



The interactive effects of climate change and land use on boreal stream fish communities



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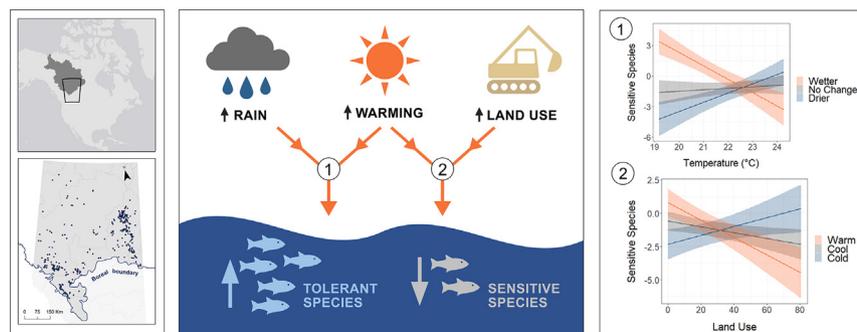
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HIGHLIGHTS

- Sensitive fish species declined owing to a combination of warming and land use.
- Land use disturbances may be providing benefits to species in cooler regions.
- Overall species richness and productivity were generally unaffected by land use.
- Sensitive species declined owing to potential drought conditions in small streams.
- Future warming may exacerbate the negative effects of co-occurring stressors.

GRAPHICAL ABSTRACT



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ABSTRACT

Ongoing and projected climate change is likely to greatly alter co-occurring stressor mechanisms, yet these potential interactions remain poorly understood in natural freshwater systems worldwide. As the global biodiversity crisis deepens, successful conservation efforts will hinge on developing mechanistic multiple stressor frameworks that have been ground-truthed in natural systems containing complex species dynamics and ecological processes. Our study examined the combined and interacting effects of potential climate and land use stressors on boreal stream fishes using data from over 300 catchments across a broad 250,000 km² region. To characterize boreal fish community health, we examined four indicators including species richness, total catch per unit effort, the proportion of lithophilic spawners (fish sensitive to sedimentation), and the assemblage tolerance index which provides a measurement of the overall community tolerance to disturbance. Land use stressors included total anthropogenic land use area and linear disturbance at multiple watershed scales as well as two site-specific habitat degradation indicators (dissolved oxygen and the proportion of fine substrate). Overall community richness and productivity were not negatively related to land use changes indicating potential compensatory dynamics (e.g. where intolerant species are replaced with more tolerant species as habitat quality degrades). In contrast, we observed declines for sensitive species, including highly valued salmonids, that varied depending on interactions between local climate, land use, and stream type. Sensitive species declines were concentrated in regions experiencing increased land use and warming, whereas increases were observed in cooler regions consistent with a subsidy-stress response. In addition, lithophilic spawners declined in watersheds experiencing warmer and wetter conditions owing to potential indirect effects on spawning habitat quality. Results from our study provide novel insight into complex climate and land

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use interactions occurring across a broad, real-world landscape, and highlight the potential for amplified species declines under future warming and land use scenarios.

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1. Introduction

The global human footprint continues to expand at an alarming rate, with a disproportionate amount of pressure being placed on vital freshwater resources (WWF, 2018). While land use change remains the leading threat to freshwater biodiversity worldwide, climate change is rapidly emerging as a significant secondary stressor with the ability to alter land use mechanisms in potentially unexpected ways (Piggott et al., 2015; Reid et al., 2018). Certain stressor combinations may produce ecological 'surprises', or dampened (antagonistic) responses, potentially nullifying or even worsening management actions based on single-stressor predictions (Côté et al., 2016). As evidence for the global biodiversity crisis continues to mount, ecosystem managers remain vastly ill-equipped for managing the numerous potential stressor interactions that may arise in ecologically complex real-world systems (Nöges et al., 2016; WWF, 2018).

The successful conservation of aquatic resources hinges on the immense task of elucidating multiple stressor relationships amid novel and potentially regional-specific direct and indirect climate change processes. Many freshwater species experience ecological advantages within their specific environmental niche, potentially making them vulnerable to any unprecedented changes in temperature, stream flow, substrate, or water quality (Magnuson et al., 1979). For instance, increased summer temperatures will likely favour the establishment of species with warmer thermal preferences, reducing the abundances of many highly valued species that are dependent on cooler waters for their survival (Heino et al., 2009). Further, climate-altered stream flows may limit fish movements or degrade water quality, shifting community assemblages towards more stationary and tolerant fishes (Schindler et al., 1996; Lake, 2003). Climate processes are also likely to vary depending on local conditions, for example, lowered stream flows may be more detrimental in smaller streams with a higher risk for low-flow stranding (Lake, 2003). Further, regions experiencing warmer summer temperatures in combination with more precipitation may experience impacts due to enhanced nutrient and sediment run-off (Goudie, 2006; Goode et al., 2012).

While there has been ample research examining potential climate change effects on fish, understanding how these effects may combine and potentially interact with co-occurring stressors remains a critical and understudied question for freshwater ecosystems (Mantyka-Pringle et al., 2014; Nöges et al., 2016). The growing body of ecological literature investigating freshwater multiple stressors indicates a high prevalence of antagonistic interactions, as well as potential reversal effects associated with warming (Jackson et al., 2016). For example, the stimulatory effect of higher temperatures may increase animal metabolism or plant assimilation, potentially dampening the negative effects of other stressors such as eutrophication (e.g., Thompson et al., 2008). Cooler, less productive regions may also be more positively impacted by low disturbance subsidies (e.g. increased sunlight or nutrients), with benefits decreasing in warmer regions (Allan, 2004; Piggott et al., 2012). Despite the prevailing evidence, there is still the possibility of negative (synergistic) interactions following increasing land use and climate change in freshwater systems, particularly when involving changes in precipitation (Murdoch et al., in review). As lotic systems are highly vulnerable to fragmentation, imposing additional thermal, high-flow, or low-flow barriers could

exacerbate local land use effects if fish are stranded in increasingly stressful environments (Radinger et al., 2017). Further, enhanced sediment and nutrient run-off in wet, disturbed watersheds could accelerate water quality degradation or bury important gravel beds for lithophilic spawners (Schindler, 2001; Bryant, 2009). However, the mechanistic understanding of climate interactions has been largely derived from small-scale experimental studies to-date, and there is an urgent need to validate potential mechanisms in natural systems containing complex ecological processes (Jackson et al., 2016; Bruder et al., 2017).

Identifying key threats to freshwater biodiversity and how they may vary depending on climate conditions is greatly needed for the successful conservation and management of northern fishes within their rapidly changing environments. Therefore, the objectives of this study were to determine: (1) how cumulative land use pressures are influencing boreal stream fish community structure, and (2) if climate is producing a buffering (antagonistic) or amplified (synergistic) effect on concurrently acting stressors across a broad, real-world landscape. We predicted that (1) sensitive species would decline in response to rising land use impacts, whereas overall community metrics would be more robust (at low-mid disturbance levels) owing to species compensatory dynamics (Vinebrooke et al., 2004), and (2) that warming would dampen the effects of co-occurring stressors on boreal fishes owing to its stimulatory effect (Jackson et al., 2016), whereas amplified (synergistic) species declines would be observed when stressors interacted with changes in summer precipitation (Murdoch et al., in review). Few others have provided field-based empirical data of cumulative land use on fishes over broad spatial scales (e.g., Esselman et al., 2011; Schinegger et al., 2012; Daniel et al., 2015; Cooper et al., 2017), and fewer have investigated climate – land use interactions beyond a local study scale (e.g., Radinger et al., 2016; Gutowsky et al., 2019), providing us with a unique opportunity to test findings from a recent freshwater meta-analysis using regional-scale *in situ* data (Jackson et al., 2016).

