INTRODUCTION

Land use change is a disturbance known to strongly affect aquatic habitat and biological diversity (Allan, 2004; Harding, Benfield, Bolstad, Helfman & Jones, 1998). Aquatic ecosystems are influenced by land use change at both regional and local scales via direct and indirect alteration of natural processes (Allan, 2004; Poff et al., 1997; Sponseller, Benfield & Valett, 2001). Ecosystem response to agricultural land use has been well established and is linked to alteration of stream geomorphology, stream flow regime, sedimentation, water chemistry and biological communities (Burcher, Valett & Benfield, 2007; Burdon, McIntosh & Harding, 2013). Oil and natural gas (ONG) development is an increasingly important land use change for which effects, mechanistic pathways and species vulnerability are not as well understood (Smith, Snyder, Hitt, Young & Faulkner, 2012).

Global energy demand is predicted to increase by 37% by 2040, and approximately half of this worldwide demand is met by ONG (International Energy Agency, 2014). The United States has seen rapid recent growth in energy development, especially for natural gas (EIA 2015; Entrekin, Evans-White, Johnson & Hagenbuch, 2011). Natural resources are likely to be affected by this development due to habitat alteration and non-point source pollution. The effects of ONG development for terrestrial species such as wild ungulates, sage grouse, Centrocercus urophasianus (Bonaparte), and shrub-steppe passerines have been increasingly studied and are a common focus of environmental planning in the Intermountain West (Gilbert & Chalfoun, 2011; Holloran, Kaiser & Hubert, 2010; Sawyer, Kauffman & Nielson, 2009). Although aquatic ecosystems have always been of concern because of the potential for contamination of ground and surface water resources, there has been limited research on the effects of ONG development for freshwater fish.

Modelling studies in the Upper Green River Basin, Wyoming, have related the occurrence of native fish species to different land use variables but found ONG development explained only a
small proportion of fish assemblage variation (Dauwalter, 2013; Dauwalter, Wenger, Gelwicks & Fesenmyer, 2011). However, at that broad spatial scale, variability in landform and fish and vegetation communities may have obscured potential patterns. An empirical study in Arkansas streams documented reduced reproductive success of redfin darter, *Etheostoma whipplei* (Girard), in areas with higher ONG development, likely due to increased siltation from surface disturbance (Stearman, Adams & Adams, 2015). Other empirical studies in Arkansas streams found increased sediment and primary productivity in streams closest to well pads; this had implications for macroinvertebrate communities but effects interacted with hydrology (Austin et al., 2015; Johnson et al., 2015).

Despite the limited empirical research, it is predicted that fish will be affected by the hydrological, chemical and physical alterations that occur with ONG development (Davis, Bramblett & Zale, 2010; Davis, Bramblett, Zale & Endicott, 2009; Weltman-Fahs & Taylor, 2013). Water use is a particular concern in water-stressed regions (Nicot & Scanlon, 2012). Hydrocarbons, saline water produced during hydrocarbon extraction and lubricants used for drilling can contaminate surface and groundwater; spills of these liquids are stochastic and vary greatly in their effect (BLM et al. 1983; EOG 2012; EPA 2010). Disturbance of soils and vegetation (surface disturbance) as a result of roads, pipelines, well pads and processing facilities fragments habitat (Weller, Thomson, Morton & Aplet, 2002) and denudes vegetation, leading to soil erosion and increased stream sediment load (Entrekine et al., 2011; McBroom, Thomas & Zhang, 2012; Reid, Metikosh & Ade, 2004). An existing research gap is if and how surface disturbance affects riparian and stream habitat and, thus, fish populations (Entrekin, Austin, Evans-White & Haggard, 2018). This research begins to address this information gap by evaluating aquatic habitat conditions and fish presence and abundance across sites with varying ONG development intensities.

A field study was conducted that compared sites from adjacent streams in the LaBarge Oil and Gas Field in the Upper Green River Basin of Wyoming. At each site, fine-scale aquatic habitat and fish data were collected to examine effects of ONG development. The study objectives were to: (1) evaluate the relative importance of stream habitat variables in describing fish species distribution; and (2) compare stream habitat and fish species catch-per-unit-effort (CPUE) between sites with varying degrees of ONG-related disturbance. The results of this study provide management agencies with needed information to justify specific management actions to conserve aquatic ecosystems and fish populations alongside ever-expanding ONG development.

**FIGURE 1** Study area with oil and gas wells denoted as orange crosses. Aerial imagery basemap depicts proximity and planform of study streams. The yellow-bordered map inset shows road and well pad development and aeration lagoons at the confluence of Dry Piney and Fogarty creeks [Colour figure can be viewed at wileyonlinelibrary.com]
2 METHODS

2.1 Study area

The study area is located in the eastern slopes of the Wyoming Range in southwest Wyoming, USA. Site and landscape data were collected from three small stream drainages, the Dry Piney, Fogarty and South Beaver, which originate at Deadline and Riley Ridge and flow east towards the Green River (Figure 1). South Beaver Creek is a tributary to South Piney Creek, which meets the Green River at Big Piney, Wyoming. Dry Piney Creek flows directly into the Green River 14 km south of Big Piney. Fogarty Creek is the northern tributary to Dry Piney Creek. Four streams in the Dry Piney Drainage (Dry Piney, Beaver Dam, Black Canyon and North Black Canyon), five in the Fogarty Drainage (North and South Fogarty, North and South Pine Grove and Sawmill) and four in the South Beaver Drainage (North Beaver, South Beaver, Middle Beaver and Spring) were sampled. All streams flow west to east.

