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Hydroclimatic Conditions, Wildfire, and Species Assemblages Influence Co-Occurrence of Bull Trout and Tailed Frogs in Northern Rocky Mountain Streams

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Abstract: Although bull trout (*Salvelinus confluentus*) and tailed frogs (*Ascaphus montanus*) have co-existed in forested Pacific Northwest streams for millennia, these iconic cold-water specialists are experiencing rapid environmental change caused by a warming climate and enhanced wildfire activity. Our goal was to inform future conservation by examining the habitat associations of each species and conditions that facilitate co-occupancy. We repurposed data from previous studies in the northern Rocky Mountains to assess the efficacy of bull trout electrofishing surveys for determining the occurrence of tailed frogs and the predictive capacity of habitat covariates derived from in-stream measurements and geospatial sources to model distributions of both species. Electrofishing reliably detected frog presence (89.2% rate). Both species were strongly associated with stream temperature and flow regime characteristics, and less responsive to riparian canopy cover, slope, and other salmonids. Tailed frogs were also sensitive to wildfire, with occupancy probability peaking around 80 years after a fire. Co-occupancy was most probable in locations with low-to-moderate frequencies of high winter flow events, few other salmonids, a low base-flow index, and intermediate years since fire. The distributions of these species appear to be sensitive to environmental conditions that are changing this century in forests of the northern Rocky Mountains. The amplification of climate-driven effects after wildfire may prove to be particularly problematic in the future. Habitat differences between these two species, considered to be headwater specialists, suggest that conservation measures designed for one may not fully protect the other. Additional studies involving future climate and wildfire scenarios are needed to assess broader conservation strategies and the potential to identify refuge streams where both species are likely to persist, or complementary streams where each could exist separately into the future.

Keywords: *Ascaphus montanus*; detection; electrofishing; *Salvelinus confluentus*; snorkeling; wildfire; winter scour

1. Introduction

Forested montane stream environments in the Pacific Northwest and northern Rocky Mountains support several endemic species and species of conservation concern. These species are at risk of range contractions and local population extirpations as their habitat conditions shift in association with climate change. The stability of these freshwater habitats over previous millennia, including through multiple glacial and interglacial cycles, has provided important refuges for species adapted to the unique thermal conditions, hydrology, and food webs of headwater streams. These refuges, however, are changing rapidly in the Anthropocene [1] as snowpacks melt and runoff earlier [2,3], flood regimes change [4], summer flows and habitat volume decrease [5,6], and stream temperatures increase [7,8]. As these changes occur, stream reaches near the downstream extent of headwater species' distributions become too warm for cold-adapted species, resulting in thermal stress, diseases, and increased risk of local extirpations [9–11]. Along with changing stream conditions, invasion by native and non-native fishes and amphibians can also cause increased predation, competition, or hybridization [12–14].

Although some streams in the Pacific Northwest are predicted to serve as long-term climate refuges for cold-water species [15,16], variability stemming from enhanced disturbance processes may also degrade the thermal conditions and overall habitat suitability in these locations [17–19]. Wildfires, in particular, are burning larger areas and at higher severity, extending to higher elevations, and interacting more frequently with stream channels in northern montane forests over the last several decades, partly influenced by drought and changes in fire weather [20–22]. Although wildfires often have long-term benefits to streams in terms of enhancing habitat diversity [23–25], cold-water species may be vulnerable to short- to medium-term (i.e., ~1–20 years) warming effects when riparian vegetation, and the shade it provides, is burned. In burned watersheds in Montana, for example, maximum stream temperatures were 1.4–2.2 °C higher compared to nearby unburned streams; the largest differences were recorded in July and August [26]. These differences persisted for years, yet dissipated as the water flowed downstream into unburned areas of the catchment. Other studies have reported even larger changes, with mean and maximum summer water temperatures increasing by 3.7 °C and 5.2 °C, respectively, in the first 13 years following wildfire [27]. While such dramatic and persistent changes are possible, stream temperature changes after wildfire are variable and influenced by riparian and watershed-level burn severity and extent, and catchment aspect, gradient, snowpack, groundwater sources, remaining tree cover, and riparian forest recovery [19,28]. Streams flowing through burned watersheds are also more vulnerable to high intensity spates, debris flows, and channel reorganizing events during the period of post-fire recovery, which can also affect stream temperatures and fish and amphibian populations [27,29,30].

The bull trout (*Salvelinus confluentus*) is a char in the family Salmonidae that is endemic to northwestern North America (Figure 1). Bull trout are typically found where water temperatures remain below 13 °C, such as in high-elevation streams and headwaters, or in deep pools [31]. Bull trout spawn in the fall and eggs incubate in the streambed for a prolonged overwinter period, potentially making them vulnerable to flood disturbances [18,32]. Population declines of bull trout led to a 1995 listing of Special Concern in Canada and a 1998 listing as Threatened under the U.S. Endangered Species Act [33]. Bull trout have garnered particular concern among biologists about how it will cope with increasing water temperatures [34]. Several studies have documented range contractions along the warm-edge distributional boundary of the species [35–37] and a recent analysis of nearly 22,000 survey sites in the northern Rocky Mountains concluded that bull trout occupancy has already decreased by 18% between 1993 and 2018, with additional decreases of 39% predicted by 2080 because of climate-driven increases in water temperature and decreases in summer flow [38]. Not accounted for in those estimates, are bull trout requirements for low-sediment gravel beds for reproduction and large, instream wood and undercut banks for cover. Wildfire is thought to have negative consequences for these habitat characteristics for bull trout, particularly when compounded by effects of climate change [39].