2. Materials and methods

2.1. Study area

The boreal ecozone of Alberta, Canada, contains several major rivers that combine to form the headwaters of the second largest drainage in North America, the Mackenzie River system (Fig. 1). Substantial anthropogenic land use has occurred within this region, including major hydroelectric development, forestry, agriculture, as well as extensive oil sands mining concentrated in the lower Athabasca watershed (Schindler and Lee, 2010; Lima and Wrona, 2019). Notably, oil extraction in Canada's western boreal is poised to quickly escalate and may eventually impact a region greater than 25 times the current areal footprint (Kreutzweiser et al., 2013). Over the 1950–2010 period, the region has also experienced substantial warming (1–4 °C change) and a range of regional-specific annual precipitation trends (Clark and Kienzle, 2019; Zhang et al., 2019). Future climate projections indicate that this region will endure considerable additional warming (1.9–6.5 °C) and an overall increase in precipitation (6–15%) by the year 2100 (Zhang et al., 2019).

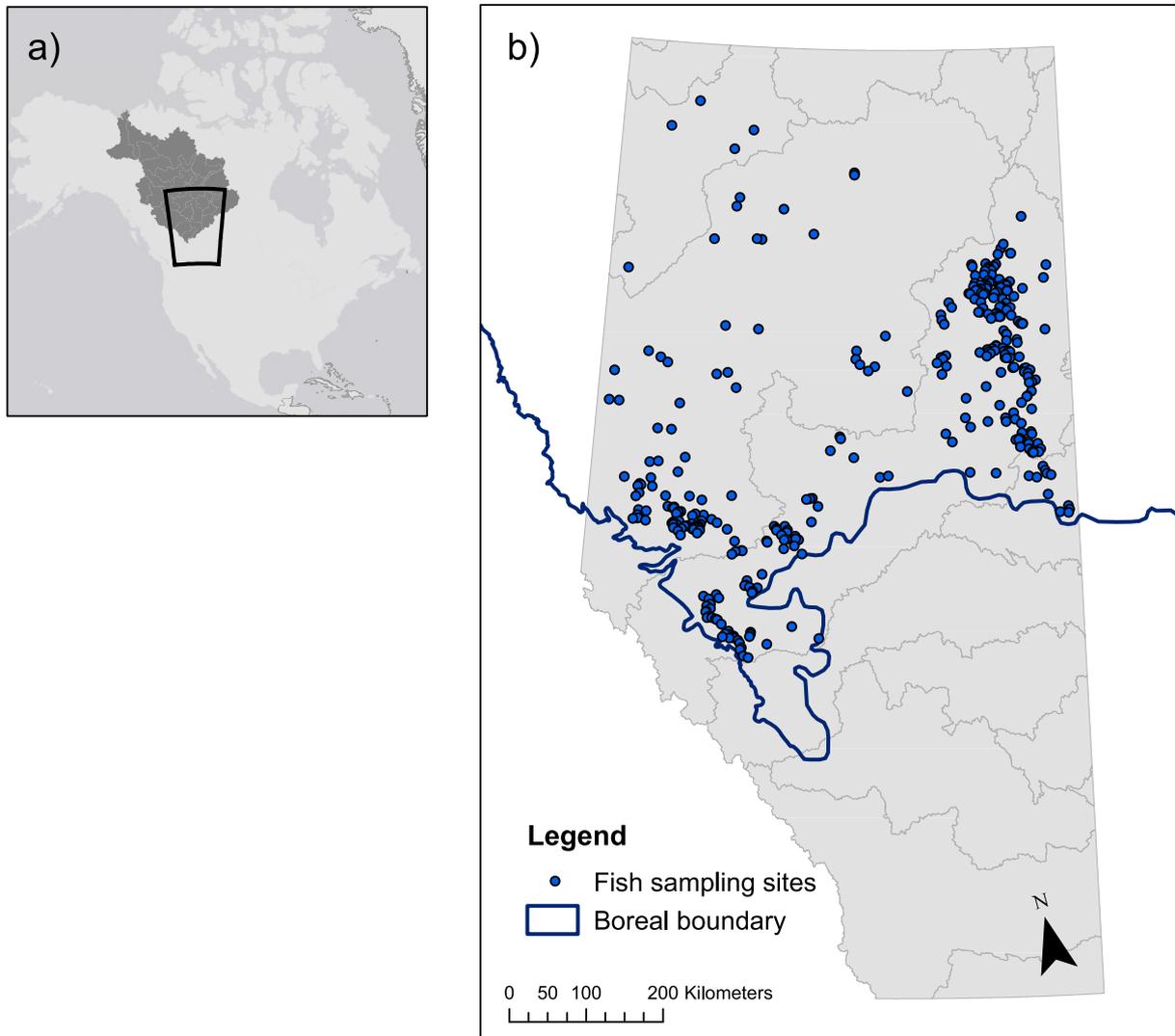


Fig. 1. Study area in the boreal region of Alberta, Canada, showing a) the Mackenzie River drainage which flows from its headwaters in the Peace-Athabasca Delta north to the Arctic Ocean and b) zoomed in view of the study area including backpack electrofishing sampling sites and the southern boundary of the boreal disturbance dataset.

2.2. Data sources and processing

Fish catch data were obtained from the Alberta Government's Fish and Wildlife Management Information System (FWMIS) (Fig. 1; AEP, 2018a). The fish dataset was subset to focus on small streams and rivers (drainage area <1000 km²; Esselman et al., 2011) sampled with backpack electrofishing, during the 2010–2016 period. We only included survey data that aimed to sample the entire fish community, which was achieved by removing any targeted species sampling (as indicated by a column in the FWMIS database). All sites were sampled during the open water season (May–October). Where available, site-specific habitat quality data (dissolved oxygen in mg/L, water temperature, conductivity, and percentage of fine substrates) were also obtained from FWMIS.