The study streams originate from small springs, approximately 2,450 m in elevation, well below the alpine zone. In the upper portions of the streams, north-facing slopes are predominantly montane conifer, and sagebrush, *Artemisia* spp., occur on south-facing aspects. Moving down in elevation, upland vegetation quickly shifts to sagebrush steppe ecotype. Willow, *Salix* spp., and sedge, *Cyperaceae* spp., are dominant riparian species, although alder, *Alnus* spp., rushes, and wetland grasses are also present. Aspen, *Populus tremuloides* Michx., is patchily distributed along the riparian areas with its presence decreasing in a downstream direction. The study area streams provide hydrological support to narrow ribbons of riparian plant communities that are surrounded by drought-tolerant upland plant species. The study streams gain discharge due to snowmelt in the early summer with some streams becoming intermittent in the late summer due to the hot, dry summers and the long distances they travel at low elevations without additional discharge from tributaries. Afternoon thunderstorms occur periodically throughout the summer but often do not contribute to increases in-stream flow; summer rain events that result in overbank flooding are rare and do not occur on an annual basis.

Oil and natural gas development density varies across the study area from stream catchments containing few ONG wells and limited infrastructure to highly developed areas with multiple phases of ONG development including processing facilities and long-term contaminant storage lagoons (Figures 1 and 2). Dry Piney and Fogarty drainages overlap the heart of the LaBarge Oil and Gas Field. Less development occurs in the South Beaver Drainage. ONG development has been occurring since the 1940s, and the area is currently being redeveloped to take advantage of new techniques such as hydraulic fracturing.

The Dry Piney and Fogarty drainages currently contain two species of fish: mottled sculpin, *Cottus bairdii* Girard, and mountain sucker, *Catostomus platyrhynchos* (Cope). Colorado River cutthroat trout, *Oncorhynchus clarkii pleuriticus* (Cope), are endemic to the study area, as has been documented by Wyoming Game and Fish Department sampling and rangewide distribution databases (Gelwicks, Gill, Kern & Keith, 2009; Kern, Keith & Gelwicks, 2006). There was some historical stocking of salmonids in the Dry Piney and Fogarty drainages; Colorado River cutthroat trout stocking ended in 2006, and brook trout, *Salvelinus fontinalis* (Mitchill), stocking ended at an unknown date prior to 2006 (Hilda Sexauer, Wyoming Game and Fish Department, personal communication). South Beaver Drainage has endemic, self-sustaining populations of Colorado River cutthroat trout, mottled sculpin, mountain sucker and speckled dace, *Rhinichthys osculus* (Girard). Speckled dace were not included in our analysis because they were found only at a few sites. Mountain sucker, mottled sculpin and Colorado River cutthroat trout are all native to the Green River Drainage and are often found sympatrically in mountain streams. Mottled sculpin and mountain sucker are common within their ranges (Dauwalter, 2013), while Colorado River cutthroat trout populations have been declining and are of conservation concern at the state and federal levels (Hirsch, Dare & Albeke, 2013).

2.2 Landscape variables

Stream elevation, slope, sinuosity, catchment area and water surface area were generated digitally in Arc GIS 10.1 (ESRI 2011). Elevation...
was extracted from a 10 m digital elevation model (DEM) at the downstream endpoint of each 100 m site. The 10 m DEM was used to generate slope rasters that were averaged along the line between the upstream and downstream point of sampling sites to generate site-specific percent slope. Sinuosity was calculated as the digitally measured straight-line distance from each site’s downstream and upstream endpoint divided by the total site length measured along the length of the thalweg.

Catchment area was calculated for each study site using the ArcGIS Watershed toolbox (ESRI 2011). The Fill (depth = 0) tool was used to eliminate sinks, which are areas that drain into themselves. Flow direction and accumulation rasters were created from the “filled” DEM. Study site point locations were snapped to the flow accumulation cell with the maximum value within the given radius, in this case, 10 m. This process results in a raster of all site locations from which the catchment area of a point is calculated by summing the cells from the flow accumulation raster that flow into it. This newly created raster was used with the Watershed tool to categorise a new raster that delineated the subcatchment boundary of each site. This sub-catchment boundary raster was converted to a polygon data set and visually checked for accuracy in ArcGIS. In the final step, sub-catchment polygons were merged so that each site included the full catchment above it. The final catchment boundary polygons were used to calculate catchment area (km²) per site.

To quantify water surface area, randomForest in Program R (R Core Team 2014) was used to model and classify habitat types from 2012 aerial imagery of the study area [National Agricultural Imagery Program (USDA) 2012; Hayes, Miller & Murphy, 2014]. The model used aspect, elevation, slope, distance to stream, texture and NAIP’s four colour bands to predict nine land cover classes, one of which was surface water. The area (m²) of surface water area within a 1 km² circular buffer of each site’s centroid in ArcGIS was quantified.

### 2.3 Oil and natural gas development variables

Well density, surface disturbance and stream fragment length were used as metrics of ONG development. ONG well data originated from the Wyoming Oil and Gas Conservation Commission GIS well layer (2013; http://wogccms.state.wy.us/flexviewers/unitmap/). All wells were included in the analysis. The catchment boundary polygon was spatially joined with the Wyoming Oil and Gas Conservation Commission well locations to calculate the number of wells per catchment area by site (wells/km²). Local well density was also calculated as the number of wells with a 1 km² circular buffer centred on the sampling site.

