

Anthropogenic land-use change intensifies the effect of low flows on stream fishes

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Abstract

1. As ecosystems experience simultaneous disturbances, it is critical to understand how multiple stressors interact to affect ecological change. Land-use change and extreme flow events are two important stressors that could interact to affect fish populations.
2. We evaluated the individual and interactive effects of discharge and land-use change associated with oil and natural gas development on populations of two stream fishes over a 7-year period. We used repeated-state (i.e. abundance trends) and rate (i.e. colonization and persistence) responses to advance our understanding of flow-ecology relationships in a multiple-stressor framework.
3. Overall, fish abundance, colonization and persistence declined as discharge decreased. The effect of land-use change associated with oil and natural gas development differed between species, with the abundance of Mottled Sculpin declining and Mountain Sucker increasing as land-use change increased. We found both synergistic and antagonistic interactions between discharge and land-use change. Land-use change intensified the effect of low flows for Mottled Sculpin and lead to greater variability in responses to flow for Mountain Sucker. These differences between species' responses are likely due to differences in their physiological tolerances and behavioural adaptations to disturbance.
4. *Synthesis and applications.* Our research provides empirical evidence for the complex interactions that can arise between discharge and anthropogenic land-use change. Management efforts to reduce inputs of sediments and chemical contaminants associated with land-use change (e.g. silt fences, vegetative buffers) and promote quality refuge habitats (i.e. in-stream habitat restoration) could help mitigate the negative effects of low-flow extremes on stream fishes. Further development of flow-ecology relationships in a multiple-stressor framework will help guide management of stream fishes, and provide a better understanding of the mechanisms underlying responses of different species.

KEYWORDS

colonization, multiple stressors, natural flow regime, oil and natural gas development, persistence, rate responses, repeated-state responses, stream fishes

1 | INTRODUCTION

The potential for multiple stressors to occur simultaneously emphasizes the importance of quantifying how stressors interact to affect ecological change (Craig et al., 2017; Jackson, Loewen, Vinebrooke, & Chimimba, 2016). Many ecosystems are affected by multiple stressors that can interact in complex ways (Matthaei, Piggott, & Townsend, 2010; Townsend, Uhlmann, & Matthaei, 2008). Yet comparatively few studies have evaluated the interactive effects of multiple stressors in freshwater ecosystems, especially for fishes (Matthaei & Lange, 2016).

Primary threats to freshwater ecosystems include increased anthropogenic disturbance (Allan, 2004; Vörösmarty et al., 2010) and altered flow regimes (Barnett et al., 2008; Ficke, Myrick, & Hansen, 2007). Oil and natural gas development (ONGD) is an emergent anthropogenic threat that has gained considerable attention because of its rapid expansion and associated land-use change (LUC; Entrekin, Evans-White, Johnson, & Hagenbuch, 2011; Olmstead, Muehlenbachs, Shih, Chu, & Krupnick, 2013). Effects of LUC associated with ONGD include increased sedimentation, nutrient loading and loss of riparian vegetation, consequently reducing habitat and water quality (Entrekin et al., 2011). Nevertheless, our understanding of the ecological consequences of ONGD is limited (Johnson et al., 2015; Stearman, Adams, & Adams, 2015; Walters, Girard, Walker, Farag, & Alvarez, 2019).

Climate change and anthropogenic practices have modified the natural flow regime (hereafter discharge) of streams in many regions (Poff et al., 1997), producing stressful flow events that can have deleterious effects on lotic organism (Lake, 2003; Steward, Von Schiller, Tockner, Marshall, & Bunn, 2012). For example reduced winter snowpack, increased winter rainfall and earlier spring runoff are expected to increase the frequency of summer low-flow events

in snowmelt-dominated streams (Poff, Brinson, & Day, 2002). Water extraction for consumptive uses have also increased low-flow conditions in many streams (Lytle & Poff, 2004). Increased frequency and magnitude of low-flow events will likely lead to declines in the distribution, local abundance and vital rates of lotic fishes whose life histories are closely linked with stream flows (Falke, Bailey, Fausch, & Bestgen, 2012; Radinger et al., 2016; Wheeler, Wenger, & Freeman, 2017).

Flow-ecology relationships are often context dependent (Walters, 2016; Wheeler et al., 2018). While the standalone effects of anthropogenic LUC (Dudgeon et al., 2006) and extreme flow events (Lake, 2000, 2003) are well documented, their interactive effects have received limited consideration (but see Lange, Townsend, Gabrielson, Chanut, & Matthaei, 2013). For instance low flows and LUC are both expected to negatively affect fishes through decreased habitat quality and availability, but their combined effect could be equal to, greater, or less than the summed effect of the individual stressors (Figure 1). Synergistic interactions would emerge if the effect of low flows were intensified by increased LUC, as might be the case if LUC decreases the availability of low-flow refuge habitats. Alternatively, antagonistic interactions could arise if the effect of low flows counteract increased LUC. This would occur if critical headwater refuge habitats contract during low-flow periods and force the downstream dispersal of fish to 'degraded' refuge habitats closer to ONGD. In addition, the response is likely to be species dependent, where species with limited dispersal abilities and lower tolerances to changes in water and habitat quality are expected to exhibit stronger reactions to low flows and LUC as compared to more tolerant, mobile species (Lange, Bruder, Matthaei, Brodersen, & Paterson, 2018).