The Rocky Mountain tailed frog (*Ascaphus montanus*) is thought to require similar habitat conditions as bull trout, but has received far less attention. The tailed frog is an ancient species, retaining the most ancestral morphological characteristics of any frog species worldwide [40]. Rocky Mountain tailed frogs are one of only two species in the family Ascaphidae and, like bull trout, they are endemic to the Pacific Northwest [41] (Figure 1). Like bull trout, tailed frogs occupy cold, clear streams with low interstitial sediment. Tailed frogs prefer water temperatures below 10–11 °C [42] and only tolerate warmer water temperatures for short periods of time [43]. Tailed frogs have among the slowest development rate known of any frog and, in the northern Rocky Mountains, tadpoles require at least 3 years to reach metamorphosis and several more years to become sexually mature. Adult survival is high (0.885–0.901) with adults living >15 years [44]. Hence, as with bull trout, there is concern that climate-induced stream degradation related to increasing water temperatures, evolving flood patterns, or sedimentation after wildfire could influence their distribution and threaten the persistence of some populations [45]. This risk could be substantial, as at least 24% of the Rocky Mountain tailed frog's range has burned since 1987 [46].

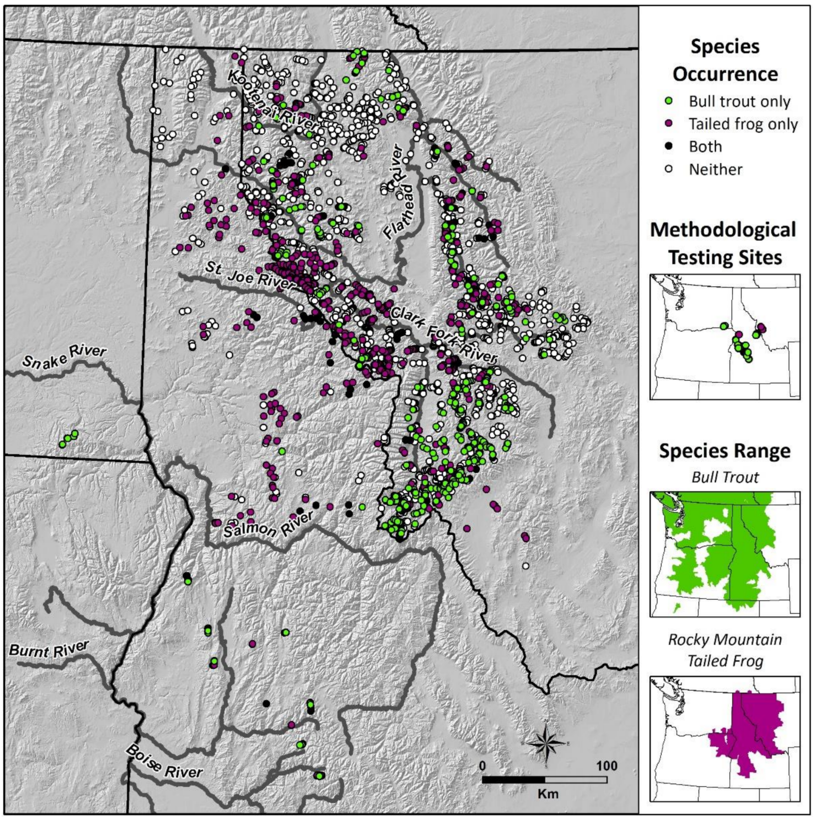

Figure 1. Map of the 2829 stream surveys used in this study. All surveys were conducted within the known range of the Rocky Mountain tailed frog (*Ascaphus montanus*) and bull trout (*Salvelinus confluentus*; see inset maps). Survey points represent 100-m reaches and are color coded based on the detection of each species during electrofishing surveys in 2006–2011. We conducted methodological tests on a smaller dataset of biological surveys conducted 1994–2002, shown in the top right inset.

Here we investigate the occupancy patterns of bull trout and tailed frogs across the northern Rocky Mountains to better understand the environmental conditions and habitat associations of these cold-water species, threats associated with climate change and wildfire, and opportunities to conserve tailed frog habitat and populations, perhaps under the umbrella of bull trout habitat management. In particular, we sought to determine if these species readily co-exist at the stream reach-scale, or whether their habitats are partitioned. To investigate this topic, we used existing electrofishing data from nearly 3000 survey sites in the northern Rocky Mountains to address several questions: (1) how often do bull trout and tailed frogs co-occur? (2) what are the characteristics of habitats occupied by each species? (3) what habitat characteristics are associated with co-occupancy? (4) how might changes in climate and wildfire influence occupancy and co-occupancy? Prior to this analysis, we conducted methodological tests on a separate set of survey sites to evaluate: (1) whether electrofishing was an effective method of detection for tailed frogs; and (2) whether geographic information system (GIS) derived environmental and habitat variables were sufficient for occupancy analysis in the absence of field-measured predictor variables. We hypothesized that bull trout and tailed frogs would occupy the coldest streams, but tailed frogs would be found at higher elevations and steeper gradients compared with bull trout because tailed frog tadpoles can occupy shallower waters and adults can cross barriers and move overland. We also hypothesized that streams where both species occurred would be relatively rare (i.e., because of niche partitioning and predation by bull trout on tailed frogs) and have environmental conditions intermediate to each species' optimal conditions. Finally, we hypothesized that both species would have lower probability of occupancy in streams flowing through watersheds burned by recent wildfires, but this effect would diminish with time since fire.