A U.S. Geological Survey well pad scar data layer (Garman & McBeth, 2014) and hand digitisation from 2013 ArcGIS Basemap imagery were used to quantify surface disturbance for each infrastructure type: facilities, wells, roads and pipelines. Facilities were hand-digitised and included processing facilities, containment ponds and storage yards. Facility polygons were added to the well pad scar data. Linear disturbance was hand-digitised using polylines and was buffered by the average disturbance width of roads and pipelines in the study area. Improved roads (roads created by grading) were buffered on each side by 5 m, two-track roads (roads created by vehicle wear) by 1 m and pipelines by 7.5 m. The hand-digitised surface disturbance layers were combined, and the % surface disturbance within the catchment of each sampling site was calculated to create a comprehensive metric of the extent of ONG development. In addition, local % surface disturbance was calculated as the % surface disturbance within a 1 km² circular buffer centred on the sampling site.

Stream fragment length was measured as the distance between hand-digitised culverts along all streams in the study area. Each fish sampling site was assigned the fragment length of the stream section on which it occurred.

### 2.4 Fish sampling

Fish sampling occurred along headwater tributaries and included streams of all sizes present as long as perennial surface water persisted at some location in that stream throughout the year. For all tributaries, potential sampling sites (100 m reach) were distributed along the National Hydrography Dataset (NHD) linear stream feature every 500 m, beginning 50 m upstream from the downstream confluence. Prior to fieldwork, sampling sites were picked randomly from these evenly distributed sites. In 2012, 73 sites for fish and aquatic habitat were sampled including sites on all study streams. In 2013, 72 sites were revisited (one site that was located in a dry wash was dropped), and 16 additional sites were added to increase the extent of sampling. These additional sampling sites were randomly chosen from remaining evenly distributed sites but only from streams that had a high probability of supporting fish populations based on results from the 2012 surveys. Sampling occurred from June 6 through July 17 in 2012, and June 6 through July 18 in 2013. Single-pass electric fishing methods (Smith-Root LR-24 backpack electric fishing unit, Smith-Root, Vancouver, WA, USA) were used with a two-person sampling crew moving in an upstream direction (Reynolds & Kolz, 2012). When sampling was complete, all fish were identified to species and released into slow-moving water. Single-pass electric fishing without block nets was used because of the small stream sizes. CPUE (fish/100 m) was calculated as the number of fish caught per pass.

The wilcoxon.test() function from Mass package in R (Ripley et al., 2017) was used to complete a paired Wilcoxon Signed-Rank Test to compare potential differences in 2012 and 2013 site CPUE. The Wilcoxon Signed-Rank Test was chosen because CPUE data were skewed towards zero values. Total site fish abundance for 2012 and 2013 was used in this analysis and was calculated by summing the CPUE for all species found at each site for that year.

### 2.5 Stream habitat characteristics

Most site-specific stream habitat data were collected based upon Bureau of Land Management field measurement protocols (Multiple Indicators Monitoring, Proper Function Condition; Prichard, 1993; Burton, Smith & Cowley, 2011). These predominantly structural
measurements were conducted once per site (100 m stream reach) in late summer of 2012 or 2013 because they tend to change slowly over time and not necessarily on a year-to-year basis. Stream morphology measurements (stream incision, width, depth and riparian width) were calculated at each sampling site as the average of measurements taken at 0, 25, 50, 75 and 100 m along the stream reach (Rosgen, 1994). Stream incision was measured from the stream bed to the height at which the stream would overtop its banks and flow onto its floodplain. Maximum water depth was recorded at each sampling site. The proportions of pool, riffle and run habitats, as well as the proportional distributions of fine, sand, gravel and cobble substrates (Wolman, 1954), was qualitatively assessed using a visual examination at each sampling site. Beaver, Castor canadensis Kuhl, dams were counted for each sampling site; most dams were inactive, but five had evidence of freshly cropped vegetation.

Streambank vegetation and in-stream cover were assessed at every metre along each sampling site. Streambank vegetation can be assessed relatively easily and is measured because it is strongly indicative of ecological, hydrological and geomorphological function. To quantify habitat variables, a metre tape was stretched along the stream edge for the length of the site (100 m). At every metre mark, the predominant streambank vegetation type within a 30 cm square centred on the metre mark and against the active stream channel edge was characterised into five categories: bare soil, upland nonwoody vegetation, riparian nonwoody vegetation, upland woody vegetation or riparian woody vegetation. Cover was assessed at each metre mark, with the presence or absence being recorded for each stream cover type if it occurred across the stream width at that metre mark and was large enough to be used by an adult fish. Percent cover was calculated as the percentage of presences recorded for potential cover types: shrub cover (woody vegetation), in-stream woody debris, undercut banks or other. Aquatic vegetation coverage was quantified at each sampling site using a qualitative visual assessment of proportional coverage of the stream bed.

Surface water parameters were measured at all sites at the time of fish sampling and again in late summer each year. At each sampling site, temperature, specific conductivity and dissolved oxygen were measured with a YSI Professional Plus Multiparameter Instrument (YSI Incorporated, Yellow Springs, OH, USA). Discharge was calculated by multiplying velocity (Marsh McBirney Flo-Mate, Marsh McBirney Inc, Frederick, MD, USA), depth and width for three equally spaced intervals across the measured stream cross section. This rapid measure of discharge was for intersite comparisons as well as to document seasonal changes at each site. For comparisons between sites, the maximum (conductivity, temperature) and minimum (discharge, dissolved oxygen percent saturation) of the measurements taken across years at that site were used.

2.6 | Fish–habitat relationships

Pearson correlation coefficients between catchment % surface disturbance, CPUE of each fish species, and all other landscape, ONG development and habitat variables were used to assess significant relationships between ONG disturbance and fish and stream habitat characteristics. Given the strong correlation between catchment area and catchment % surface disturbance, partial correlation coefficients were also calculated that account for catchment area. Catchment % surface disturbance was used as the ONG development variable for these comparisons, but both local and catchment level metrics of well density and % surface disturbance were included as ONG development variables in the other fish–habitat relationship analyses.