Here, we evaluated the individual and interactive effects of increased LUC and discharge on populations of two stream fishes with

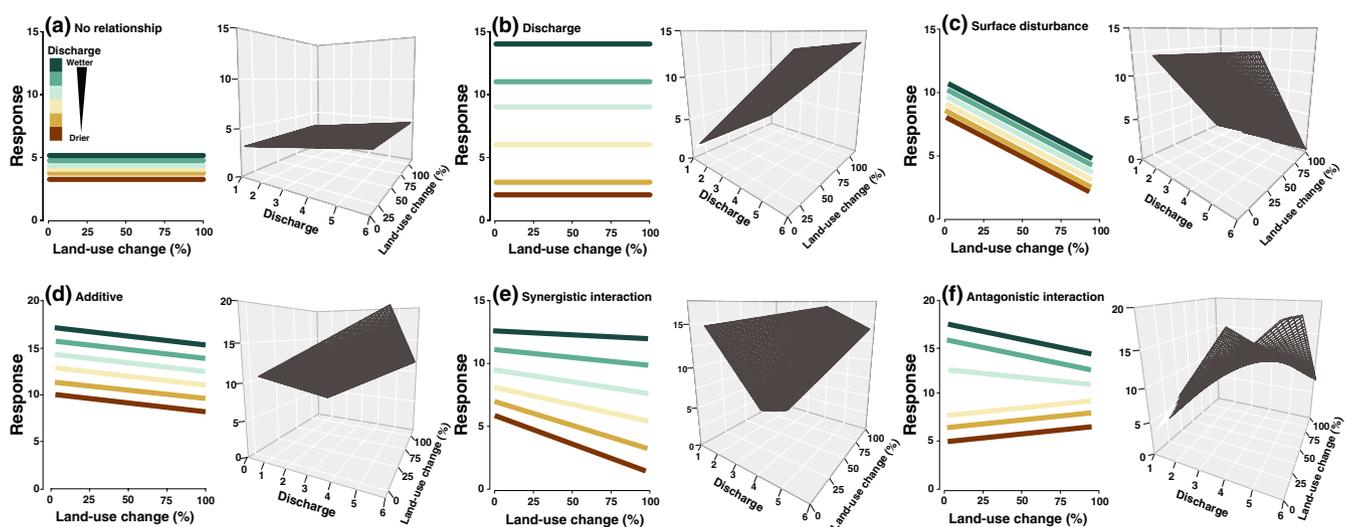


FIGURE 1 Simulated linear and three-dimensional response surfaces predicting the individual and interactive relationships that could arise between discharge and percent land-use change (%LUC). Slopes and intercepts varied across the stressor gradients depending on the interaction type. Lines in each linear plot reflect differences in annual discharge across the %LUC gradient. See methods section for simulation details

different dispersal abilities and tolerances to disturbance: Mottled Sculpin (*Cottus bairdii*) and Mountain Sucker (*Catostomus platyrhynchus*). To provide a mechanistic understanding of flow-ecology relationships for stream fishes, we combined multiple-year (7-year) repeated-state (i.e. trends in abundance) and rate responses (i.e. colonization and persistence rates; Wheeler et al., 2017) in a multiple-stressor framework. We predicted the individual effect of: (a) discharge would be positively related to fish abundance, colonization rates and persistence rates, and (b) LUC associated with ONGD would be negatively related to fish responses. We also predicted: (c) the interaction between discharge and LUC would be greatest at sites with more LUC, generally resulting in synergistic declines in fish responses and (d) that species with limited dispersal and lower tolerance to stressors (i.e. sculpin) would exhibit stronger responses compared to mobile, tolerant species (i.e. sucker). To our knowledge, no other studies have evaluated flow-ecology relationships for stream fishes in a multiple-stressor framework using repeated-state and rate responses.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study was conducted in two stream drainages, Dry Piney and South Beaver, which originate on the eastern flank of the Wyoming Range in the Upper Green River basin (Figure 2; 42°26.553N, 110°22.298W). The study area is within the LaBarge Oil and Gas Field. The South Beaver drainage to the north is less developed (0.71 ± 1.43 wells/km²), and is a tributary to South Piney Creek, flowing into the Green River in Big Piney, Wyoming. The Dry Piney drainage to the south flows through more ONGD (8.20 ± 6.17 wells/km²), entering the Green River approximately

14 kilometres south of Big Piney. Additional characterization of in-stream habitat and riparian conditions can be found in Girard and Walters (2018).

2.2 | Fish sampling

We randomly selected 64 sites of 100 m length along the National Hydrography Dataset from 150 evenly distributed sites every 500 m along the stream network (Figure 2). All sites were between 2,105 and 2,458 m in elevation. We collected age 1+ fish using single-pass (2012–2013) and multiple-pass (2014–2018) backpack electrofishing (Smith-Root LR-24, Vancouver, WA, USA) with two dip netters between June and August of each year. Block nets were used to ensure closed populations during sampling. All fish were identified to species, measured (standard length), and released to the original site. Other fish species included native Colorado River Cutthroat Trout (*Oncorhynchus clarki pleuriticus*) and Speckled Dace (*Rhinichthys osculus*), and non-native Fathead Minnow (*Pimephales promelas*), White Sucker (*Catostomus commersonii*) and Brook Trout (*Salvelinus fontinalis*), composing 11% of all fish collected. These species were not included in any statistical analyses because of low sample size and lack of model convergence.