2. Materials and Methods

2.1. Study Area

Study sites were selected within the known range of both bull trout and Rocky Mountain tailed frogs in central Idaho, western Montana, and eastern Washington (Figure 1). We used a subset of data from Isaak et al. [42], filtered to include 2829 electrofishing surveys that met four criteria: (1) they were conducted within the range of both species, (2) they included presence/not detected information for both species, (3) they represented unique sites, with no repeat surveys of stream reaches within, or between, years, and (4) they were conducted 2006–2011, to represent a more contemporary timespan where detection information was consistently recorded. We used this dataset to address Questions 1–4. Prior to our primary analysis, we conducted methodological tests using a subset of data from Peterson et al. [47] and Thurow et al. [48] to evaluate the effectiveness of electrofishing for detecting tailed frogs (106 surveys) and to assess the relative importance of variables measured in-stream versus those derived from remote sensing or GIS (96 surveys). These electrofishing surveys met the same criteria as mentioned above, except that data were collected 1994–2002 and we restricted surveys to those which collected each of 20 field-measured predictor variables relating to benthic substrates, stream habitat type, water depth, flow, and temperature, large woody debris, and riparian vegetation (Table S1). GIS-derived variables corresponding to those reported by Isaak et al. [42] were also extracted for this dataset. All sites were sampled by trained state and federal fisheries biologists during summer baseflow periods that typically occurred July–September.

2.2. Electrofishing Detection of Tailed Frogs

Before conducting occupancy analyses, we evaluated the reliability of three-pass electrofishing for detecting tailed frogs by comparing detections against snorkel surveys in 106 sites (~100-m long stream reaches) in 1st through 3rd order streams. Peterson et al. [47] and Thurow et al. [48] had selected these sites using sampling strata based on environmental data derived from previously sampled bull trout streams in the region; hence this smaller dataset covered a broad range of habitat conditions. Sample sites were selected within each stratum. Strata were defined by features including channel wetted width, gradient, large wood density, and length of undercut banks [47,49]. To meet the assumption of a closed population, they used 7 mm square-mesh nets secured to the streambed to block off each site prior to sampling and they selected locations with abrupt changes in channel gradient as hydraulic controls for upper and lower boundaries of each site to ensure adequate closure. All block nets were maintained in place until sampling was concluded.

Sites were sampled via day snorkeling between 1000 and 1700 h and night snorkeling between 2230 and 0230 h within the same 24-h period (following Thurow et al. [48]). For logistical and safety reasons, at most sites they completed day snorkel surveys first. They used identical sampling techniques during day and night, except that night snorkel counts included a hand-held underwater halogen light. Day snorkelers occasionally also used a halogen light to inspect shaded locations. All snorkeling began at the downstream end of each study site and was completed in a single upstream pass. After snorkeling, sites were undisturbed for an average of 4 h prior to electrofishing surveys, which consisted of three consecutive upstream passes using a backpack electrofisher set predominately on unpulsed DC (following Peterson et al. [47]). During each electrofishing pass, captured tailed frog tadpoles and adults were held in live wells at stream margins and approximately 0.5 h elapsed between successive electrofishing passes. Previous research has found that tailed frogs are not harmed by electrofishing [50]. After the final electrofishing pass, frogs were positively identified and released back into the site. All three sampling methods were completed within a 24–28 h period to minimize between-method variations in weather or site conditions at each study site.

We used these data to compare tailed frog detection probabilities for day snorkeling, night snorkeling, and electrofishing. Detections of tailed frog tadpoles and adults were recorded separately, but only tadpoles were used in the analysis because adults are often terrestrial and fewer adults were observed using the methods we employed.

2.3. Importance of GIS-Derived versus Field-Measured Predictor Variables

To assess the relative importance of GIS-derived versus field-measured environmental and habitat predictor variables, we developed occupancy models for both species using a subset of the data (n = 96 sites) from Peterson et al. [47] and Thurow et al. [48]. This subset was determined by sites where all instream variables were measured. This step was important because few of the 2829 electrofishing surveys that had been previously compiled [51] had field-measured habitat variables and, for those that did, they were often not measured consistently. Hence, we needed to understand what information might be lost in the absence of instream-measured predictor variables. We conducted this preliminary analysis using non-parametric multiplicative regression (NPMR) in HyperNiche 2.30 [52]. We developed separate models for each species, with response variables as either occurrence of bull trout in a survey reach (i.e., presence of any life stage versus species not detected) or occurrence of pre-metamorphic tailed frogs in a survey reach (i.e., presence versus non-detection of tadpoles) during electrofishing surveys (Table 1). For each NPMR analysis, we used a local mean (LM) model option with Gaussian weighting functions. All combinations of predictor variables were available for selection and models were identified with the greatest fit for each number of included predictor variables. The final model for each response variable met an improvement criterion of having a fit at least 5% better than the best model with one fewer predictor variables. NPMR is well suited to these, and subsequent, analyses because it allowed us to model occupancy as a function of non-linear, multiplicatively interacting combinations of predictor variables [52].

Table 1. Variables used in the occupancy models for bull trout and tailed frogs across 2829 sites. All species detections were based on observations from three-pass electrofishing surveys. See Isaak et al. [42] and Table 1 in Isaak et al. [51] for rationale for inclusion of variables in bull trout and tailed frog occupancy models (except where noted).

