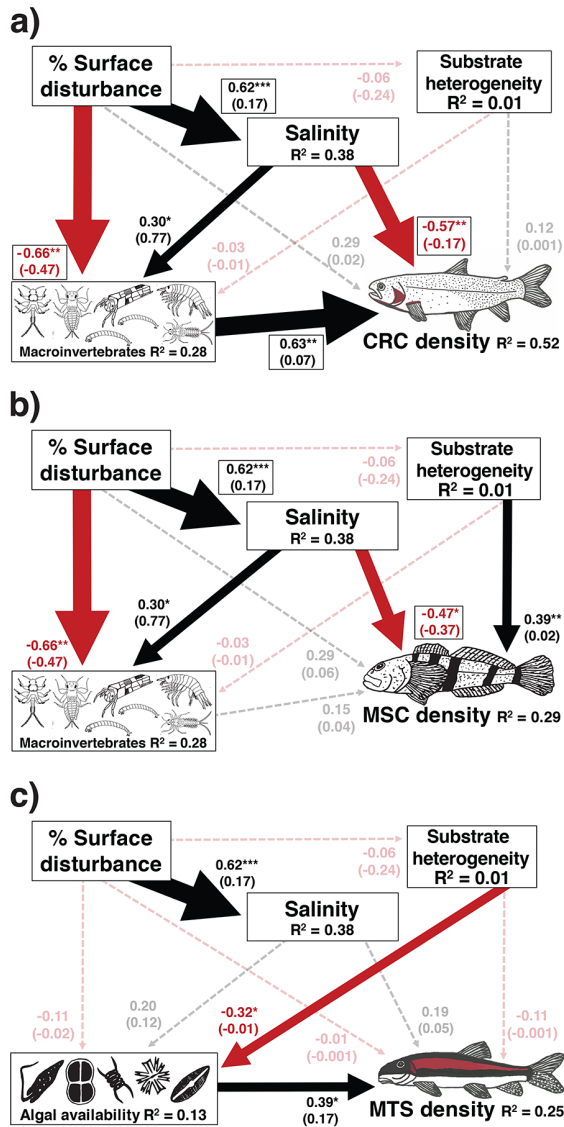
Fig. 5. Final structural equation model results with standardized and unstandardized path coefficients for each fish species. Values outside parentheses represent standardized path coefficients, while values inside parentheses represent unstandardized path coefficients. Pathway significance is denoted by the following: $*P \leq 0.05$, $**P \leq 0.01$, $***P \leq 0.001$. Significant positive pathways are indicated by black arrows, while significant negative pathways are indicated by red arrows. Nonsignificant pathways are indicated by dashed, transparent arrows. Outlined path coefficients indicate significant indirect pathways. Arrow thickness reflects the magnitude of the standardized path coefficients. The amount of variation explained by all pathways connecting a specific variable is shown by the R^2 values.

unpublished manuscript). Another explanation could be related to the scale and resolution at which variables were measured (Larsen et al. 2009). For example, macroinvertebrate assemblages were sampled at the patch scale (0.02 m^2), while habitat and fishes incorporated measurements at a coarser site scale (100 m). This corroborates other studies that suggest site-scale metrics may not be the best predictor of patch-scale macroinvertebrate assemblages (Larsen et al. 2009, Burdon et al. 2013), even though site-scale measurements are more logical for management goals.

The effect of LUC on the mechanistic pathways was generally in the predicted directions, being positive (i.e., salinity) and negative (i.e., macroinvertebrate prey availability), but sometimes unrelated (i.e., substrate heterogeneity and algal availability). Activities associated with ONGD and many other anthropogenic practices are known to increase ion concentrations in nearby streams through unintended leaks and spills from infrastructure and intentional releases (Patz et al. 2004, Peterson et al. 2009). In fact, recent studies have found that increased salinity was positively related to ONGD (Olmstead et al. 2013, Walters et al. 2019). Consequently, this increase could significantly affect ion regulation for many freshwater organisms, potentially resulting in the decline of many salinity-intolerant species (Kefford 2019).

Food availability was related to LUC in three models, only being negatively related to macroinvertebrate prey availability. We expected algal availability to be positively associated with LUC, and that CBOM, FBOM, and SPOM availability would be negatively related to LUC due to reductions in riparian vegetative cover and allochthonous inputs, but instead these relationships were insignificant. We speculate that the lack of LUC effect on algal resources is related to the dominance of filamentous algae (i.e., *Dichotomosiphon* sp.) across all sites late in the growing season, when basal food resources were sampled. By August, even those sites in the less disturbed South Beaver drainage are overgrown with filamentous algae (R. H. Walker, *personal observations* 2014–2017), likely overpowering any relationship that might arise between algal availability and LUC in this system.