2.3 | Hydrologic metrics

We deployed HOBO water-level loggers (Onset Computer Corporation, Bourne, Massachusetts, USA) at similar elevations on Black Canyon, Fogarty and South Beaver creeks to estimate continuous stream discharge (Figure 2). Loggers were set to record depth hourly from mid-April to mid-September in each year. We measured in situ discharge (m³/s) every 7–10 days using the cross-sectional method with a Marsh McBirney Flo-Mate™ velocity meter (Model 2000; Buchanan & Somers, 1969). We estimated continuous discharge by constructing a rating curve between measured discharge and logger depths. We compared average daily, maximum and cumulative discharge metrics between all water-level loggers and two nearby USGS gages (Fontenelle (#09210500) and Hams Fork creeks (#09223000)), which were approximately 45 and 35 km downstream respectively. Because discharge metrics were highly correlated ($r = .79-.99$; see Table S1 in Appendix S1), and we did not have site-specific discharge, we used average discharge from the Fontenelle Creek gage as our global hydrologic metric and extended available discharge to an entire 'water year' (Figure 3; e.g. 10-01-2011 to 09-30-2012 represented 2012 discharge). We ran mixed-effects and occupancy models using discharge for an entire water year and for the water year truncated on June 1st (i.e. beginning of fish sampling). These models provided similar results; therefore, we used discharge for a full water year in all models. We calculated average discharge for both the current and previous year (antecedent discharge), as fish responses may be driven by the current year's discharge or have a lagged response associated with antecedent discharge (Balcombe & Arthington, 2009). We also calculated average snow water

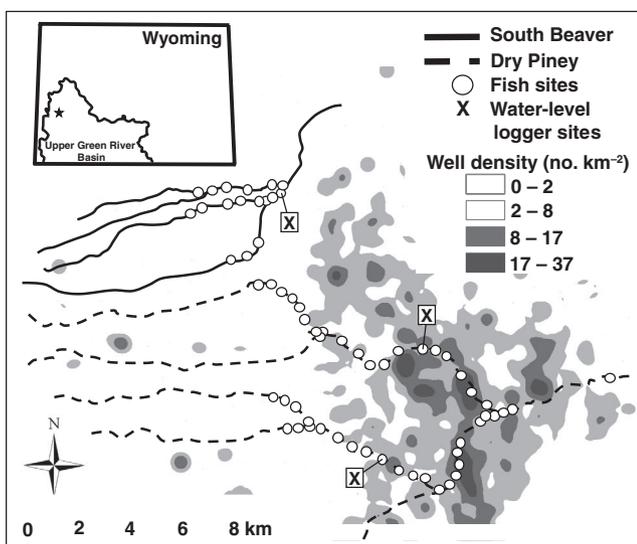


FIGURE 2 Map of study area in the Wyoming Range in the Upper Green River Basin depicting well density (no. per km²) with fish (64 sites) and water-level logger sites (3 sites) sample locations 2012–2018

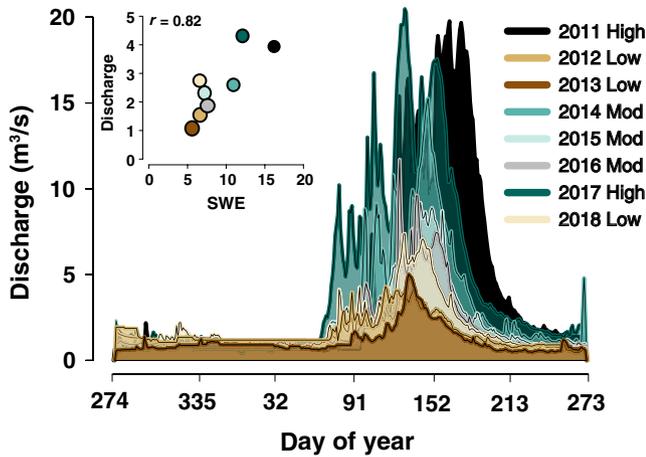


FIGURE 3 Average daily discharge from the Fontenelle Creek USGS gage for each water year (09,210,500; 35 km downstream). Average discharge (m^3/s) was highly correlated with average snow water equivalent (SWE) at Snyder Basin SNOTEL site at 2,457 metres (Station ID: 765). Colours correspond to a gradient of discharge with orange representing drier years and blue to black representing wetter years. High refers to years with higher than average discharge, moderate (mod) refers to years with average discharge and low refers to years with lower than average discharge. The Snyder Basin SNOTEL site is within the headwaters of the South Beaver drainage approximately 10 km northwest of our sites. Snow water equivalent was positively correlated with average discharge ($r = 0.82$, $n = 8$, $p = .01$)

equivalent from the Snyder Basin SNOTEL site (Station ID: 765; within headwaters of the South Beaver drainage, approximately 10 km northwest of our highest elevation sites) between October and May of each water year, which was then correlated with discharge to determine if variation in stream flows in this system are driven by snowfall dynamics.

2.4 | Land-use change

We calculated percent land-use change (%LUC) to represent our LUC stressor metric, which was the amount of surface area disturbed by all infrastructure associated with ONGD (i.e. roads, well pads, facilities and pipelines). We calculated %LUC at the site- and catchment-level to determine at which scale effects of ONGD on fish were greatest, by combining well location data with hand-digitized disturbed areas from GIS Basemap imagery within a 1 km buffer of each site and within each site's contributing catchment.