Variable Type	Variable Name	Variable Description
Response variables	Tailed frog occupancy	Binary variable for whether tailed frog tadpoles were detected at a site
	Bull trout occupancy	Binary variable for whether bull trout were detected at a site
	Co-occupancy	Binary variable for whether tailed frog tadpoles and bull trout were detected at a site, where a value of 1 indicates both species were detected and a value of 0 indicates only bull trout were detected
Environmental predictor variables	HUC	8-digit Hydrologic Unit Code (4th code HUCs) containing the survey site
	Slope	Slope of the stream reach, calculated as the drop in elevation divided by segment length (m/m) [53] (accessed on 15 May 2021)
	Drainage area	Cumulative drainage area in the watershed upstream from the survey site [53]
	Lakes upstream	Percentage of watershed upstream composed of lake or reservoir Surfaces [53]
	Base-flow index	Base-flow index calculated as the ratio of base flow to total flow (%, https://water.usgs.gov/GIS/metadata/usgswrd/XML/bfi48grd.xml, accessed on 15 May 2021)
	Winter high flow events	Number of days during winter when flows are in the upper 95% of the flow record
	August discharge	Mean August stream discharge (m^3/s; http://waterdata.usgs.gov/nwis/rt, accessed on 15 May 2021)
	August stream temperature	Mean August stream temperature (°C) for a baseline climate period (1993–2011) derived from the NorWeST model [51]

Table 1. *Cont.*

Variable Type	Variable Name	Variable Description
Wildfire predictor variables	Riparian canopy cover	Percent canopy derived from the NLCD 2011 USFS Tree Canopy Cartographic layer (https://www.mrlc.gov/data/nlcd-2011-usfs-tree-canopy-cover-conus, accessed on 15 May 2021)
	Presurvey fires	The number of wildfires [54], (accessed on 7 October 2021) intersecting a portion of the survey reach's upstream area, prior to the survey year
	Years since fire	Years between the most recent wildfire prior to the survey and the survey year [54]
	Years since oldest fire	Years between the oldest recorded wildfire prior to the survey and the survey year [54]
Predictor variables for biotic interactions	pSACO	In models predicting tailed frog occupancy, this binary variable indicated whether bull trout were detected at a site
	nSACO	In models predicting tailed frog occupancy, this variable indicated the number of bull trout detected
	pASMO	In models predicting bull trout occupancy, this binary variable indicated whether tailed frog tadpoles were detected at a site
	nTrout	The cumulative number of non-bull trout salmonids detected at a site
	nONCL	The number of cutthroat trout individuals detected at a site
	nSAFO	The number of brook trout individuals detected at a site
	nONMY	The number of rainbow trout individuals detected at a site
	nSATR	The number of brown trout individuals detected at a site

Abbreviations include: ASMO = *Ascaphus montanus*; ONCL = *Oncorhynchus clarkia lewisii*; ONMY = *Oncorhynchus mykiss*; SATR = *Salmo trutta*; SAFO = *Salvelinus fontinalis*; SACO = *Salvelinus confluentus*.

During modeling, we included both field-measured biotic and abiotic predictor variables and GIS-derived predictor variables. Field-measured predictor variables are listed in Section 2.1, and further described in Thurow et al. [48] and in our supplement. Biotic data were collected during electrofishing surveys and included presence versus non-detection of tailed frogs and counts of fish observed by species (Table 1). We used counts of five fish species (westslope cutthroat trout, *Oncorhynchus clarkia lewisii*; rainbow trout, *Oncorhynchus mykiss*; brown trout, *Salmo trutta*; brook trout, *Salvelinus fontinalis*; and bull trout) with sufficient sample sizes and dropped Chinook salmon (*Oncorhynchus tshawytscha*) because of extremely low prevalence. The GIS-derived predictor variables included for each study reach are described in Table 1, in Isaak et al. [51], or in the case of wildfire variables, in Section 2.7, below. GIS variable values were derived for the survey location in the stream (i.e., downstream point of a 100-m survey reach), but each GIS layer had a different spatial resolution ranging from 30 m (e.g., Slope) to 1 km (e.g., Riparian Canopy Cover) to entire watersheds (e.g., HUC and Drainage Area), as described by Isaak et al. [51]. Hence, the potential scale of inference of each predictor variable on species occupancy is unique to that variable.

In addition to the variables described in Table 1, we assessed several other variables that were later dropped because of high inter-correlations or redundancy with factors that had more direct influence on target species occupancy. For example, summer stream temperature and summer stream flow were dropped because they were correlated with August stream flow and temperature, which were stronger predictors in preliminary model runs. Likewise, latitude and longitude were dropped because they primarily described geographical subsets in the data and these subsets were already accounted for by including 4th level Hydrologic Unit Codes (HUC). Elevation and precipitation were excluded after initial inspection because these variables were highly correlated with stream temperature and flow metrics. We did, however, plot these data in Figure S1 to provide additional context for species occupancy and co-occupancy patterns.

2.4. How Often Do Bull Trout and Tailed Frogs Co-Occur?

To assess the frequency of co-occupancy (Question 1), we quantified the percent of 2829 randomly selected sites within the two species' ranges that were occupied by four different combinations of species occupancy: neither species detected (Neither), tailed frogs detected and bull trout not-detected (Tailed Frog only), bull trout detected and tailed frogs not detected (Bull Trout only), and both species detected (Both).

2.5. What Are the Characteristics of Habitats Occupied by Each Species?

We used NPMR analysis using GIS-derived variables to assess which factors predict occupancy of each species at 2829 sites within the overlapping portion of the species' ranges (Question 2). See Section 2.3 for a description of the modeling approach and GIS-derived variables.