The randomForest package in R (Breiman, Cutler, Liaw & Wiener, 2012; Liaw & Wiener, 2002) was used to model presence and absence of each fish species as it relates to site landscape, ONG development and habitat variables (Table 1). A classification tree approach was used in which many classification trees were created based on a bootstrap of the data, and variation in fish species presence/absence was partitioned based on predictor variables. A fish species was considered to be present at a sampling site if it was found in 2012 or 2013 sampling and absent if it was not found in either year. The Colorado River cutthroat trout model only included landscape, ONG development and habitat variables from the South Beaver Drainage. This was performed to reduce potential drainage level effects that could be introduced in the model because this species was only found in the South Beaver Drainage. Four sites with missing values for some habitat variables were removed from the analysis. Random Forest models were run with 1,001 trees. Random Forest models can handle large numbers of variables but including a large number of variables can make ecological interpretation difficult and decrease explanatory power, so variable selection was performed as described in Murphy, Evans and Storfer (2010). The variables selection code calculates a model improvement ratio for each variable and sets a threshold for number of variables retained. The variable set that minimises model mean squared error and maximises percentage of variation explained was retained as the top model. Top models were evaluated using out-of-bag error, a comparison of model predictions to species occurrence from site data. Relative importance plots were used to quantify and rank the relative ability of retained variables to predict the occurrence of each fish species. For the selected variables for each species, probability partial plots that plot the variable range against the probability of fish species occurrence were generated.

Non-metric multi-dimensional scaling (NMDS) was used to visualise differences in aquatic habitat conditions among sites. All landscape, ONG development and habitat variables were retained, but sites with missing values were removed. NMDS analysis was performed with the "vegan" package (Oksanen et al., 2015). Bray–Curtis dissimilarity indices were used, and data were Wisconsin double standardised and square root transformed. Two-dimensional and three-dimensional solutions were explored. The envfit() function was used to fit vectors corresponding to fish species' CPUE, averaged between years, onto the ordination. The ordisurf() function, which creates a smooth surface estimated with a general additive model, was used to fit contours corresponding to catchment % surface disturbance onto the ordination.
<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean (range)</th>
<th>Correlation with catchment % surface disturbance</th>
<th>Partial correlation with catchment % surface disturbance controlling for catchment area</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Landscape</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Catchment area (km²)</td>
<td>31.4 (1.5–174.8)</td>
<td>0.67</td>
<td></td>
</tr>
<tr>
<td>Elevation at the downstream point (m)</td>
<td>2,333 (2,106–2,503)</td>
<td>-0.71</td>
<td>-0.37</td>
</tr>
<tr>
<td>Average % slope</td>
<td>7.9 (0.3–42.0)</td>
<td>-0.38</td>
<td>-0.12</td>
</tr>
<tr>
<td><strong>Oil and gas development</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Catchment % surface disturbance</td>
<td>4.3 (0.4–9.2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Catchment well density (wells/km²)</td>
<td>0.9 (0–2.8)</td>
<td>0.87</td>
<td>0.75</td>
</tr>
<tr>
<td>Stream fragment length (m)</td>
<td>4,705 (442–11,882)</td>
<td>0.23</td>
<td>0.26</td>
</tr>
<tr>
<td>Local (1 km² area) well density (wells/km²)</td>
<td>5.7 (0-23.1)</td>
<td>0.58</td>
<td>0.30</td>
</tr>
<tr>
<td>Local (1 km² area) % surface disturbance</td>
<td>11.7 (0.2–61.1)</td>
<td>0.69</td>
<td>0.35</td>
</tr>
<tr>
<td><strong>Catch-per-unit-effort</strong></td>
<td></td>
<td></td>
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<tr>
<td>Colorado River cutthroat trout a</td>
<td>0.6 (0–13.5)</td>
<td>0.12</td>
<td>0.08</td>
</tr>
<tr>
<td>Mottled sculpin</td>
<td>2.6 (0–37.5)</td>
<td>-0.20</td>
<td>-0.12</td>
</tr>
<tr>
<td>Mountain sucker</td>
<td>1.9 (0–11)</td>
<td>0.04</td>
<td>-0.30</td>
</tr>
<tr>
<td><strong>Stream morphology</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Riparian width (m)</td>
<td>30.9 (0–234)</td>
<td>-0.13</td>
<td>-0.01</td>
</tr>
<tr>
<td>Sinuosity</td>
<td>0.70 (0.38–0.97)</td>
<td>-0.02</td>
<td>0.09</td>
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<tr>
<td>Average width (cm)</td>
<td>84.0 (21.2–245.0)</td>
<td>-0.08</td>
<td>-0.22</td>
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<tr>
<td>Average depth (cm)</td>
<td>11.1 (3.0–34.4)</td>
<td>-0.20</td>
<td>-0.29</td>
</tr>
<tr>
<td>Width-to-depth ratio</td>
<td>8.1 (1.7–23.4)</td>
<td>0.18</td>
<td>0.13</td>
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<tr>
<td>Entrenchment ratio</td>
<td>32.3 (0.3–541.5)</td>
<td>-0.13</td>
<td>-0.08</td>
</tr>
<tr>
<td>Maximum depth (cm)</td>
<td>25.1 (21.2–121.9)</td>
<td>-0.07</td>
<td>-0.12</td>
</tr>
<tr>
<td>Area of standing water (m²)</td>
<td>226.4 (0–3,300.5)</td>
<td>-0.29</td>
<td>-0.21</td>
</tr>
<tr>
<td>Average incision (cm)</td>
<td>86.5 (0–246.2)</td>
<td>0.55</td>
<td>0.15</td>
</tr>
<tr>
<td>% Pool habitat</td>
<td>14.9 (0–75)</td>
<td>-0.26</td>
<td>-0.18</td>
</tr>
<tr>
<td>% Riffle habitat</td>
<td>27.1 (0–80)</td>
<td>-0.36</td>
<td>-0.26</td>
</tr>
<tr>
<td>% Run habitat</td>
<td>58.0 (10–100)</td>
<td>0.43</td>
<td>0.30</td>
</tr>
<tr>
<td>Number of beaver dams</td>
<td>1.1 (0–8)</td>
<td>-0.30</td>
<td>-0.07</td>
</tr>
<tr>
<td><strong>Substrate</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Cobble substrate</td>
<td>6.2 (0–60)</td>
<td>0.25</td>
<td>0.12</td>
</tr>
<tr>
<td>% Gravel substrate</td>
<td>31.3 (0–0)</td>
<td>-0.39</td>
<td>-0.31</td>
</tr>
<tr>
<td>% Sand substrate</td>
<td>1.1 (0–12)</td>
<td>0.04</td>
<td>0.12</td>
</tr>
<tr>
<td>% Fine substrate</td>
<td>61.2 (8–100)</td>
<td>0.26</td>
<td>0.22</td>
</tr>
<tr>
<td><strong>Streambank vegetation</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>% Bare soil</td>
<td>12.3 (0–49)</td>
<td>0.22</td>
<td>0.08</td>
</tr>
<tr>
<td>% Upland nonwoody vegetation</td>
<td>10.8 (0–15)</td>
<td>-0.07</td>
<td>-0.16</td>
</tr>
</tbody>
</table>