2.5 | Data analyses

2.5.1 | Simulations

We simulated fish responses that could arise from the individual and interactive effects of LUC and discharge (Figure 1). For each relationship, we simulated variation in the slopes and intercepts of response variables across the two stressor gradients, reflecting their individual and interactive effects. If fish responses were

unrelated to either stressor, the slopes and intercepts would not vary along either stressor gradient (Figure 1a). If the individual effect of one stressor had an overwhelming effect compared to the other stressor, the intercepts would vary significantly along that stressor gradient, whereas the slopes would not (Figure 1b and c). Additive relationships would emerge if the sum of the two stressors in isolation was equal to their combined effect, reflecting changes in the intercepts along both stressor gradients, but not the slopes (Figure 1d). Synergistic interactions would arise if the interaction between two stressors was greater than their summed effect (Crain, Kroeker, & Halpern, 2008; Jackson et al., 2016), indicated by a steeper slope at the extremes of both stressors. In the example, the effect of low flows is greatest at sites with greater LUC (Figure 1e). Antagonistic interactions occur if the effect of one stressor is weakened or reversed along the gradient of the other stressor (Crain et al., 2008; Jackson et al., 2016). For example the effects of lower flows are greatest at sites with the least LUC (i.e. slopes vary by flows; Figure 1f).

2.5.2 | Mixed-effects abundance modelling

We modelled the effects of discharge and %LUC on fish abundance using a mixed-effect modelling approach (R package GLMMADMB; Skaug, Fournier, Nielsen, Magnusson, & Bolker, 2016). For each species, we constructed 13 mixed-effect models to evaluate the individual effect of antecedent discharge, the current year's discharge, catchment %LUC and site %LUC, as well as their two-way interactions. We included a model for all two-way interactions between the two discharge and two LUC metrics for both additive and multiplicative relationships (see Table S2 for the entire candidate set of models). This allowed us to test the hypothesized individual and interactive effects of discharge and %LUC on fish abundance (Figure 1). In all mixed-effects models, we used fish abundance per 100 m from the first pass in each year as it was highly correlated with abundance estimates calculated from multiple-pass depletion between 2014 and 2018 ($r = .87$, $n = 256$, $p < .0001$; Carle & Strub, 1978; Seber & Le Cren, 1967).

We conducted initial data-exploration steps that included examination of response variable distributions, evaluation of the number of zeros (Zuur, Ieno, Walker, Saveliev, & Smith, 2009a) and collinearity between predictors (Zuur, Ieno, & Elphick, 2010). We visually inspected model assumptions using plots of fitted values against residuals, evaluated overdispersion and tested for autocovariance in model residuals. To account for spatial autocorrelation and repeated sampling at sites, we included a random effect of site nested within drainage in all models. We used a negative binomial distribution to account for overdispersion in discrete, positive data (Bolker, 2008), with zero-inflation to deal with more zeros than expected (Zuur et al., 2009a). We used log₁₀-transformed area (m^2) as an offset in all models to account for differences in sample area. We calculated sample area as the product of site length (100 m) and mean wetted width from 16 equidistant transects measured in August 2016. Average (\pm SD) wetted width

across sites was 2.01 ± 0.89 m in 2016, and changed by the same relative proportions at each site in each year (Walker, personal observations).

We used Akaike's Information Criterion corrected for small sample size in model selection (AIC_c), ΔAIC_c and AIC_c weights to compare the relative strength of each model (Burnham & Anderson, 2002; Mazerolle, 2015). To account for model uncertainty, we used model averaging to calculate parameter estimates and standard errors for all models with a cumulative AIC_c weight ≥ 0.90 . We considered parameters insignificant at an $\alpha > .05$ and if the predictor's confidence limits (CL) overlapped zero in the final model set (Nakagawa & Cuthill, 2007). We evaluated the importance of random effects, where variance values ≤ 0.1 indicated unimportant random effects (Zuur, Ieno, Walker, Saveliev, & Smith, 2009b). All mixed-effects analyses were performed in Program R (R Development Core Team, 2018).

2.5.3 | Occupancy modelling

We used multi-season occupancy models to separately estimate detection, occupancy, colonization and persistence rates for each species as a function of the defined covariates (MacKenzie et al., 2006). This approach combines state process and observation models that account for imperfect detection (MacKenzie et al., 2006; Wheeler et al., 2017). In these models, occupancy probability of a site was estimated based on the occupancy status of that site in the previous season $t-1$. Site-level persistence and colonization rates were estimated based on the probability that a species persists at a site or recolonized an unoccupied site between seasons respectively. All rates are based on probabilities and range from zero to one. Because multi-season occupancy models estimate rates between intervals, we limited discharge to the current water year to estimate changes between yearly sampling intervals. We only used site %LUC in occupancy models because of its overwhelming AIC_c support in the mixed-effects models (AIC_c weight ≥ 0.89 ; Table S2). We used a three-stage approach to estimate rate responses, where the top model(s) within the 90% confidence set from each stage was progressed to the next stage of model selection (see Table S3 for all candidate models). In stage one, occupancy, colonization and persistence were held constant (.), whereas competing detection models varied across the gradient of %LUC, discharge or were held constant. In stage two, colonization and persistence were

held constant, whereas occupancy varied with %LUC or was held constant. In stage three, we used the top stage two model(s) to construct a set of competing models that evaluated the individual and interactive effects of discharge and %LUC on colonization and persistence rates (Table S3). All occupancy models were conducted using program PRESENCE (<https://www.mbr-pwrc.usgs.gov/software/presence.html>).