2.6. What Habitat Characteristics Are Associated with Co-Occupancy?

To assess which habitat characteristics are associated with co-occupancy of bull trout and tailed frogs within a stream reach (Question 3), we developed one model using GIS-derived variables to predict stream reaches classified as Both versus Bull Trout Only, under the assumption that predatory bull trout could potentially exclude tailed frogs [55] or that tailed frogs have unique conditions under which they will occur regardless of the presence of bull trout. This model was developed using 481 observations (150 Both and 331 Bull Trout-only sites) and associated predictor variables (Table 1). We further examined habitat variables associated with our four occupancy categories (i.e., Neither, Tailed Frog only, Bull Trout only, Both; n = 2829) by plotting each in a series of distribution plots.

2.7. What Are the Wildfire Trends across Occupancy and Co-Occupancy Categories?

To assess wildfire trends across the four occupancy categories (Question 4) and to create wilfire predictor variables for other questions, we extracted fire occurrence data [54] for each of the 2829 survey location watersheds (HUC12) using GIS processing. This resulted in 1578 instances where fires overlapped portions of our study site watersheds, ranging from 1878 to 2019. For each site, we calculated the number of reported pre-survey wildfires, the time between the first (i.e., oldest on record) fire and the survey, and time between the most recent pre-survey fire and the survey to use as potential predictor variables in occupancy models (Table 1). To quanitify wildfire trends through time, we calculated the proportion of sites in each of our four occupancy categories that experienced some wildfire in each decade in the 1878–2019 timespan. Since record-keeping, reporting, and wildfire data centrialization have improved over time, we acknowledge that older fires may be underreported in these analyses [54].

3. Results

3.1. Was Electrofishing Effective for Detecting Tailed Frogs?

In 106 sites where all three survey methods were conducted, tailed frog tadpoles were detected by at least one method in 69.8% of reaches sampled. Electrofishing and day snorkeling were comparable, with tadpoles detected in 22.6% of sites. These methods were not as accurate as night snorkeling, however, which detected tadpoles in 55.7% of reaches sampled. In contrast, adult frogs were detected by at least one method in only 39.6% of reaches sampled, mostly by electrofishing (33.0% of sites), followed by day snorkeling (10.4%) and night snorkeling (7.5%). Despite this apparent high detection rate of tailed frog adults using electrofishing compared with other methods, adults were detected without tadpoles in only three sites using electrofishing. Adult frogs were mostly detected along with tadpoles (32 of 106 electrofishing surveys) or tadpoles were detected without adults (34 of 106 electrofishing surveys). Most importantly, we only failed to detect tadpoles using electrofishing at 8 of 74 sites where the species was determined present using other methods (Table S2). Hence, using electrofishing, our detection probability for tailed frog tadpoles was 89.2% and tadpole occupancy was indicative of species occupancy.

3.2. What Was the Relative Importance of Field-Measured versus GIS-Derived Predictor?

When we included both field-measured and GIS-derived variables as potential predictors in occupancy models for each species, a total of 11 predictor variables were included in the models, but only one of them was a field-measured variable (percent undercut bank was predictive of tailed frog occupancy; Table 2). No field-measured variables were selected for bull trout. These models suggest that our pool of GIS-derived predictor variables is capable of explaining much of the variability in occupancy and that both species tend to occur in locations with colder summer water temperatures and low-to-intermediate winter high flow events. Tailed frog occupancy was related to cool August water temperatures (~10 °C), intermediate numbers of winter high flow events, intermediate amounts of undercut bank morphology, and the absence of bull trout ($\log\beta = 9.9$; $p = 0.02$, $N^* = 8.1$; Figures S2 and S3). The presence of bull trout (pSACO) reduced the probability of tailed frog occupancy by about 40%, a strong negative relationship. Bull trout occupancy was highest in locations with fewer winter high flow events, cold August water temperatures, and relatively high riparian canopy cover ($\log\beta = 15.3$; $p < 0.001$, $N^* = 41.9$; Figure S4).

Table 2. Top predictor variables in occupancy models for Rocky Mountain tailed frogs and bull trout in 96 sites where both field-measured and GIS-derived predictors were collected. We also report the source, model Sensitivity (relative importance), Tolerance (niche breadth), and % Tolerance (percent of the variable's range) for each selected variable. Na indicates test statistics that could not be calculated because the predictor variable was binary.

Response	Predictor	Source	Sensitivity	Tolerance	% Tolerance
Tailed frog occupancy	August stream temperature	GIS	0.36	0.67	15
	Winter high flow events	GIS	0.25	1.89	15
	Percent undercut bank	Field	0.25	14.50	20
	Bull trout occupancy (pSACO)	Field	na	na	na
Bull trout occupancy	August stream temperature	GIS	0.36	0.90	20
	Winter high flow events	GIS	1.26	0.63	5
	Riparian canopy cover	GIS	0.07	34.68	45

3.3. How Often Do Bull Trout and Tailed Frogs Co-Occur?

Neither species was detected in nearly 60% of the 2829 surveyed sites. Sites where tailed frogs but no bull trout were observed (Tailed Frog Only) accounted for 23.5% of sites, whereas Bull Trout Only were detected in 11.7% of sites. Co-occupancy was rare, with only 5.3% of sites having detections of both species (i.e., Both). After combining Tailed Frog Only- and Both sites, tailed frogs were detected in a total of 29% of sites, whereas combining Bull Trout Only with Both sites resulted in a total of 13.1% of sites having bull trout detections (Figure 2).