Watersheds were delineated using spatial data from the Alberta ArcHydro Phase 2 dataset (AEP, 2018b). We used pre-defined local catchments (the immediate catchment where the fish survey was located), and delineated network catchments (the entire upstream area) using ArcHydro tools version 2.0 (Redlands, CA, USA). In addition, we used Unit 8 from the Hydrologic Unit Code Watersheds of Alberta spatial dataset to represent an even larger, watershed-level spatial scale (AEP, 2017). We further refined the fish dataset based on available data in each local catchment. First, we selected local

catchments with a minimum of 15 individual fish sampled, and then summarized this data at the catchment level ($n = 301$ local catchments, mean = three surveys per catchment) to minimize sampling bias and high spatial autocorrelation from repeated sampling (Fig. 2). As a result, each catchment had an average of four species (standard deviation = 3, minimum = 1, maximum = 15) and 132 individual fish captured (standard deviation = 542, minimum = 15, maximum = 8169), with lake chub, brook stickleback, white sucker, and longnose sucker being the most dominant species present (Table A.1). Further, each catchment received an average electrofishing effort of 926 s per survey \pm one standard deviation of 641 s. Mean elevation for each watershed was calculated using data from the Canadian Digital Elevation Model (Natural Resources Canada 2017). Local catchment slope (%) was derived using elevation data.

Land use data were obtained from the Boreal Ecosystem Anthropogenic Disturbance dataset (2008–2010), which was originally created to assess anthropogenic effects on boreal caribou (Pasher et al., 2013). The dataset is unique in that it quantifies all disturbed areas for a range of development activities in a standardized way (e.g., agriculture, cutblocks, hydroelectric dams, settlements, and oil and gas), and it includes many features that are commonly missed in other geospatial datasets, such as forestry

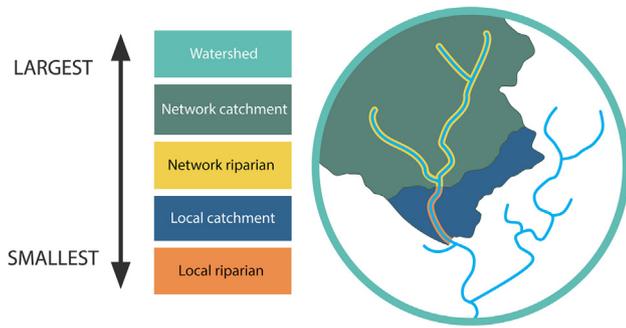


Fig. 2. Five spatial scales used for calculating human disturbance variables. Local spatial scales encompass the immediate catchment where the fish survey was conducted. Network spatial scales include the local catchment and the entire upstream catchment. Riparian areas were defined as areas within 30 m of the stream line. Watershed-level catchment includes the network catchment, as well as the greater area surrounding it as defined by Alberta's Hydrologic Unit Code 8 (AEP, 2017).

roads and seismic lines. Total linear density (m/km^2) and anthropogenic land use (%) were calculated for five different spatial scales: local riparian, local catchment, network riparian, network catchment and HUC8 watershed level (Fig. 2). Multiple spatial scales were considered as the spatial extent of disturbance pathways are known to vary depending on disturbance type and the life histories of response biota (Allan, 2004; Esselman et al., 2011). On average, local, network and HUC8 catchments represented a median area of 10 km^2 , 58 km^2 , and 1710 km^2 , respectively. The riparian area was defined as land within 30 m on either side of the drainage line. All GIS data processing was conducted in ArcMap Desktop 10.6.

Climate data were obtained from the ClimateNA program (version 5.5) (Wang et al., 2016). Climate data were extracted at each sampling site, and then averaged by catchment. Current weather means were based on the thirty years prior to the fish collection date and included maximum July air temperature ($^{\circ}\text{C}$), summer precipitation (June–August) (mm), and frost free period (days). Change in summer precipitation (mm) and summer temperature ($^{\circ}\text{C}$) were calculated as the difference between the current thirty year mean and the previous thirty-year mean.

2.3. Data analysis

Fish metrics representing biological integrity in Albertan watersheds were calculated (Table 1), including species richness, fish catch per 100 s of electrofishing effort (CPUE = catch per unit effort), percent lithophils, and the assemblage tolerance index (ATI) (e.g., Bramblett et al., 2005; Whittier et al., 2007; Stevens et al., 2010). The ATI provides an index of the overall community

tolerance, with a high score indicating relatively more tolerant individuals and a low score indicating relatively more intolerant individuals. Species richness was rarefied using the *rarefy* function from the *vegan* package to 15 individuals. Pearson's correlation coefficients between response variables ranged from -0.54 to 0.34 , with ATI and lithophils having the strongest correlation ($r = -0.54$). To improve normality, we log-transformed CPUE, summer precipitation, drainage area, elevation, and slope, square-root transformed species richness and linear disturbance, and logit-transformed percent lithophils and land use. As many disturbance variables had high disturbance outliers, we corrected outliers to the 99th percentile value for each variable (e.g., Esselman et al., 2011).

Prior to analyses, we checked for potential multicollinearity between predictor variables resulting in the omission of two variables, summer precipitation and change in summer temperature, as they were highly correlated with maximum July air temperature (Table A.2). July temperature was positively correlated with change in summer temperature ($r = 0.77$) and negatively correlated with summer precipitation ($r = -0.9$). Further, regions that were warming the fastest (i.e., change in summer temperature) tended to have lower current summer precipitation ($r = -0.82$) and were experiencing more summer drying (i.e., change in summer precipitation; $r = -0.6$). We retained July temperature due to its demonstrated influence on species fitness, including implications for overall freshwater productivity (Schindler, 1997; Sharma et al., 2007; Ficke et al., 2007). However, because summer precipitation was also moderately correlated with change in summer precipitation ($r = 0.48$), and both precipitation variables were expected to produce similar effects on important streamflow processes (Ashmore and Church, 2001), we additionally explored competing models to determine which variable would provide the greatest statistical fit (Table A.3; see more detailed methods information below for linear mixed models). Summer precipitation did not alter model interpretation or improve model performance for any metric and was therefore omitted from further analyses. All other predictor variables demonstrated low potential for multicollinearity issues and were retained for further analyses (Pearson correlation coefficients < 0.7 and variance inflation factors < 2 ; Dormann et al., 2013).

Linear mixed models were used to analyze relationships between fish community metrics and predictor variables. For each metric, an initial model was run using all explanatory variables: total linear density, total land use percent, catchment slope, drainage area, maximum July temperature, frost free period, and change in summer precipitation. We included quadratic terms to represent potential nonlinear relationships. In addition, we incorporated interaction terms between maximum July temperature and the two disturbance variables to test our second objective. Further, we included interactive terms to represent two potential

Table 1
Fish assemblage metrics representing the biological integrity of Albertan fish communities.

Fish Metric	Description	Predicted Effect	Catchment Mean \pm SD
Species richness	Total number of species present in a catchment	Highly stressed watersheds will support less biodiversity	3.1 ± 1.5
Fish catch per 100s of electrofishing (CPUE)	Fish catch is an index of relative abundance	Highly stressed watersheds will have a lower carrying capacity	7.0 ± 16.0
Percent lithophil ^c	The percentage of individuals requiring coarse unembedded substrate for reproduction	Expected to decline with land use that may increase stream sedimentation (e.g. forestry, agriculture)	44 ± 38
Assemblage Tolerance Index (ATI)	An index of the overall community tolerance to disturbance	Expected to decline with land use that may degrade habitat or water quality	5.9 ± 2.2

SD = standard deviation.