3 | RESULTS

3.1 | Abiotic characteristics

Average discharge (m^3/s^1 ; $\pm SE$) was lowest in 2012 ($1.59 \pm 0.05 m^3/s$) and 2013 ($1.13 \pm 0.04 m^3/s$), moderate in 2014 ($2.62 \pm 0.17 m^3/s$), 2015 ($2.22 \pm 0.10 m^3/s$), 2016 ($1.91 \pm 0.11 m^3/s$) and 2018 ($2.73 \pm 0.24 m^3/s$), and greatest in 2011 ($3.94 \pm 0.28 m^3/s$), and 2017 ($4.34 \pm 0.26 m^3/s$; Figure 3). Discharge in 2012 and 2013 was approximately 1.6 and 2.3 times lower than the long-term average ($2.65 m^3/s$; 1990–2018), whereas values for 2011 and 2017 were 1.5 and 1.6 times higher respectively. Site-level %LUC averaged $13.36\% \pm 1.68$ across all 64 sites, ranging from 1% to 7% and 0.02% to 61.14% in the South Beaver and Dry Piney drainages respectively.

3.2 | Abundance models

Site-level %LUC was by far the best LUC metric explaining fish abundance for both species (Table S2). Sculpin abundance was driven by a synergistic interaction between antecedent discharge and % LUC ($\beta = .03$, 95%CL = 0.02 to 0.54, $z = 4.13$, $p < .0001$; Table 1; Table S2; Figure 4a), which had overwhelming support (AIC_c wt = 1.00). %LUC negatively affected sculpin abundance and the greatest effect of discharge occurred at sites with more %LUC (i.e. stronger declines in abundance in low flow years at sites with greater LUC). The random effect of drainage and site accounted for a significant amount of the variation in sculpin abundance ($\sigma_{\text{drainage}}^2 = 0.28$; $\sigma_{\text{site}}^2 = 5.98$), suggesting that individual sites and drainage accounted for substantial variability in sculpin abundance with greater abundances occurring at sites in the South Beaver drainage.

Based on model averaging, antecedent discharge was the only predictor that had a statistically significant effect on sucker abundance with higher abundances associated with greater discharge

TABLE 1 Overview of model results for Mottled Sculpin (*Cottus bairdii*) and Mountain Sucker (*Catostomus platyrhynchus*) abundance, colonization rates and persistence rates. + or – symbols represent the direction for each corresponding relationship. NS refers to no significant relationship

Species	Response metric	Discharge	Land-use change	Relationship
Mottled Sculpin	Abundance	+	–	Synergistic
	Colonization	+	+	Additive
	Persistence	+	–	Synergistic
Mountain Sucker	Abundance	+	NS	None
	Colonization	+ and –	+ and –	Antagonistic
	Persistence	NS	+	None

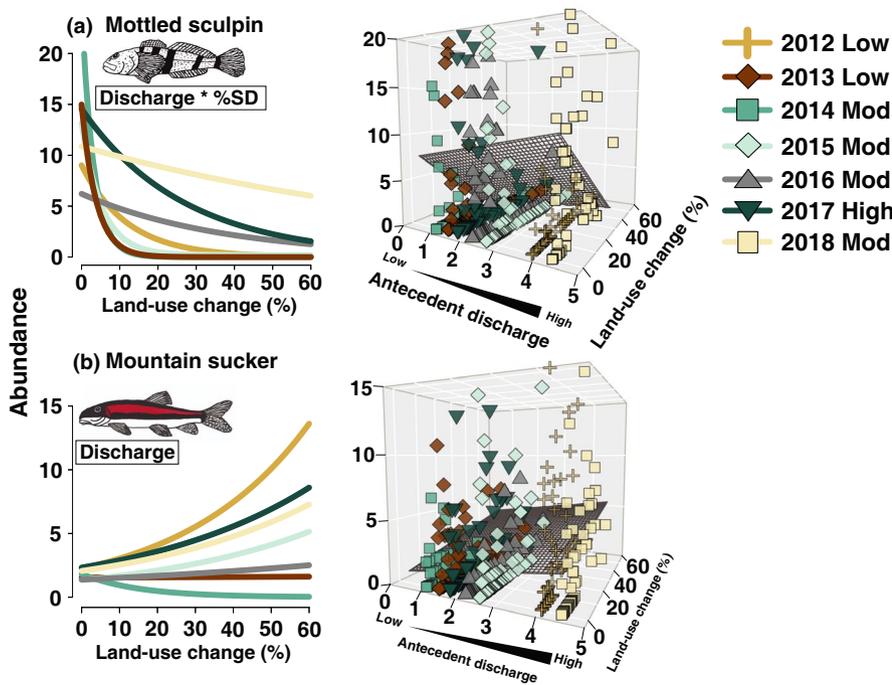


FIGURE 4 Representative relationships for the top mixed-effect model evaluating the individual and interactive effects of discharge and percent land-use change (%LUC) on Mottled Sculpin (*Cottus bairdii*) and Mountain Sucker (*Catostomus platyrhynchus*) abundance across 64 sites in the Wyoming Range between 2012 and 2018. Shown are the predicted linear responses and three-dimensional response surfaces with shapes and colours reflecting different years of discharge. High refers to years with higher than average discharge, moderate (mod) refers to years with average discharge and low refers to years with lower than average discharge. Sculpin abundance (a) was driven by a synergistic interaction between antecedent discharge and %LUC. Sucker (b) abundance was positively related to the antecedent discharge

($\beta = .05$, 95%CL = 0.001 to 0.23, $z = 1.93$, $p = .05$; Table 1; Table S2; Figure 4b). While included in the top model set, sucker abundance was not significantly related to an interaction between discharge and %LUC ($\beta = .10$, 95%CL = -0.01 to 0.02 , $z = 1.67$, $p = .10$). The random effect of drainage was unimportant ($\sigma^2_{\text{drainage}} < 0.01$), whereas site accounted for significant variation in sucker abundance ($\sigma^2_{\text{site}} = 1.27$).