(Continues)
3 | RESULTS

3.1 | Landscape variables

The slope and elevation of each drainage reflected typical catchment characteristics, decreasing smoothly in a downstream direction. Elevation, slope and catchment area were all correlated with catchment % surface disturbance, likely due in part to the development being preferentially sited at lower elevation sites with lower slope, which would have larger catchment areas (Table 1).

3.2 | Oil and natural gas development variables

Catchment well density ranged from 0 to 2.8 wells/km², and local (within 1 km² circular buffer) well density ranged from 0 to 23.1 wells/km² (Table 1). Catchment % surface disturbance ranged from 0.4% to 9.2%, and local % surface disturbance ranged from 0.2% to 61.1%. Stream segment length between road crossings varied from 442 m to 11 km and was positively correlated with catchment % surface disturbance. All ONG development variables were correlated.

3.3 | Fish

Fish were present in 47 of the 73 sampling sites in 2012 and in 45 of the 88 sites in 2013. In 10 of the 13 streams sampled, fish sampling was completed at sites beyond the upstream extent of fish presence in that stream (Figure 3). Colorado River cutthroat trout was only found in the South Beaver Drainage and was found at 10 sites in both years (Figure 3a). Mottled sculpin was most common in the South Beaver Drainage and found occasionally in the other drainages; mottled sculpin occupied 21 sites in 2012 and 18 sites in 2013 (Figure 3b). Mountain sucker was the most widely distributed fish species and was present at 38 sites in 2012 and 30 sites in 2013 (Figure 3c).

Fish CPUE per site averaged 7.0 fish/100 m in 2012 and decreased to 3.8 fish/100 m in 2013. The decrease in fish CPUE between 2012 and 2013 was statistically significant (Wilcoxon Signed-Rank Test, V = 1,007.5, p = <0.01). The average site CPUE of mountain sucker, mottled sculpin and Colorado River cutthroat trout at sites with fish was 3.5 (SD = 3.1), 9.94 (SD = 11.88) and 4.14 (SD = 3.63) fish/100 m, respectively.

3.4 | Stream habitat

The predominant habitat was run, which was positively correlated with catchment % surface disturbance; riffle habitat was negatively correlated with catchment % surface disturbance (Table 1). Run habitat comprised the entire site in some rare cases, but more commonly stream habitats were a heterogeneous mixture of pools, riffles and

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</tr>
</thead>
<tbody>
<tr>
<td>% Riparian nonwoody vegetation</td>
<td>41.2 (0–95)</td>
<td>0.24</td>
<td>0.29</td>
</tr>
<tr>
<td>% Upland woody vegetation</td>
<td>6.0 (0–32)</td>
<td>0.20</td>
<td>0.01</td>
</tr>
<tr>
<td>% Riparian woody vegetation</td>
<td>27.8 (0–87)</td>
<td>−0.36</td>
<td>−0.22</td>
</tr>
<tr>
<td>Stream cover</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Shrub cover</td>
<td>28.4 (0–95)</td>
<td>−0.35</td>
<td>−0.20</td>
</tr>
<tr>
<td>% In-stream woody debris</td>
<td>16.3 (0–67)</td>
<td>−0.59</td>
<td>−0.47</td>
</tr>
<tr>
<td>% Cut-bank</td>
<td>1.9 (0–38)</td>
<td>−0.05</td>
<td>0.01</td>
</tr>
<tr>
<td>% Aquatic vegetation</td>
<td>18.3 (0–100)</td>
<td>0.35</td>
<td>−0.10</td>
</tr>
<tr>
<td>% Other forms of cover</td>
<td>2.9 (0–18)</td>
<td>−0.09</td>
<td>−0.06</td>
</tr>
<tr>
<td>Surface water</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum specific conductivity (μS/cm)</td>
<td>542 (392–1,597)</td>
<td>0.07</td>
<td>0.05</td>
</tr>
<tr>
<td>Maximum temperature (°C)</td>
<td>19.5 (6.8–29.5)</td>
<td>0.53</td>
<td>0.17</td>
</tr>
<tr>
<td>Minimum % dissolved oxygen saturation</td>
<td>73.3 (53.7–95.9)</td>
<td>0.42</td>
<td>0.05</td>
</tr>
<tr>
<td>Minimum discharge (L/s)</td>
<td>7.3 (0–46.7)</td>
<td>−0.22</td>
<td>−0.15</td>
</tr>
</tbody>
</table>

Notes. Significant correlation coefficients are in bold.