^c Lithophils included Arctic grayling, brook trout, bull trout, burbot, lake chub, lake whitefish, longnose dace, longnose sucker, mountain whitefish, rainbow trout, spottail shiner, trout-perch, walleye and white sucker.

climate interactions: an interaction between maximum July temperature and change in summer precipitation, and an interaction between drainage area and change in summer precipitation. These interactions were included based on predictions that (1) warmer and wetter regions may experience negative effects due to the higher potential for water quality and substrate degradation following climate-induced sedimentation (e.g., Goudie, 2006; Bryant, 2009; Goode et al., 2012), and (2) that smaller drainages would be at greater risk to drought, whereas larger drainages may experience detrimental high flows (e.g., Brooks, 2009; Leppi et al., 2014; Shanley and Albert, 2014). Two potential random effects levels (watershed hydrological codes 4 and 6) were first tested for significance using a log-likelihood test, and if both levels were significant we retained the HUC level that provided the best model fit. As a result, HUC6 was used for all models with the exception of lithophil models which used HUC4. Further, elevation was included as a random intercept after being categorized into six equal levels. We used the *lme4* package for running mixed models, and the *dredge* function in the *MuMin* (Multi-Model Inference) package for model selection (Barton, 2018). The *dredge* function runs all possible model combinations as potential competing hypotheses and identifies the top model based on the lowest AICc value (Johnson and Omland, 2004; Grueber et al., 2011). Models that were within 2 AICc from the lowest score were considered to be equally valid models, following Burnham and Anderson (2002). In the event that a higher order term was selected in the final model, we also retained related lower order terms. All variables were standardized using the function *standardize* in the *arm* package which converts all variables to a comparable, unitless scale (Gelman et al., 2018). Using the partial regression coefficients as indicators of effect size, we interpreted values between 0.1 and 0.3 as weak, between 0.3 and 0.5 as moderate, and greater than 0.5 as strong (Nakagawa and Cuthill, 2007). Pseudo-R² values for mixed models were obtained using the *r.squaredGLMM* function from the *MuMin* package (Barton, 2018).

Using fish survey records that had accompanying site-specific habitat quality data (n = 340), we also ran regression tree models to examine any potential important climate or habitat quality thresholds for four community indicators (square-root transformed species richness, log-transformed catch per unit effort,

logit-transformed percentage of lithophilic individuals, and the assemblage tolerance index). Regression trees employ a recursive binary partitioning algorithm, minimizing node variability at each subsequent split using the best possible predictor variable (De'ath and Fabricius, 2000). Further, regression tree modelling is an effective tool for identifying potential ecological thresholds and interactions within complex ecological datasets. For better alignment with site-specific predictors, we used individual fish survey data records rather than the local catchment summaries used in the land use models described above. However, because some surveys had very low catch data (minimum = 1, median = 10), we were unable to use species rarefaction and instead corrected for the influence of effort on species richness using log-transformed electrofishing effort as a model offset.

3. Results

Fish community indicators demonstrated variable responses to climate and land use variables (Tables 2 and 3). The top species richness models included drainage area, frost free period, and watershed-level linear disturbance (R² = 44%; Table 2). However, there was equal support ($\Delta AICc < 2$) for models that did not retain watershed-level linear disturbance. More species were found in larger drainages (Table 3; std. coefficient = 0.55 ± 0.05, P < 0.01), with intermediate growing seasons (quadratic std. coefficient = -0.28 ± 0.09, P < 0.01), and intermediate linear disturbance (quadratic std. coefficient = -0.20 ± 0.06, P < 0.01; Fig. 3). Overall, drainage size was the strongest predictor of species richness, with the frost-free period and linear disturbance demonstrating relatively weak effect sizes. Species richness peaked in watersheds with approximately 1225 m/km² of linear disturbance (Fig. 3), however few watersheds exceeded disturbance levels greater than 1600 m/km². There was no evidence for a climate-land use interaction for species richness.

Total community catch was best explained by maximum July temperature and drainage area (R² = 35%; Table 2), with higher abundances found in small catchments (std. coefficient = -0.14 ± 0.05, P < 0.01) and with warmer summer temperatures (std. coefficient = 0.39 ± 0.09, P < 0.01; Fig. 4). Human disturbance variables were unrelated to total catch.

Table 2

Linear mixed model results for four community metrics. Disturbance scale indicates the spatial scale of potential disturbance variables (linear disturbance or polygonal land use), ranging from disturbance in the riparian buffer of the local catchment to the entire watershed at the HUC-8 level (AEP, 2017). Predictors that contributed to the top models at each scale are reported, along with the AICc, difference in AICc to the best model for each metric, and the conditional pseudo R² followed by the marginal R² in brackets. Highlighted rows indicate where a single top disturbance scale model was identified for each biological metric ($\Delta AICc > 2$).

Biological Metric	Disturbance Scale	AICc	$\Delta AICc$	R ²	Important Predictors ⁴
Species richness ¹	Watershed	322.3	0	44 (37)	Area, FFP, FFP2, linear, linear2
	Riparian local	322.7	0.4	46 (35)	Area, FFP, FFP2
	Local	322.7	0.4	46 (35)	Area, FFP, FFP2
	Riparian network	322.7	0.4	46 (35)	Area, FFP, FFP2
	Network	322.7	0.4	46 (35)	Area, FFP, FFP2
Total catch ²	All	389.4	-	35 (12)	Area, July
Lithophils (%) ³	Riparian network	292.4	0	53 (42)	Area, July, slope, $\Delta SMPP$, $\Delta SMPP^*July$, linear, linear*July
	Watershed	297.1	4.7	50 (40)	Area, July, slope, $\Delta SMPP$, $\Delta SMPP^*July$, land
	Riparian local	299.6	7.2	49 (39)	Area, July, slope, $\Delta SMPP$, $\Delta SMPP^*July$
	Local	299.6	7.2	49 (39)	Area, July, slope, $\Delta SMPP$, $\Delta SMPP^*July$
	Network	299.6	7.2	49 (39)	Area, July, slope, $\Delta SMPP$, $\Delta SMPP^*July$
Assemblage Tolerance Index	Watershed	284.4	0	56 (45)	Area, July, slope, $\Delta SMPP$, $\Delta SMPP^*area$, land, land*July
	Riparian local	288.6	4.2	51 (44)	Area, July, July2, slope, $\Delta SMPP$, $\Delta SMPP^*area$
	Riparian network	288.6	4.2	51 (44)	Area, July, July2, slope, $\Delta SMPP$, $\Delta SMPP^*area$
	Network	288.6	4.2	51 (44)	Area, July, July2, slope, $\Delta SMPP$, $\Delta SMPP^*area$
	Local	293.4	9.0	55 (43)	Area, July, July2, $\Delta SMPP$, $\Delta SMPP^*area$, linear, land, land2

¹ Species richness was square-root transformed.

² Total catch was log-transformed.

³ Lithophils were logit transformed.

⁴ Area = drainage area, FFP = frost free period, land = land use (%), slope = catchment slope, July = maximum July air temperature, $\Delta SMPP$ = change in summer precipitation, linear = linear disturbance (m/km²); a suffix of "2" indicates a quadratic term and an asterisk indicates an interactive term.

Table 3
Top model standardized coefficients for four community metrics.