TABLE 2 Colonization and persistence rates ($\pm SE$) from multiple-season occupancy modelling for Mottled Sculpin (*Cottus bairdii*) and Mountain Sucker (*Catostomus platyrhynchus*) at 64 sites in the Wyoming Range of the Green River Basin, Wyoming from 2012 to 2018

Response	Species	
	Mottled Sculpin	Mountain Sucker
Colonization		
2012–2013	0.00 \pm 0.00	0.19 \pm 0.24
2013–2014	0.07 \pm 0.05	0.26 \pm 0.14
2014–2015	0.15 \pm 0.07	0.26 \pm 0.17
2015–2016	0.05 \pm 0.04	0.38 \pm 0.08
2016–2017	0.17 \pm 0.07	0.28 \pm 0.34
2017–2018	0.41 \pm 0.10	0.46 \pm 0.05
Persistence		
2012–2013	0.57 \pm 0.12	0.69 \pm 0.03
2013–2014	1.00 \pm 0.00	0.69 \pm 0.03
2014–2015	0.68 \pm 0.06	0.69 \pm 0.03
2015–2016	0.92 \pm 0.09	0.69 \pm 0.03
2016–2017	0.97 \pm 0.04	0.69 \pm 0.03
2017–2018	1.00 \pm 0.00	0.69 \pm 0.03

This suggests that individual sites accounted for substantially more variability in sucker abundance than drainage.

3.3 | Occupancy models

Based on the top-ranked occupancy model (AIC_c wt = 0.94), sculpin detection averaged 0.79 ± 0.06 and varied by year, ranging from 0.64 ± 0.07 in 2014 to 0.92 ± 0.04 in 2016 (Table S3). Sculpin occupancy probability was 0.48 ± 0.07 and remained relatively constant over the study. Sculpin colonization was explained by a simple, additive multiple-stressor response between discharge and %LUC (Table 1). On average, colonization rates for sculpin were 0.14 ± 0.04 with little colonization occurring during the low-flow intervals between 2012 and 2014, and the greatest colonization occurring at all sites during the high-flow interval between 2017 and 2018 (Table 2; Figure 5a). Sculpin persistence was best explained by a synergistic interaction between discharge and %LUC with the negative effect of discharge being greatest at sites with greater LUC, as signified by steeper slopes at higher %LUC and during low-flow years (Table 1; Figure 5b). Sculpin persistence rates averaged 0.86 ± 0.05 across all sites and years with lower persistence occurring at sites with higher %LUC during the 2012 and 2013 low-flow interval and the first moderately wet interval between 2014 and 2015 (Table 2).

Sucker detection probability was 0.71 ± 0.06 and varied by year, ranging from 0.54 ± 0.07 in 2014 to 1.00 ± 0.00 in 2012 (Table S3). Sucker occupancy probability was 0.84 ± 0.13 over this study and was positively related to %LUC, ranging from 0.52 ± 0.01 to 1.00 ± 0.00 . Sucker colonization rates were driven by an antagonistic interaction between discharge and %LUC (Table 1; Figure 5c). In low flow years, colonization was negatively related to %LUC, but positively related to %LUC in high-flow years—indicating greater variability in colonization rates at greater %LUC (Figure 5c). Sucker colonization rates averaged