Substrate heterogeneity was unrelated to increased LUC in our study. We predicted that

substrate heterogeneity would be negatively related to LUC due to increased soil exposure and erosion on the landscape, resulting in augmented sediment deposition in streams (Waters 1995, Moore and Palmer 2005), but our findings do not support this. We propose two explanations for this result. The first being, many of the study sites downstream of heavier ONGD had sections with deep, fine sediments that covered coarse substrates and were interspersed with sections of exposed coarse substrates. And this relationship seems to mimic our headwater sites, which are influenced more by current and historic beaver activity. Overall, beavers are beneficial to many streams and wetlands (Rosenfeld et al. 2000, White and Rahel 2008), but their activities slow stream flows and increase the buildup of fine sediments in localized areas (Rosell et al. 2005), often resulting in a patchy mosaic of fine sediments and coarse substrates that can mirror downstream LUC effects. This is further supported by low substrate heterogeneity values and high percentage of coarse substrates across all sites. Another potential reason for the lack of LUC–habitat relationship in the models could be similar cattle grazing across our sites. While no data are available for historic grazing practices, all sites are currently within the same grazing allotment and receive a relatively equal number of cattle each year, which are progressed upstream in a seasonal manner to follow vegetative forage.

The effects of LUC were indirectly mediated through the mechanistic pathways in five instances. We found that macroinvertebrate predator, *O. clarki,* and *C. bairdii* densities were indirectly affected by LUC through changes in food availability, increasing at sites with more macroinvertebrate prey. The remaining indirect effects of LUC were mediated through water quality (i.e., salinity), but these relationships were not always in the anticipated direction. For example, the mechanistic pathway driving changes in water quality was mostly negative, as expected, but not for collector–gatherer and scraper densities. Instead, collector–gatherer and scraper densities were positively related to LUC through an indirect increase in salinity. Upon further investigation of individual taxa, we found that this positive relationship for scrapers was mostly explained by greater densities of riffle

beetles (Coleoptera: Elmidae) at sites with greater salinities. Coleopterans are frequently found to tolerate wide salinity ranges (Akünal and Aslan 2017), with Elimdae being one of the most widely distributed families (Pérez-Bilbao et al. 2014). It is hypothesized that this resulted in greater physiological tolerances to increased salinity for Elimdae and reduced competitive and predatory interactions via chemical refuge (Arribas et al. 2019).

Mechanistic pathways

Substrate heterogeneity and water quality had variable effects on food availability. In all macroinvertebrate assemblage SEMs, food availability (i.e., food PCA-1) was negatively associated with substrate heterogeneity (i.e., habitat PCA-1) and positivity associated with salinity. In the collector–filterer and collector–gatherer models, SPOM and FBOM availability were positively related to increased salinity. We also found that substrate heterogeneity was negatively related to algal and FBOM availability, suggesting reduced food availability at sites with a combination of coarser substrates and fewer depositional habitats. These relationships are not surprising, in that OM and fine sediments accumulate in stream habitats that are deeper and experience less scour (Bilby 1981, Frissell et al. 1986), which often corresponds with increased ion concentrations downstream—unless streams or groundwater with drastically different ion concentrations enter (Ilg et al. 2001, Lods-Crozet et al. 2001).

The physical environment is frequently viewed as one of the most important factors regulating species' responses in many ecosystems (Chapman 1966, Poff and Ward 1990, Tews et al. 2004), but our results did not support this paradigm. Our substrate heterogeneity index was an important mechanistic pathway for only *C. bairdii* and %EPT species, which are generally considered habitat specialists. It is especially interesting that other benthic macroinvertebrate groups were not related to habitat complexity, as the filling of interstitial spaces and loss of coarse substrates are frequently linked to declines in diversity (Benoy et al. 2012, Burdon et al. 2013). We offer four explanations that could help clarify the limited habitat relationships in our study. First, while our macroinvertebrate sampling design

specifically targeted riffle and run habitats within a narrow range of depths (10–21 cm) to reduce potential microhabitat differences, not targeting the same habitat type may have unintentionally introduced random noise to the data. The second explanation could be related to our habitat sampling framework, as mentioned above—where a site-scale habitat metric may not be the best predictor of our patch-scale macroinvertebrate assemblages (Larsen et al. 2009). But the habitat sampled for benthic macroinvertebrates tended to be the dominant habitat within a given site; therefore, we expected habitat to have a greater influence in our models. The third explanation could be that the variation in substrate heterogeneity across our sites may have been too small to be reflected in the fish and macroinvertebrate responses. Finally, our substrate heterogeneity index (i.e., habitat PCA-1) may not be the most relevant habitat metric for every species. For example, we focused attention on substrate heterogeneity, fine sediments, and coarse substrates, which represent the quality and availability of spawning and feeding habitat for many aquatic species. But other habitat metrics such as structural cover (e.g., wood, overhanging vegetation, undercut banks; Hughes et al. 2010), the availability of different microhabitats within each site (Robson and Chester 1999), or stream flows (Poff et al. 1997) could be more important.