Biological Metric	Disturbance Scale	Important Predictors ⁴	Standardized Coefficient	SE	P-value
Species richness ¹	Watershed	Area	0.55	0.05	<0.01
		FFP	0.04	0.06	0.53
		FFP2	-0.28	0.09	<0.01
		Linear	0.10	0.05	0.04
Total catch ²	n/a	Linear2	-0.20	0.06	<0.01
		Area	-0.14	0.05	<0.01
Lithophils (%) ³	Riparian network	July	0.39	0.09	<0.01
		Area	0.34	0.05	<0.01
		Slope	0.14	0.06	0.01
		July	-0.03	0.09	0.7
		Δ SMPP	0.17	0.08	0.04
		July* Δ SMPP	-0.84	0.14	<0.01
		Linear	-0.09	0.04	0.06
		Linear* July	-0.39	0.1	<0.01
Assemblage Tolerance Index	Watershed	Area	-0.15	0.05	<0.01
		Slope	-0.17	0.06	<0.01
		July	0.21	0.10	0.04
		Δ SMPP	-0.11	0.08	0.17
		Land	-0.14	0.07	0.05
		Area* Δ SMPP	0.51	0.09	<0.01
		Land* July	0.63	0.15	<0.01

¹ Species richness was square-root transformed.

² Total catch was log-transformed.

³ Lithophils were logit transformed.

⁴ Area = drainage area, FFP = frost free period, land = land use (%), slope = catchment slope, July = maximum July air temperature, Δ SMPP = change in summer precipitation, linear = linear disturbance (m/km²); SE = standard error; a suffix of "2" indicates a quadratic term and an asterisk indicates an interactive term.

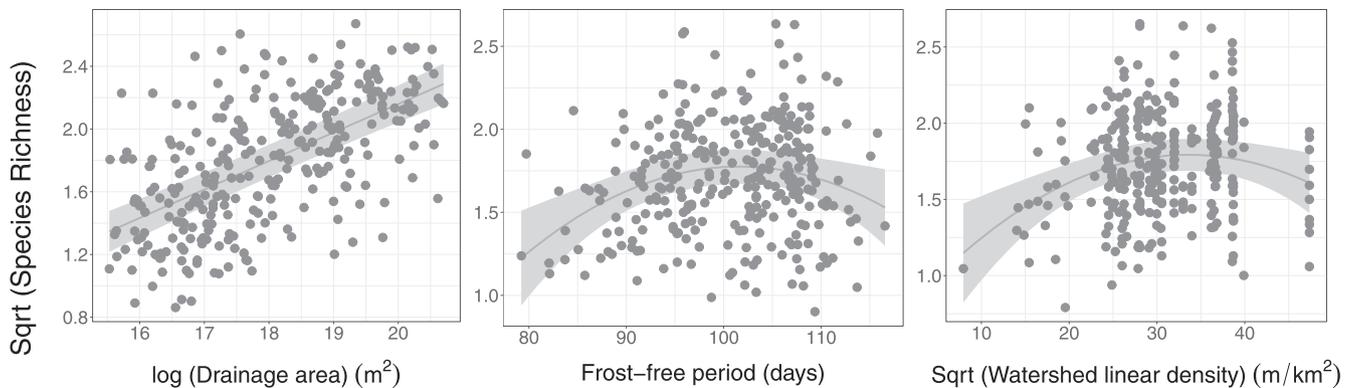


Fig. 3. Partial plots for square-root transformed species richness with drainage area, frost-free period and watershed linear density. For partial plots, all additional model variables have been corrected to their mean values for improved model interpretation. Shaded areas represent the 95% confidence intervals.

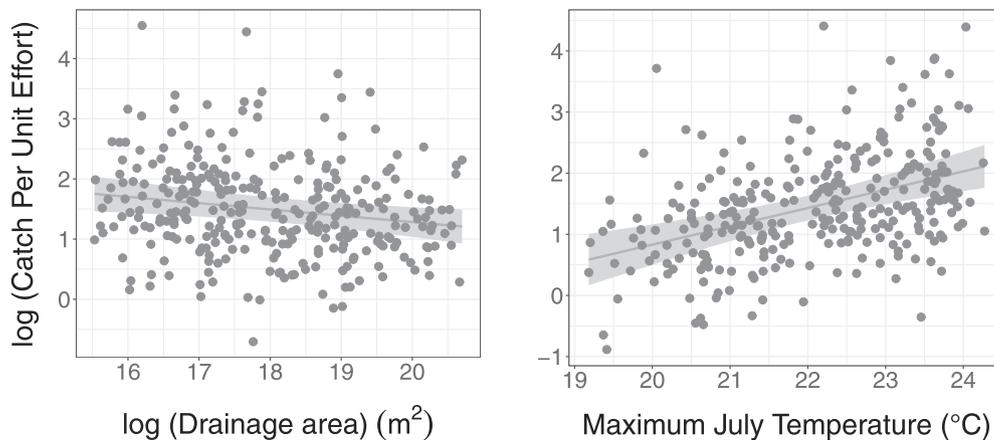


Fig. 4. Partial plots for log-transformed catch per unit effort with drainage area and maximum July temperature. For partial plots, all additional model variables have been corrected to their mean values for improved model interpretation. Shaded areas represent the 95% confidence intervals.

The riparian network disturbance model best explained the proportion of lithophilic spawners ($R^2 = 53\%$; Table 2). More lithophils were found in larger, higher gradient drainages that were receiving more summer precipitation (Fig. 5, Table 3). However, lithophils declined sharply in regions experiencing the warmest and wettest climate due to a strong synergistic interaction between July temperature and change in summer precipitation (std. coefficient = -0.84 ± 0.14 , $P < 0.01$) (Fig. 5). Further, a moderate linear disturbance – climate interaction (std. coefficient = -0.39 ± 0.1 , $P < 0.01$) revealed a potential increase in regions with cooler summers, whereas lithophils declined with increasing disturbance in regions with the warmest summers (Fig. 5).

The assemblage tolerance index (ATI) was best explained using the watershed-level disturbance model ($R^2 = 56\%$, Table 2). Community tolerance was generally higher in smaller, lower gradient drainages (Fig. 6, Table 3). We identified a strong interaction between watershed-level land use and maximum July temperature, with similar trends noted as above for lithophils (std. coefficient = 0.63 ± 0.15 , $P < 0.01$; Fig. 6). Community tolerance increased in regions experiencing warmer summer temperatures in conjunction with higher land use stress (synergistic), whereas a decrease was observed in regions experiencing cooler summer temperatures. Another strong synergistic interaction was observed between change in summer precipitation and drainage area (std. coefficient = 0.51 ± 0.09 , $P < 0.01$; Fig. 6), where more precipitation was associated with lower community tolerance in small streams and higher community tolerance in large streams.