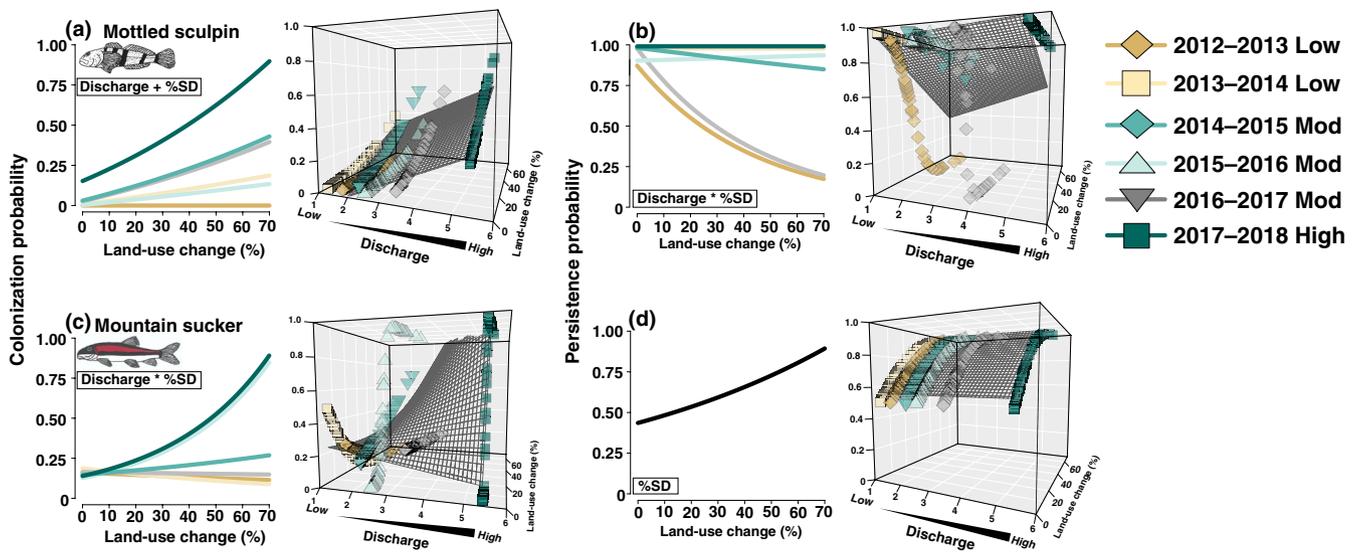


FIGURE 5 Estimated annual colonization (left) and persistence (right) rates from occupancy models for Mottled Sculpin (*Cottus bairdii*; top) and Mountain Sucker (*Catostomus platyrhynchus*; bottom) across 64 sites in the Wyoming Range between 2012 and 2018. Shown are linear model predictions across a gradient of percent land-use change (%LUC) with corresponding three-dimensional response surfaces. High refers to yearly intervals with higher than average discharge, moderate (Mod) refers to yearly intervals with average discharge, and low refers to yearly intervals with lower than average discharge. Sculpin colonization (a) was driven by a simple, additive multiple-stressor response. Sculpin persistence (b) was best described by a synergistic interaction, whereas sucker colonization (d) was described by an antagonistic interaction. Sucker persistence (c) was driven by the individual effect of %LUC, but not discharge

0.31 ± 0.17 , being lowest during the 2012 and 2013 low-flow interval and greatest during the 2017 and 2018 high-flow interval. Persistence rates (0.69 ± 0.03) were positively related to the individual effect of %LUC (Table 1; Figure 5d), being consistent at all sites across years (Table 2),

4 | DISCUSSION

We are aware of no other studies that have used repeated-state and rate responses to evaluate flow-ecology relationships for stream fishes in a multiple-stressor framework. We found consistent negative effects of low flows on fish abundance, colonization rates and persistence rates, which have been shown for many other fish species (Poff & Zimmerman, 2010; Walters, 2016). The effect of LUC varied by species. In addition, sites with the greatest LUC generally had the highest variation in effects, suggesting a strong effect of discharge at these sites. These results were mostly aligned with our predictions, though we were surprised that sculpin colonization and sucker persistence and colonization increased with LUC. Our findings provide empirical evidence for the complex interactions that can arise between discharge and anthropogenic LUC, emphasizing the need to establish flow-ecology relationships in a multiple-stressor framework for more species.

4.1 | Individual stressor responses

Discharge is a key factor regulating populations and assemblages of stream fishes (Bunn & Arthington, 2002; Poff et al., 1997). In our

study area, we found that discharge was strongly correlated with snowpack, with years of low snowpack corresponding to low-flow years. Low-flow years can be stressful for stream fishes; as surface waters contract, habitat availability, connectivity and quality correspondingly decrease, often resulting in lower abundances, colonization rates and persistence rates (Balcombe & Arthington, 2009; Falke et al., 2012; Walters, 2016). Overall, we found that abundance and vital rates of both fish species declined concomitantly with low flows (i.e. 2012 and 2013), supporting our first hypothesis. For fish abundance, the most important flow metric was antecedent discharge, with low-flow years resulting in declines in abundance and moderate- to high-flow years resulting in increases in abundance the following year. This suggests between year persistence and colonization dynamics are important mechanisms underlying responses in fish abundance to streamflow in our system. High-flow years can also be stressful (Lake, 2000), but the limited effect in our study suggests that high-flow events are not as important or did not exceed a stressful discharge threshold for these fish populations. Our study incorporated multiple low- and high-flow years over a 7-year period and included the 2011 event, which was equivalent to a 10-year flood, though fish sampling did not start until 2012. These results corroborate other stream fish studies showing that antecedent flows influence stream fishes (Balcombe & Arthington, 2009; Chang, Tsai, Wu, Chen, & Herricks, 2011), and emphasize the need for more long-term, flow-ecology research.

Humans have significantly modified the landscape with increased LUC frequently having deleterious effects on the ecological integrity of lotic ecosystems (Allan, 2004; Vörösmarty et al., 2010). We predicted LUC would have an overall negative effect on both

species. We found that sculpin abundance and persistence rates declined with increasing LUC, ostensibly due to decreased water quality and available refuge habitat, but sucker abundance, colonization rates and persistence rates generally increased with LUC in contrast to predictions. This result was somewhat surprising as other studies have demonstrated that sucker populations have declined across its range (Belica & Nibbelink, 2006; Patton, Rahel, & Hubert, 1998). But those studies found declining Mountain Sucker populations were mainly associated with factors such as introduced predatory salmonids (i.e. Brown Trout; *Salmo trutta*), stream intermittency and algal food availability (Dauwalter & Rahel, 2008; Schultz, Bertrand, & Graeb, 2016). Thus, suckers may tolerate some degree of LUC, especially if it is associated with increased algal availability, as was the case in our study system (Walker and Walters, 2019). The positive relationship between sucker populations and increased ONGD could also be because suckers favour small, low-gradient perennial streams (Dauwalter & Rahel, 2008) that correspond with where ONGD is situated (Entriken et al., 2011). Unexpectedly, sculpin colonization was positively related to LUC, reflecting lower occupancy and persistence rates at sites with greater LUC and successive recolonization—albeit at slower rates (4 years)—at these sites in higher flow years. Our findings suggest that colonization rates are intrinsically linked to dispersal dynamics for both species and poor persistence of sculpin in areas with comparably more LUC, where some nearby sites with less LUC still serve as source populations.