*Only includes data from South Beaver drainage.
runs. Stream incision, % pools and beaver dams were significantly correlated with catchment % surface disturbance but had nonsignificant partial correlations when catchment area was controlled for. Stream width and depth had significant negative partial correlations with catchment % surface disturbance, but correlations were not significant before the influence of catchment area was removed. The most common substrates throughout the study area were fine and gravel substrates. Fine substrate was positively correlated with catchment % surface disturbance, while gravel substrate was negatively correlated.

Riparian woody and non-woody vegetation were the dominant streambank vegetation types, and riparian woody streambank vegetation was negatively correlated and riparian non-woody streambank vegetation positively correlated with catchment % surface disturbance. Willows and sedges were the dominant riparian woody and non-woody streambank vegetation, respectively. Sagebrush and grasses were the predominant upland woody and nonwoody streambank vegetation, respectively. Willows comprised most of the shrub cover. Shrub cover was negatively correlated and aquatic vegetation cover was positively correlated with catchment % surface disturbance, but these correlations were no longer significant when catchment area was accounted for. In-stream woody debris cover was negatively correlated with catchment % surface disturbance. Several surface water variables were correlated with catchment % surface disturbance, but the partial correlations suggest this was driven by catchment area.

3.5 | Fish–habitat relationships

Colorado River cutthroat trout CPUE was not correlated with catchment % surface disturbance in the South Beaver Drainage (Table 1, Figure 4a). Mottled sculpin CPUE was also not significantly correlated, although CPUE was highest at sites with 2%-4% catchment surface disturbance and declined with higher catchment % surface disturbance (Figure 4b). Mountain sucker CPUE also was not correlated with catchment % surface disturbance, but when the effect of catchment area was accounted for mountain sucker CPUE was negatively correlated (Table 1; Figure 4c).

Colorado River cutthroat trout were present in 64% of the sampling locations in the South Beaver Drainage. The overall accuracy of the Colorado River cutthroat trout Random Forest model classification was 81%, with higher accuracy for predicting presences (92%) than absences (62%). The top model had 10 variables, and average depth had by far the highest relative importance value (Figure 5a). The probability of Colorado River cutthroat trout occurrence increased above 50% when depth averaged 10 cm or greater (Figure S1a). Probability of Colorado River cutthroat trout occurrence also increased with less upland woody streambank vegetation, more shrub and in-stream woody debris cover and less aquatic vegetation cover. Catchment characteristics including elevation and slope were included in this model, with sites below 2,425 m more likely to contain Colorado River cutthroat trout (Figure S1a). Local well density and % surface disturbance were included in the top Colorado River cutthroat trout model, with sites experiencing the lowest levels of disturbance having a lower probability of occurrence. There was a very limited range of ONG development in South Beaver Drainage, but high elevation sites that occurred above the extent of fish presence in these streams had the lowest amount of ONG disturbance.
Mottled sculpin were present at 28% of the sites. The top mottled sculpin Random Forest model included 10 variables with an overall classification accuracy of 84%. The absence was predicted with high accuracy (95%), but the presence was predicted with lower accuracy (54%). Elevation, minimum discharge, shrub cover, gravel substrate, catchment well density and riparian woody streambank vegetation were important variables in the mottled sculpin model (Figure 5b). Mottled sculpin were primarily found in sites below 2,350 m and probability of the presence increased with increasing shrub cover, minimum discharge, riparian woody streambank vegetation, gravel substrate and stream width (Figure S1b).

Mountain sucker was present at 54% of sites. The overall classification accuracy for the top mountain sucker Random Forest model was lowest (72%) of the species models. Accuracy for predicting the presence was higher (76%) than the absences (67%). Occurrence increased at lower slope, lower elevation (<2,360 m) and greater catchment area (Figures 5c and S1c). In contrast to the other fish species, shrub cover or riparian woody streambank vegetation was not included in the top model; instead, probability of mountain sucker presence increased with higher % aquatic vegetation cover (Figure S1c).

The stress for the NMDS was acceptable with two dimensions (stress = 0.19) and improved with three dimensions (stress = 0.13; Kruskal, 1964). In the NMDS plot of axes 1 and 2 of the three-dimensional solution (ordination was similar in two-dimensional solution), there was a trend of sites with higher catchment % surface disturbance being associated with higher loadings on NMDS axis 1 (Figure 6). High loading on NMDS axis 1 was associated with ONG development variables, catchment area and habitat variables such as run, incision, bare soil along streambanks and fine substrate, while low loading was associated with riparian woody streambank vegetation, other cover, beaver dams and area of standing water. Colorado River cutthroat trout and mottled sculpin CPUE were significantly associated with lower loadings on NMDS axis 1, while a significant relationship did not exist for mountain sucker CPUE (Figure 6).