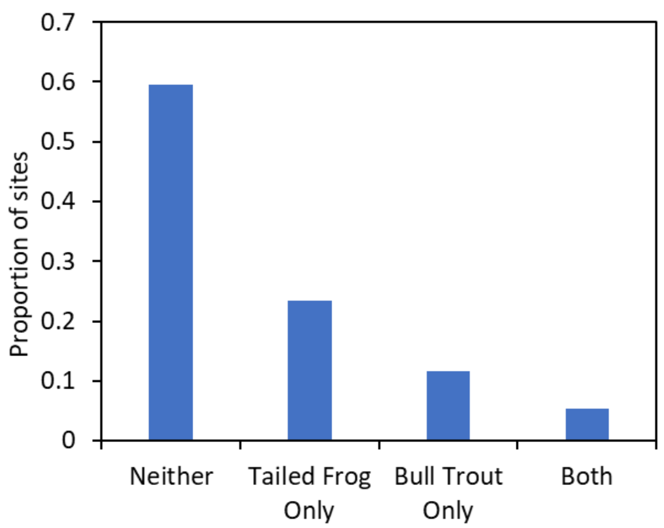

Figure 2. The proportion of 2829 stream electrofishing surveys, within the Northern Rocky Mountain range of Rocky Mountain tailed frogs (*Ascaphus montanus*) and bull trout (*Salvelinus confluentus*), where neither species was detected, only tailed frog tadpoles were detected (Tailed Frog Only), only bull trout were detected (Bull Trout Only), and where both species were detected in the same site.

3.4. What Are the Characteristics of Habitats Occupied by Each Species?

Occupancy models for each species indicate that both tailed frogs and bull trout are most sensitive to summer water temperatures and hydrologic flow regimes. In particular, the variable representing winter high flow events was selected in all models and August stream temperature appeared in both tailed frog and bull trout occupancy models (Table 3). Tailed frog occupancy was highest in locations with high riparian canopy cover, colder August water temperatures, lower base flow index, intermediate years since fire (i.e., 60–80 years), and fewer winter high flow events, except where base flow index was high (logβ = 59.4; p < 0.01, N* = 156.4; Table 3; Figure 3). Of these important predictors, tailed frog occupancy was most sensitive to site differences in riparian canopy cover, followed by base-flow index and August stream temperature. Tailed frog occupancy was least sensitive to year since fire and winter high flow events.

Table 3. Important predictors of tailed frog occupancy, bull trout occupancy, and co-occupancy. For each predictor variable, we show its Sensitivity (relative importance), Tolerance (niche breadth), and % Tolerance (percent of the variable's range) values for each model.

Response	Predictor	Sensitivity	Tolerance	% Tolerance
Tailed frog occupancy (n = 2829)	Riparian canopy cover	0.1967	19.5	20
	Base-flow index	0.1841	3	10
	August stream temperature	0.1781	1.91	15
	Years since fire	0.1443	22.35	15
	Winter high flow events	0.1126	3.138	25
Bull trout occupancy (n = 2829)	Winter high flow events	0.4519	1.26	10
	Number of cutthroat trout (nONCL)	0.4348	35.45	5
	Slope	0.2767	0.03	10
	August stream temperature	0.1062	2.534	20
Co-occupancy (n = 481)	Winter high flow events	0.8312	0.52	5
	Number of salmonids (nTrout)	0.6196	77.55	5
	Base-flow index	0.3674	1.95	15
	Years since fire	0.0851	52.15	35