Site-specific regression tree models identified several important climate and habitat quality variables for three of four community metrics (Fig. A.1). More species were found at warmer sites ($>21^\circ\text{C}$), however, richness was similarly high at cooler sites that had lower water conductivity ($R^2 = 0.26$, CV $R^2 = 0.19$; Fig. A.1a). The model for catch per unit effort did not identify any important predictor variables and cross validation error was 100%, indicating very poor model fit. Lithophilic spawners declined in smaller streams receiving less summer precipitation, and in larger drainages that were dominated ($>71\%$) by fine substrates ($R^2 = 0.38$, CV $R^2 = 0.29$; Fig. A.1b). Lastly, intolerant species declined at warmer sites (July air temperatures $>21^\circ\text{C}$ and water temperatures $>11^\circ\text{C}$), and when either fine substrates exceeded 72% or dissolved oxygen levels fell below 7.1 mg/L ($R^2 = 0.53$, CV $R^2 = 0.42$; Fig. A.1c).

4. Discussion

Results from this study highlight the importance of considering potential climate interactions in real-world environments for the improved conservation and management of freshwater resources. In particular, the significance of cumulative human disturbance variables was often contingent on the inclusion of climate interactions due to opposing, climate-dependent land use effects. We observed unexpected positive associations with human disturbance in cooler regions that may be indicative of a subsidy-stress response, whereas community integrity declined with increasing catchment disturbance stress in warmer regions. Further, climate interactions revealed potential indirect effects on habitat quality as well as the important role of stream type in determining potential drought or flooding risks. Site-specific habitat quality models further supported land use model results, demonstrating the combined negative effect of warming and habitat degradation on sensitive species including highly valued coldwater fishes such as Arctic grayling and rainbow trout. However, overall community richness and productivity were not negatively affected by land use, underscoring the importance of field-based multiple stressor studies that may reveal complex species compensatory responses.

4.1. Climate interactions

The potential buffering effect of climate on other stressors has been raised by numerous experimental studies (reviewed in Jackson et al., 2016), however, we observed only partial evidence for climate antagonisms. In this study, the proportion of sensitive species (lithophilic spawners and intolerant species) increased with greater anthropogenic land use, but only in cooler regions (Figs. 5 and 6). Positive land use effects at low to moderate disturbance levels may be indicative of a subsidy-stress response, possibly due to increased nutrients or water temperatures in these naturally cooler and less productive regions (e.g., Piggott et al., 2012). A potential subsidy-stress response was also noted by Scrimgeour et al. (2008), where increased disturbance area was associated with higher occurrences of Arctic grayling and mountain whitefish in higher elevation regions of west-central Alberta. In contrast, we observed a predominance of synergistic interactions in warmer and wetter regions experiencing greater land disturbance (Figs. 5 and 6). As many lithophilic and intolerant species are sensitive to warming water temperatures (Hasnain et al., 2010), fish in regions experiencing the greatest July air temperatures may be experiencing thermal stress, potentially lowering their abilities to withstand concurrent stress following catchment disturbance (Vinebrooke et al., 2004; Lyons et al., 2015). Further, the synergistic interaction between maximum July temperature and change in summer precipitation may be explained by indirect effects such as increased sedimentation run-off, which would compromise lithophilic spawning habitat (e.g., Goudie, 2006; Bryant, 2009; Goode et al., 2012). Notably, sites experiencing both high July temperatures and higher rates of summer wetting were also characterized as having lower current summer precipitation regimes, with sites being concentrated in the northern portion of our study area (Fig. A.2d). Despite having naturally lower precipitation regimes, dry regions are disproportionately sensitive to changes in precipitation which may result in increased flooding events (Ashmore and Church, 2001). Furthermore, sedimentation impacts may be particularly detrimental in northern boreal streams that are being rapidly altered by permafrost loss (Chin et al., 2016). In agreement with our predictions, the interaction between drainage area and change in summer precipitation identified potential benefits of increasing streamflow in smaller streams that may be increasingly vulnerable to stranding and degraded water quality with ongoing climate change (e.g., Brooks, 2009; Leppi et al., 2014; Shanley and Albert, 2014).

Findings from the few field-based freshwater multiple stressor studies that have incorporated climate interactions further highlight the importance of considering ecological context, as well as the great need for an improved mechanistic understanding of combined stressors within a natural setting (Radinger et al., 2016; Bruder et al., 2017; Gutowsky et al., 2019). In this study, the higher prevalence of synergistic climate interactions observed may be specific to northern boreal ecosystems experiencing amplified climate change rates, although future work will be required to substantiate this possibility (Schindler and Lee, 2010). In contrast, Radinger et al. (2016) identified predominantly antagonistic climate – land use interactions on freshwater fish distributions which were attributed to the potential for dominance effects (where one stressor greatly outweighs another) commonly found in smaller lotic systems. However, within the same river system, synergistic interactions were observed in larger rivers experiencing higher land use pressures, suggesting the potential for systems to shift from an antagonistic to a synergistic state once certain stressor thresholds are surpassed. An additional example of ecological context comes from observing the interaction between warming and land use degradation on freshwater trophic state, which can produce either dampened or synergistic net effects depending on the