4 | DISCUSSION

Fisheries managers are increasingly asked to predict how fish assemblages and the habitat they depend on will respond to land use change. ONG development is a large-scale environmental disturbance that has been occurring since the late 1800s but has recently attracted research attention due to rapid expansion of natural gas development within the United States (Entrekin et al., 2011; McDonald et al., 2012; Souther et al., 2014). ONG development has the potential to affect aquatic habitats through multiple mechanisms including physical habitat alteration, hydrological shifts and impaired water quality (Entrekin et al., 2011). Degraded stream habitat conditions in the study streams, especially decreased riparian woody streambank vegetation, increased fine substrate, decreased riffle habitat and less area of standing water were associated with higher catchment % surface disturbance. Of specific concern were decreased riparian woody streambank vegetation and decreased shrub cover, which appeared to be important factors affecting fish distribution in the study area. Colorado River cutthroat trout and mottled sculpin occurrence were both more probable when shrub cover exceeded 50% and were absent and in low abundance, respectively, in the more developed Dry Piney and Fogarty drainages.

Willow, the predominant riparian woody streambank vegetation in the study area, was an important habitat variable that could be influencing many other habitat characteristics. Riparian woody streambank vegetation, especially willow, is commonly used as a metric for stream habitat quality in sagebrush steppe streams (Booth, Cox, Simonds & Sant, 2012; Prichard, 1993). Riparian woody streambank vegetation both reduces streambank erosion and provides habitat complexity, as their branches and roots are often in the stream channel, while also effectively confining the stream channel and increasing the stream energy exerted on the stream bed (Polvi & Wohl, 2013). As a result, fine sediments are mobilised and gravel remains clean of fine sediments, which is important for mottled sculpin and Colorado River cutthroat trout spawning and feeding (Magee, McMahon & Thorow, 1996; McGinley, Reasly & Willaim, 2013). Riparian streambank vegetation, especially an overstory of woody vegetation, can also buffer against water temperature swings by shading the stream (Kauffman, Beschta, Otting & Lytjen, 1997).

Beaver dam habitat is also known to be important for overwintering and rearing of Colorado River cutthroat trout in the region, and depth was the most important predictor of Colorado River cutthroat trout occurrence (Lindstrom & Hubert, 2004). Streams in the Dry Piney and Fogarty drainages had decreased riparian woody streambank vegetation, lower stream depths and less in-stream woody debris, which is typical of degraded sagebrush steppe streams (Booth et al., 2013).

**FIGURE 4** Catch-per-unit-effort (CPUE) for (a) Colorado River cutthroat trout, (b) mottled sculpin and (c) mountain sucker for 2012 (circles) and 2013 (triangles) plotted against catchment % surface disturbance. The Colorado River cutthroat trout graph only includes South Beaver drainage data.
et al., 2012). The degraded habitat and water quality condition in the Dry Piney Drainage have resulted in the Wyoming Department of Environmental Quality evaluating the need to classify these as impaired streams (Hargett, 2003; Thorp, 2014).

Site-scale habitat characteristics observed across the range of ONG development intensities, combined with knowledge of habitats associated with the presence of the study area’s three native fish species, provide expectations for how ONG disturbance may affect these species. Colorado River cutthroat trout was only found in the relatively undisturbed streams and, although known to be present historically, is now absent from streams in the Dry Piney and Fogarty drainages. Mottled sculpin was found in all drainages but abundances were low at sites with higher catchment % surface disturbance. The presence of Colorado River cutthroat trout and mottled sculpin was primarily associated with stream habitat features indicative of low relative ONG disturbance, specifically locations that had deeper water and greater shrub cover. Gravel substrate was also a good indicator of mottled sculpin presence. Mountain sucker was found in all drainages, and CPUE was not directly correlated with catchment % surface disturbance; but when catchment area was controlled for, there was a negative correlation. This suggests that the presence of mountain sucker at sites with higher ONG development may be a consequence of their preference for lower elevation and lower gradient sites, which is also where ONG development tends to be sited. Previous work suggests mountain sucker is sensitive to disturbance (Schultz, 2011). The study results are broadly consistent with previous modelling work in the Upper Green River Basin that suggested native species and salmonids (native and non-native) were more sensitive to increasing well density (Dauwalter, 2013). Mottled sculpin was one of four indicator species identified as having a negative threshold response to well density (Dauwalter, 2013).

The differential sensitivity of the fish species to habitat degradation is likely related to their physiological tolerances and life history requirements (Baxter & Stone, 1995; Grabarkiewicz & Davis, 2006). Lack of Colorado River cutthroat trout in Dry Piney and Fogarty drainages suggests their sensitivity to disturbance, which is supported by existing research that describes their relatively narrow thermal requirements, sensitivity to contaminants and spawning requirements of clean sediment and clear water (Baxter & Stone, 1995; Grabarkiewicz & Davis, 2006). Existing information about mottled sculpin reveals a preference for cool, clear and oxygenated water without contaminants and that they are especially sensitive to dropping water tables and riparian degradation due to their thermal requirements (Grabarkiewicz & Davis, 2006). Mottled sculpin had similar habitat preferences to Colorado River cutthroat trout, but mottled sculpin has a more stationary life history. This may make them especially susceptible to local habitat degradation and may limit their ability to escape disturbance events or re-establish following population declines (Albanese, Angermeier & Peterson, 2009). However, mottled sculpin may also be able to use small patches of good habitat and be buffered from effects of fish passage barriers by not requiring a spawning migration. In the Fogarty and Dry Piney drainages, mottled sculpin populations were small, possibly due to prevalence of fine substrates and less riparian woody streambank vegetation. Unlike mottled sculpin and Colorado River cutthroat trout, mountain sucker was more tolerant of degraded habitat conditions. Mountain sucker may be better adapted to disturbance because they tolerate warmer temperatures, reproduce at a young age and produce large numbers of eggs capable of hatching in as few as 8 days (Belica & Nibbelink, 2006).