4.2 | Interactions between discharge and LUC

Disentangling multiple-stressor interactions can be challenging as the underlying mechanism driving the resultant interactions are not always straightforward (Piggott, Townsend, & Matthei, 2015). We predicted synergistic declines, and found that for sculpin populations, but interactions were antagonistic for sucker populations. For sculpin, the combination of low flows (e.g. 2012 and 2013) and increased LUC produced synergistic declines in abundance via reduced occupancy and persistence rates at sites with greater LUC, likely due to the lack of available refugia at more developed sites in low-flow years. This interaction supports the prediction that the effect of discharge is greatest at sites with the most LUC, suggesting increased LUC can exacerbate the effect of low flows. In contrast, sucker colonization rates were driven by an antagonistic interaction, where occupancy and colonization rates were more variable at sites with greater LUC, implying the effect of LUC varied with different flows. This relationship suggests that the effect of LUC is context dependent, reflecting greater variability in sucker populations with greater dispersal abilities in higher flows years compared to low flow years.

4.3 | Species comparison

Our focal study species differed in their response to each evaluated interaction between discharge and LUC, suggesting the underlying mechanisms are species dependent. This followed our predictions

and previous work demonstrating that species respond differentially to stressor interactions, presumably because species differ in their physiological tolerances and behavioural adaptations to stressors (Lange et al., 2018). We suspect that species differences in this study are due to limited dispersal abilities and lower tolerance thresholds of sculpin (Petty & Grossman, 2004; i.e., lower occupancy and persistence rates with greater LUC) compared to more mobile, tolerant species like sucker (i.e. greater colonization and persistence rates with more LUC).

4.4 | Management implications

Like other multiple-stressor studies, low flows were an important predictor driving population responses (Matthaei et al., 2010), negatively affecting fish abundance and vital rates of both species. In streams where anthropogenic modifications have altered flows, managers can influence stream-flow management (Poff & Schmidt, 2016), potentially mitigating negative effects of low-flow extremes, through reduced water extraction. In addition, mitigation efforts targeted at reversing the effects of development to in-stream habitat could reduce its interactive effect with discharge. For example the implementation of proper, best management practices (e.g. maintaining riparian buffer zones, reducing linear features to minimize overland flow, silt fences, vegetation replanting and in-stream restoration) could decrease inputs of sediments and contaminants and help maintain in-stream refugia. In doing so, the synergistic interactions observed for more sensitive, sedentary species, like sculpin may be diminished. These mitigation efforts would likely have similar, stabilizing effects on populations of more mobile species, like the sucker, as high-quality refuge habitats should promote resistance and/or resilience to low-flow extremes (Magoulick & Kobza, 2003).

While studies have found that catchment-level characteristics are generally better predictors of ecological change than site-level characteristics (Esselman et al., 2011; Wang, Seelbach, & Lyons, 2006), the effect of site-level LUC had overwhelming support in our models. This has been found in other studies (Wang et al., 2003, 2006), and suggests that site-level effects are generally more influential in relatively undisturbed catchments, where the relative importance of local-scale factors become overridden as catchment-scale disturbance increases. Our highest catchment-level LUC was 9%, potentially below a threshold where catchment-level LUC would strongly influence fish populations relative to site-level LUC (Dauwalter, 2013). In addition, the proximity of energy development and associated infrastructure to our study streams, increases the probability for a direct effect of environmental degradation on aquatic life (Entrekin et al., 2011). Thus, effects of future development could be reduced by maintaining larger buffer zones near headwater streams.

Knowledge of the underlying mechanisms that drive species' abundance and distributional responses (i.e. colonization and persistence rates) in a multiple-stressor framework can improve our understanding of fish population dynamics. Our results demonstrate the need for more research evaluating flow-ecology relationships

for different species over long time periods and under different environmental contexts. As hydrologic shifts associated with climate change and human alterations continue, a better understanding of flow-ecology relationships, especially where additional stressors may be present, will be crucial for the conservation of stream fishes. Resource managers frequently have access to large, spatial and/or temporal datasets that include species' abundance and presence/absence data. These data can be matched with various land-uses and in-stream characteristics to better predict flow-ecology relationships for different species. Our multiple-stressor, flow-ecology framework provides a useful approach for evaluating the potential mechanisms underlying species' responses, which can improve the management and conservation of stream fishes.

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AUTHORS' CONTRIBUTIONS

R.H.W. and A.W.W. developed the research idea. A.W.W. secured funding. R.H.W., C.E.G. S.L.A. collected and managed the data. R.H.W. analysed the data and wrote the first manuscript draft. All authors contributed to revisions.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.474qt46> (Walker, Girard, Alfrord, & Walters, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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