SEMs indicated that differences in food availability and water quality were often better predictors of species' responses in our system than habitat complexity. These results generally agree with previous studies which found that food availability, water quality, and biotic interactions are better predictors of population abundance and density, while the physical environment is a better predictor of species' distributions across the landscape (Anderson 1985, Orth 1987). For example, Wilzbach (1985) found that *O. clarki* densities were greatest where prey availability was highest because of reduced emigration rates, regardless of habitat complexity. More importantly, these findings also suggest that it is necessary to simultaneously consider multiple mechanistic pathways when evaluating drivers of ecological change.

Increased LUC associated with ONGD and other anthropogenic activities has significantly altered the mechanistic pathways regulating ecological responses. But the consequences of those alterations are ultimately contingent on several other interacting factors such as specific characteristics of the stressor(s) (i.e., type, intensity, duration, and timing; Lake 2000, Miller et al. 2011), as well as the species' degree of habitat and dietary specialization (Gray et al. 2007, Devictor et al. 2008) and sensitivity to pollution (Posthuma et al. 2001). And there is sufficient evidence showing that sensitive, specialist species from many taxonomic groups are disappearing at an alarming rate due to LUC (Julliard et al. 2004, Munday 2004, Goulson et al. 2005). We found several mechanistic pathways that could represent species' specialization on food and habitat, and sensitivity to pollution. For example, densities of *O. clarki*, a species of conservation concern (Hirsch et al. 2013), were driven by a combination of water quality and food availability, suggesting they are intolerant to water quality changes and specialized in feeding on benthic macroinvertebrates in this system. Densities of *C. platyrhynchus* were driven by food availability, reflecting their specialization on algal food resources, which has been found in other systems (Dauwalter and Rahel 2008, Schultz et al. 2016). In addition, *C. bairdii* densities were associated with substrate heterogeneity, specializing in habitats with coarser substrates and fewer fine sediments. Thus, using this approach to help identify important pathways and the relative strength of those pathways for sensitive, specialist species would be fruitful for conservation efforts.

Conclusions

Ecological systems (e.g., populations, communities, and ecosystems) are inherently complex, requiring a multifaceted approach to evaluate the diverse links and pathways connecting all components within a given system. SEMs can be a useful statistical approach for understanding ecological systems because they allow for simultaneous hypothesis testing and compare the relative importance of different mechanistic pathways within a given model. We used SEMs to evaluate the effect of LUC associated with ONGD on multiple mechanistic pathways regulating freshwater fish populations and macroinvertebrate

assemblages. Similarly, resource managers and ecologists can use SEMs in any system to gain a better understanding of the underlying mechanisms driving ecological responses across gradients of environmental degradation (Grace 2006, Burdon et al. 2013). Therefore, this approach can provide guidelines for when management actions should be applied to mitigate negative effects of increased LUC in the future.

With the myriad of multiple anthropogenic stressors that can interact on the landscape, resource managers are challenged with understanding the causes and consequences of environmental degradation (Craig et al. 2017). To identify the best management practices necessary for reducing effects of environmental degradation due to anthropogenic LUC, it is critical to understand both the patterns and mechanisms underlying ecological responses. Although the important mechanistic pathway driving responses in our study was highly variable, our results provide general insight into some management practices that could be advantageous. For example, we found that changes to water quality and food availability were important mechanisms regulating *O. clarki* populations, whereas water quality and substrate heterogeneity were important for *C. bairdii* populations. Thus, if managers are interested in sustaining fish populations in streams disturbed by LUC, management actions that enhance water quality (e.g., reduce leaks, spills, and intentional releases) and increase macroinvertebrate prey availability (e.g., increased riparian cover and adequate erosion control) should positively influence *O. clarki* populations, while changes to water quality and available coarse substrates would influence *C. bairdii* populations.

ACKNOWLEDGMENTS

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DATA AVAILABILITY

Data are available from the ScienceBase Repository at https://doi.org/10.5066/p96seka2

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2907/full