Differing feeding preferences may also drive differential vulnerability of these fish species. Colorado River cutthroat trout and

**FIGURE 5** Scaled variable importance for the variables included in the top Random Forest model for (a) Colorado River cutthroat trout, (b) mottled sculpin and (c) mountain sucker.
mottled sculpin feed predominantly on aquatic macroinvertebrates (Baxter & Stone, 1995; Grabarkiewicz & Davis, 2006). Being an algivore, mountain sucker food availability may increase with light availability. Physical alterations to stream habitat could therefore have different effects on these fish species, due to differing trophic level and feeding habits.

In addition to habitat and resource requirements, interspecific interactions can also influence species’ distributions. Colorado River cutthroat trout and mottled sculpin are potential predators and competitors for juvenile mountain suckers (Belica & Nibbelink, 2006). Mountain sucker may therefore benefit from the lack of Colorado River cutthroat trout and a smaller mottled sculpin population in the Dry Piney and Fogarty drainages. The study results suggest that mountain suckers can use a wide range of stream conditions, improving their ability to persist where other native stream fishes cannot.

In observational studies it is difficult to attribute causal mechanisms. The variability in habitat characteristics and fish presence and abundance seen between sites could occur independent of ONG disturbance, but the observed habitat conditions are consistent with expectations of watershed alteration. By focusing on similar-size streams that are near one another, the influence of natural variation related to climate and geology was reduced, and the ability to compare sites with differing degrees of disturbance was improved. However, the small spatial extent of the study area does not provide a robust control for drainage level effects. The downstream extent of Dry Piney Creek where it enters the Green River is dry in many years, so there is unlikely to be substantial fish movement between the drainages. It is unknown how the observed presence and abundance of fish species is affected by the different downstream connectivity to the Green River of the South Beaver Drainage relative to the Dry Piney and Fogarty drainages. This is especially true given the differences in ONG development density in these different drainages. Therefore, unmeasured drainage level effects could contribute to differences between fish presence and CPUE regardless of ONG development.

The extent of temporal variability is also unknown. Fish presence and CPUE decreased between 2012 and 2013, and this is likely due to the stress of low water in the summer of 2012 and winter of 2012/2013. In 2012, site discharge averaged 55% of 2013 discharge. Not all habitat variables were collected in both years so this variation between years could have affected values for some stream morphology variables, such as average width, depth and maximum depth and water quality variables. However, the majority of habitat data (82%) was collected in 2012 so a large effect on results is not expected. There were no substantial changes in direction or significance of correlation analysis results for landscape, oil and natural gas development, fish and habitat variables when just run with 2012 data; there were some small changes with just 2013 data, but this could have been a sample size issue.

The study area was chosen for two primary reasons: existing sampling data confirming the native fish assemblage and because ONG development is a predominant watershed disturbance. For example, even the few homesteads that occurred historically in the study area have been long since vacated, and their access roads have been repurposed for ONG. The ability to use catchment % surface disturbance as a metric for ONG development in this study area is relatively high due to the limited amount of other infrastructure-related land uses and is supported by strong correlation between catchment % surface disturbance and catchment well density.

It is acknowledged that grazing was not controlled for in the study’s design, although it is a known contributor to watershed degradation. Cattle grazing is ubiquitous across the Intermountain West, including areas with ONG development (Waldner, Ribble, Janzen & Campbell, 2001). Currently, all study sites are part of the same grazing allotment and receive similar cattle numbers, although
there are some seasonal differences with grazing starting earlier at lower elevations and cattle being moved up in elevation to track forage production as the season progresses. Historical grazing use is not well understood. Environmental degradation from the potential interaction between cattle grazing and ONG development has not been thoroughly examined. Despite similar grazing across the drainages, grazing may have a larger effect in areas experiencing more ONG development because surface disturbance such as roads and pipelines fragment woody riparian streambank vegetation and result in direct loss of forage. Less overall forage that occurs in smaller patches may increase the potential for cattle to degrade riparian habitat. Where woody riparian streambank vegetation is lost due to disturbance, cattle grazing can suppress reestablishment. When livestock consumption exceeds forage production, degradation is the expected outcome, including the elimination of browse-sensitive plant species, soil erosion and stream incision (Belsky, Matzke & Uselman, 1999). Although the relationship between cattle grazing and ONG development associated surface disturbance is not well studied, it is acknowledged by ranchers and land managers with the implementation of exclusionary fencing following vegetation disturbing activities.

Native fish populations in the Intermountain West are often isolated in small headwater populations that are susceptible to habitat degradation and species extirpation (Cook, Rahel & Hubert, 2010). In the LaBarge Oil and Gas Field, the development has disturbed 4% of the land surface (Weller et al., 2002), and data from this study suggest that this ONG development is a potential contributor to stream habitat degradation with implications for fish populations. The extent of effects varied by fish species highlighting that ONG disturbance is similar to other watershed disturbances and predictive capabilities depend on an understanding of fish–habitat relationships. The study streams are exhibiting degraded riparian conditions including streambanks dominated by nonwoody, instead of woody, riparian vegetation. Common best management practices for protection and restoration of riparian habitats align well with the modelled habitat conditions indicative of Colorado River cutthroat trout and mottled sculpin presence, such as high shrub cover and sufficient in-stream flow (WYDEQ 2013). These same best management practices could help with recovery of native fish assemblages in areas experiencing ONG development.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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