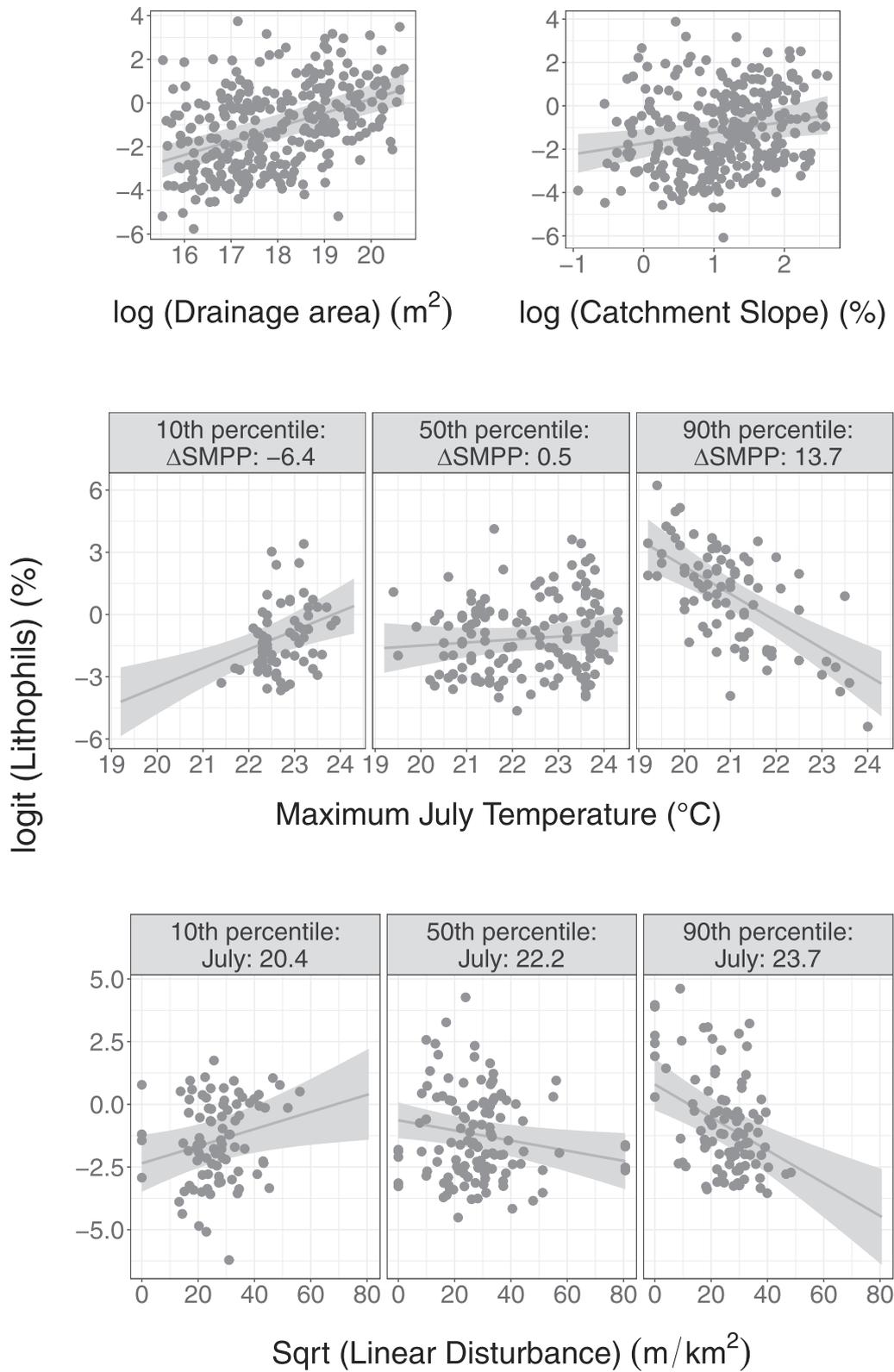


Fig. 5. Partial plots for logit-transformed lithophils (%) with log-transformed drainage area and slope (top), with maximum July temperature by change in summer precipitation (Δ SMPP) (mm) (middle), and with square-root transformed linear disturbance by maximum July temperature ($^{\circ}$ C) (bottom). Cross sectional plots are shown at the 10th, 50th, and 90th percentiles of the interacting variable. For partial plots, all additional model variables have been corrected to their mean values for improved model interpretation. Shaded areas represent the 95% confidence interval.

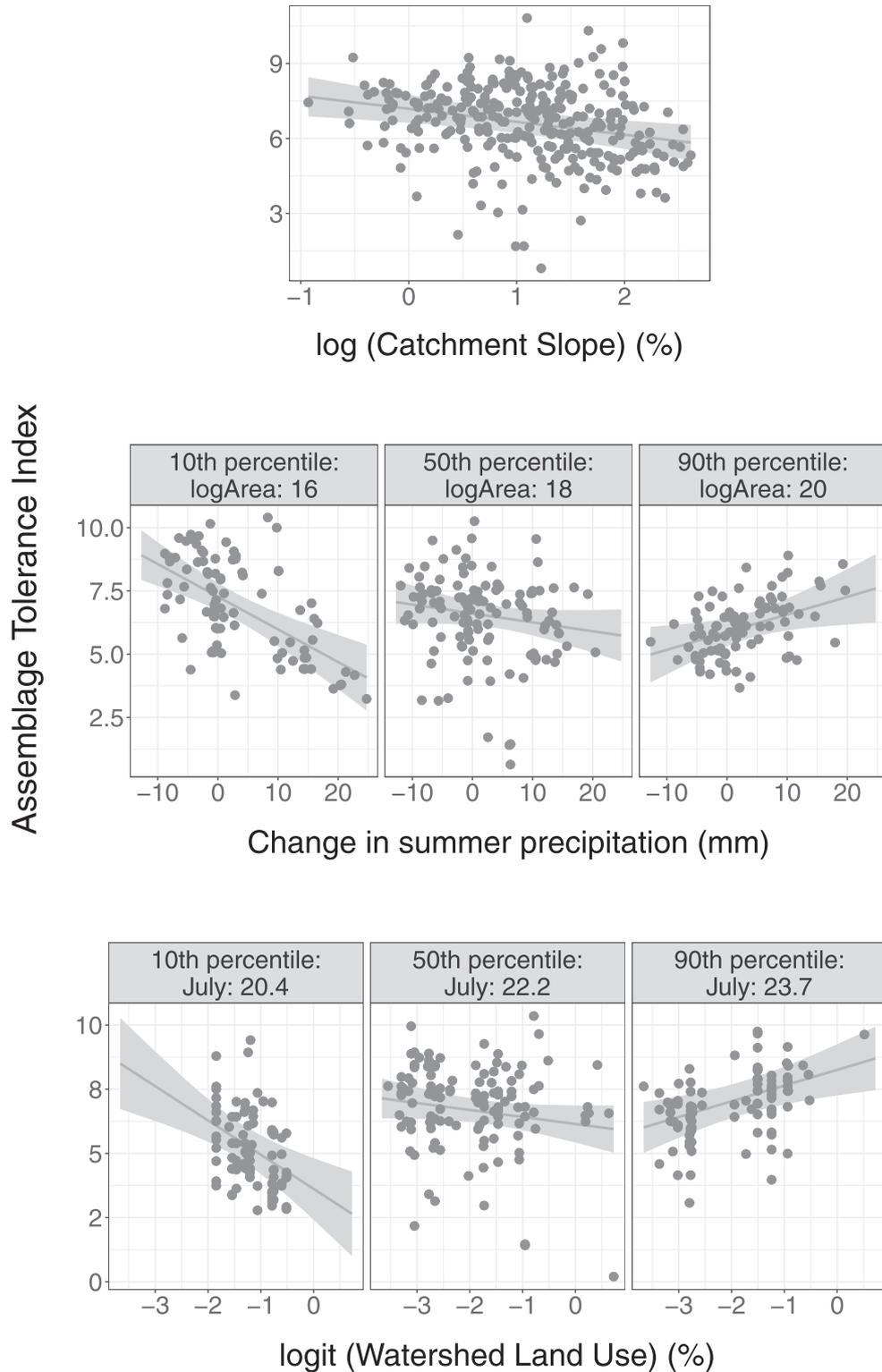


Fig. 6. Partial plots for the Assemblage Tolerance Index (ATI) with log-transformed slope (top), with change in summer precipitation by log-transformed drainage area (m^2) (middle), and with logit-transformed land use by maximum July temperature ($^{\circ}C$) (bottom). The ATI is a scale from one to ten, with a high value indicating a more tolerant community, and a low value indicating a more sensitive community. Cross sectional plots are shown at the 10th, 50th, and 90th percentiles of the interacting variable. For partial plots, all additional model variables have been corrected to their mean values for improved model interpretation. Shaded areas represent the 95% confidence intervals.

original state, the rate of ecological change, and the response of freshwater biota (Smith et al., 1999; Heino et al., 2009; Jacobson et al., 2010; Porter et al., 2013). For instance, Gutowsky et al. (2019) observed an antagonistic interaction between warming and forest cover loss on lake fish biomass, indicating that warming-induced productivity may be partly offsetting concurrent land use effects in regions with naturally lower trophic states. In contrast, climate and land use-mediated eutrophication of freshwaters has been widely observed at lower latitudes, producing devastating consequences for aquatic biodiversity (Heino et al., 2009).