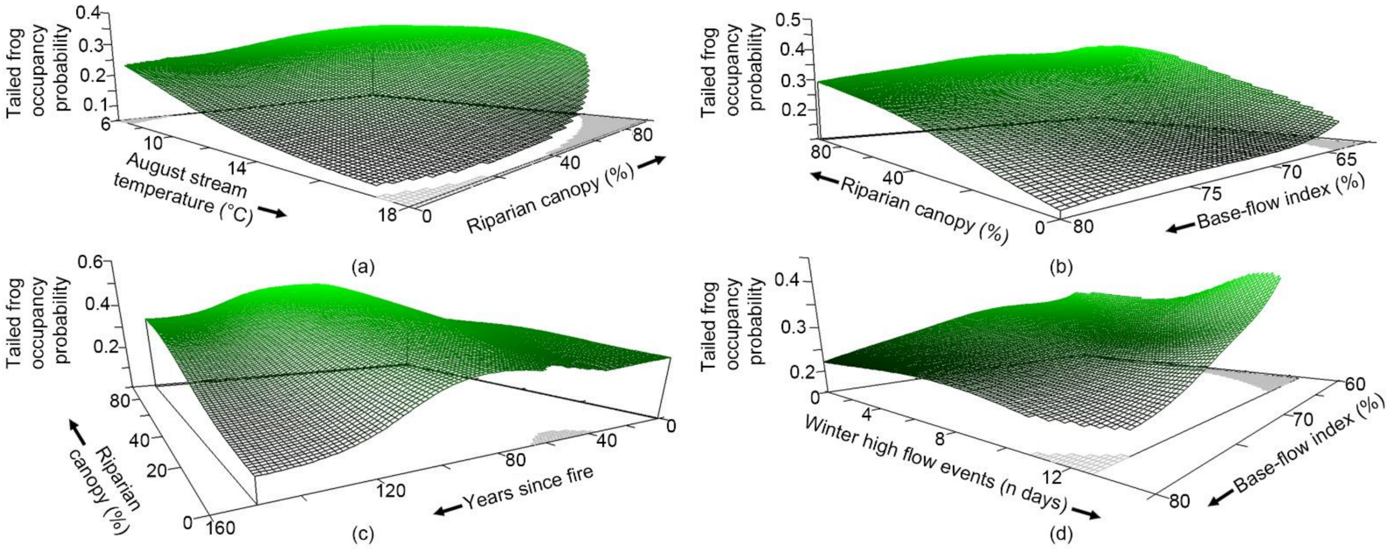

Figure 3. NPMR modeled relationships between tailed frog occupancy rate (vertical axes) and (**a**) mean stream temperature in August and riparian canopy cover, (**b**) riparian canopy cover and base-flow index, a measure of streamflow stability, (**c**) riparian canopy cover and number of years elapsed between wildfire and sampling year, and (**d**) winter high flow events (the number of winter days when stream flows are in >95 percentile of the flow of record) and base-flow index. This model was developed from 2829 sites sampled within the ranges of the Rocky Mountain tailed frog and bull trout. Gray shading in each panel indicates regions of predictor space with insufficient data for predictions to be made.

Bull trout occupancy was highest in locations with fewer winter high flow events, lower slope, larger numbers of cutthroat trout, and lower August stream temperatures ($\log\beta = 81.4$; $p < 0.01$, $N^* = 285$; Table 3; Figure 4). Of these important predictors, bull trout occupancy was most sensitive to site differences in winter high flow events and numbers of cutthroat trout, followed by slope. August stream temperature was important for bull trout occupancy (Table 3), but is not shown in figures.

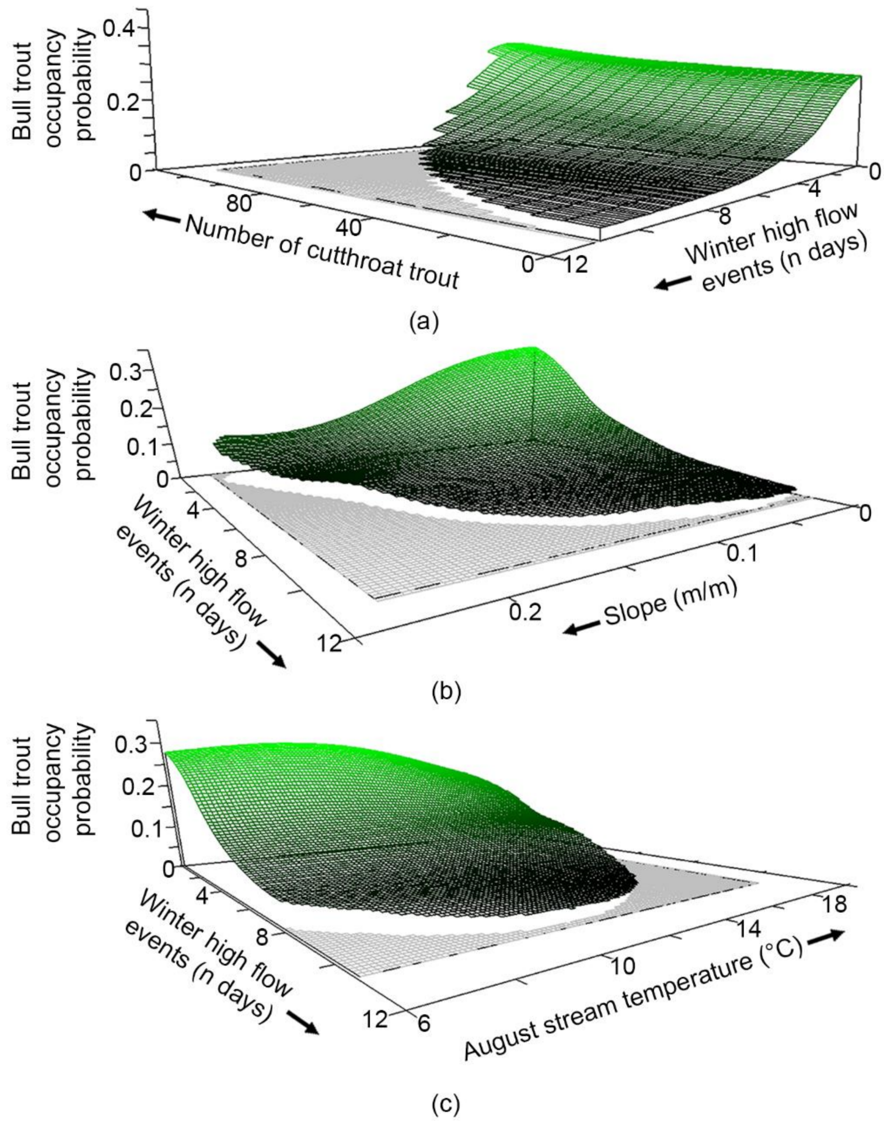

Figure 4. NPMR modeled relationships between bull trout occupancy rate (vertical axes) and (**a**) number of cutthroat trout detected in the stream reach and winter high flow events (number of winter days when stream flows are in >95 percentile of the flow of record), (**b**) winter high flow events and stream reach slope, and (**c**) winter high flow events and stream temperature in August. This model was developed from 2829 sites sampled within the ranges of the Rocky Mountain tailed frog and bull trout. Gray shading in each panel indicates regions of predictor space with insufficient data for predictions to be made.