4.2. Independent effects of land use, climate, and stream size on overall richness and productivity

Potential species compensatory dynamics and subsidies at low-moderate disturbance levels may be masking land use effects, particularly for richness and productivity metrics which contain a wider species tolerance portfolio (Vinebrooke et al., 2004; Jackson et al., 2016). Increasingly degraded habitats may favour the success of more tolerant or generalist species over intolerant species, which has been observed in many lotic systems (Bramblett et al., 2005), including watersheds in southern and central Alberta (Stevens et al., 2010; Cantin and Johns, 2012). We observed tenuous support for linear disturbance in the top species richness models, and caution that further investigation would be required to confirm this potential relationship. However, we speculate that the observed increase in species richness with low levels of linear disturbance up to a peak of approximately 1225 m/km² may be attributed to potential stream subsidies (Fig. 3; Allan, 2004; Wagenhoff et al., 2011). Another potential explanation for this trend may be the intermediate disturbance hypothesis, where moderately disturbed ecosystems are theorized to have higher species richness due to a reduction in competitive exclusion (Connell, 1978). In this case, systems with intermediate catchment disturbance may produce indirect effects such as flashier flows, increased sedimentation, or altered water quality, that may keep the watershed in a slightly higher state of flux compared to baseline conditions (Townsend et al., 1997).

Species richness and community catch were greater in regions with longer growing seasons, and higher July temperatures, respectively (Figs. 3 and 4). It has been well established that warmer regions generally support greater species diversity and productivity due to higher and more seasonally stable resources (e.g., species energy theory), combined with a lower risk of overwinter mortality (Krebs, 2008; Shuter et al., 2012; Rypel and David, 2017). Further, warmer regions are closer to recent glacial refugia, facilitating higher species dispersal rates (Abell et al., 2008). Drainage area was an important predictor in all community models, however mixed results were observed (Figs. 3–6). In particular, species richness was strongly related to increased drainage area, which is in agreement with the species-area hypothesis and typical of small lotic systems that support increased habitat heterogeneity required for varying fish life stages, including more critical overwintering habitat, in areas further downstream (Gorman and Karr, 1978; Connor and McCoy, 1979). However, both community catch and the ATI index were higher in smaller catchments, which may be related to sampling methodology or species preferences specific to the dataset used. For example, our finding that more fish are found in smaller catchments is likely an artefact of backpack electrofishing, as it is more effective in smaller drainages where fish are unable to escape (Portt et al., 2006). Further, the positive relationship with the ATI may be explained by the prevalence of small-bodied tolerant species (e.g., brook stickleback) in this dataset that are commonly found in small watercourses with low to moderate flows (Langhorne et al., 2001).

4.3. Study limitations

While we selected an extensive human disturbance dataset available for the study region, the dataset still had several potential limitations. First, grouping of all disturbance variables was necessary to avoid low individual gradients, however this removed our ability to distinguish disturbance types that may have yielded differing impacts on watershed integrity (Esselman et al., 2011). The disturbance data may have also been limited due to spatial and temporal constraints, for example all disturbance data was identified using 2008–2010 satellite imagery yet some of these effects may have been in place for many years prior. Conversely, watershed alteration that occurred after 2010 would not have been accounted for in our analyses, possibly masking the detection of disturbance trends.

We did not have data for several key variables, such as nutrient levels or streamflow, which have been demonstrated as good predictors of land use stress elsewhere (Stevens et al., 2010; Cantin and Johns, 2012; Lange et al., 2014). Further, reductions in fishing pressure over time may influence results, as was suggested by Arciszewski et al. (2017) as a possible explanation for a recently observed rise in fish abundance near the Athabasca oil sands. While we used the most up to date hydrology dataset for the region (AEP, 2018b), we did not have information regarding any previous instream habitat loss or alterations that may have altered local fish community structure. Lastly, we note that potential stressor mechanisms identified in this study would require testing in controlled, experimental settings to determine causation. Until then, it is possible that relationships observed here are due to correlation with untested variables, for example spatially correlated variables relating to differing species assemblages or disturbance mechanisms, watershed connectivity, or fine-scale processes.

4.4. Conservation and management implications

Despite the mounting threat of climate change worldwide, potential climate interactions with other cumulative stressors continue to be overlooked in typical conservation and management planning (Mantyka-Pringle et al., 2016). The inherent risk in ignoring potential climate interactions is likely to accelerate over time, and poorly informed management actions may lead to (at best) ineffective outcomes to (at worst) negative consequences for biodiversity (Côté et al., 2016). Modified solutions may be required for stressors involved in antagonistic interactions, as mitigation of a non-dominant stressor could lead to a net negative outcome. Further, identifying additive or synergistic interactions that may reach detrimental ecological threshold points under future climate and land use scenarios will be critical for prioritizing conservation efforts and thereby minimizing future biodiversity losses.

Regionally specific multiple stressor studies that include field-based validation will help to expedite successful conservation outcomes, particularly if they are designed for integration with current environmental management frameworks. For example, the Government of Alberta, Canada, has implemented an adaptive cumulative effects management framework that incorporates semi-quantitative dose-response relationships for facilitating informed management decisions (MacPherson et al., 2014). Regional multiple stressor studies such as ours could be used for refining their models, including the consideration of novel stressor interactions, and identifying potential stressor hotspots that could be used for conservation prioritization (Fig. A.2). For instance, we identified that lower Athabasca River fish populations may be at a higher risk to future warming and oil sands development, possibly warranting more strategic land use planning and/or climate adaptation strategies for this quickly evolving region (Schindler and Lee, 2010). The Athabasca watershed supports many highly

valued and already threatened coldwater fishes that may be increasingly vulnerable to the combined effects of warming and disturbance, including Arctic grayling (listed as a species of special concern in Alberta; AEP and ACA, 2015), rainbow trout (listed as endangered under COSEWIC; COSEWIC, 2014), and bull trout (listed as a species of special concern under COSEWIC; COSEWIC, 2012). In contrast, potential land use subsidies observed in cooler, higher elevation regions suggest currently low levels of stress, however, this interaction has the potential to tip from antagonistic to synergistic under future warming scenarios.

5. Conclusion

Our study provides evidence for complex interactions between warming and co-occurring stressors in a northern boreal region experiencing substantial land use and climate changes pressures. In particular, sensitive fish species (e.g. rainbow trout, Arctic grayling) declined owing to synergistic interactions between warming, increased rainfall, and land use intensity. Our use of an extensive field dataset allowed the identification of regions that may be increasingly vulnerable to ongoing climate change and land use impacts (e.g. warmer and wetter regions), versus regions that may be temporarily benefiting from low-moderate land use subsidies (e.g. cooler and less productive regions). Based on our results, we caution that the continued exclusion of mounting climate change effects in standard conservation and management plans may result in detrimental long-term impacts on freshwater biodiversity.

CRedit authorship contribution statement

Alyssa Murdoch: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization, Project administration, Funding acquisition. **Chrystal Mantyka-Pringle:** Conceptualization, Methodology, Writing - review & editing, Supervision. **Sapna Sharma:** Conceptualization, Methodology, Writing - review & editing, Supervision.

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Appendix A. Supplementary data

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