3.5. What Habitat Characteristics Are Associated with Co-Occupancy?

Using 481 observations (150 Both and 331 Bull Trout Only sites), co-occupancy, as opposed to bull trout only occupancy, was most likely in locations with low-to-moderate winter high flow events, low numbers of other salmonids, a low base-flow index, and intermediate years since fire ($\log\beta = 12.2$; $p < 0.01$, $N^* = 40.4$; Table 3; Figure 5). Of these important predictors, co-occupancy was more sensitive to site differences in winter high flow events then the abundance of other salmonids or base-flow index. Co-occupancy was least sensitive to differences in time since fire.

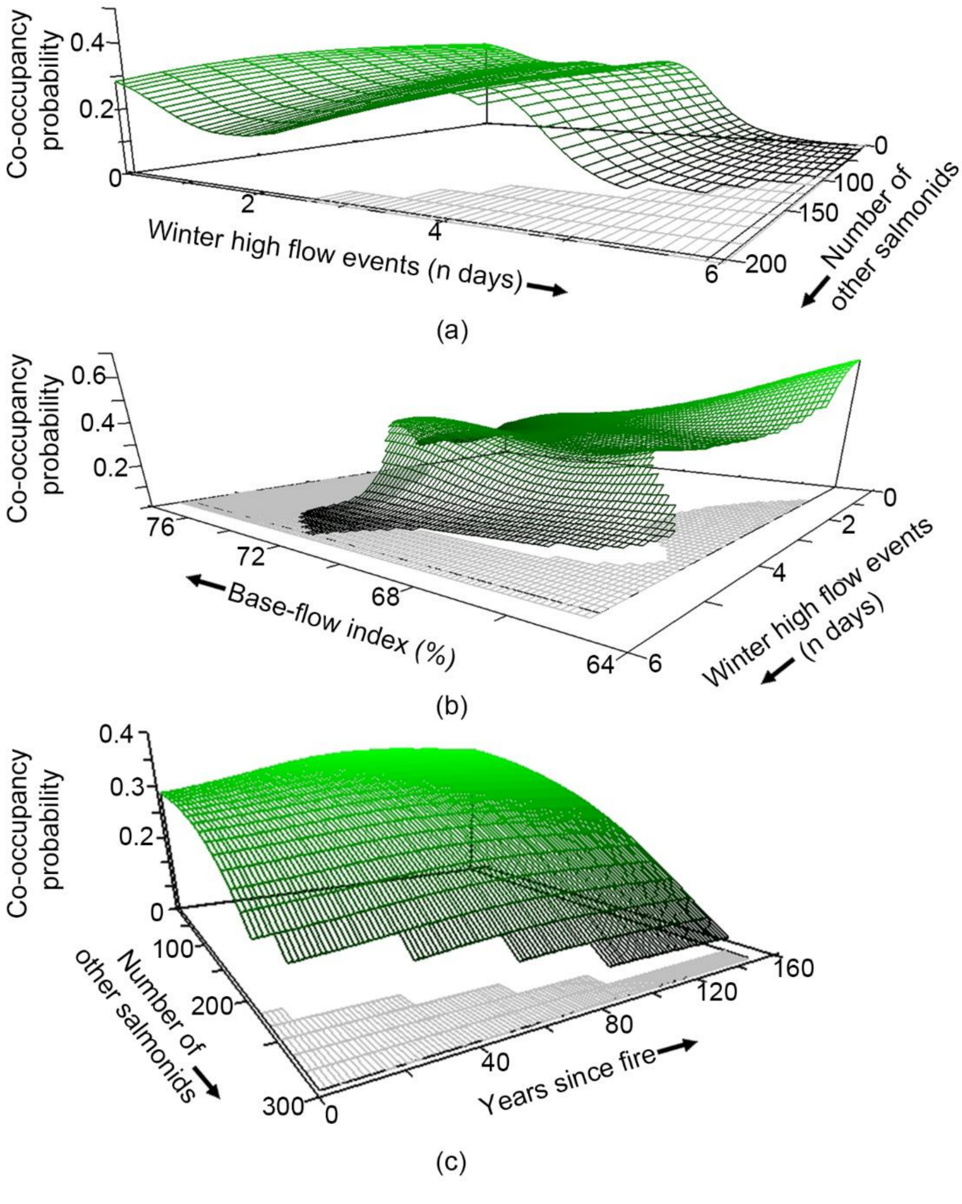

Figure 5. NPMR modeled relationships between tailed frog and bull trout co-occupancy rate (vertical axes) and (**a**) number of salmonids detected in the stream reach (other than bull trout) and winter high flow events (number of winter days when stream flows are in >95 percentile of the flow of record), (**b**) Base-flow index, a measure of streamflow stability and winter high flow events, and (**c**) number of other salmonids and number of years elapsed between wildfire and survey. This model was developed from 481 sites sampled within the ranges of the Rocky Mountain tailed frog and bull trout. Gray shading in each panel indicates regions of predictor space with insufficient data for predictions to be made.

When we compared the attributes of survey sites across four combinations of tailed frog and bull trout occupancy (i.e., Neither, Tailed Frog Only, Bull Trout Only, or Both), co-occupancy sites had lower numbers of salmonids (other than bull trout), particularly westslope cutthroat trout and brook trout, than other site types (Figure S5). Co-occupancy sites (i.e., Both) had slightly cooler August stream temperatures than Neither sites and

Bull Trout Only sites (Figure 6). Co-occupancy sites also tended to be less steep and have fewer winter high flow events than Tailed Frog Only sites, but occurred in larger drainages (Figure 6). Co-occupancy and Tailed Frog Only sites had more riparian canopy cover than Bull Trout Only sites. Sites where neither species was detected (i.e., Neither) had the least riparian canopy cover. Base-flow index, a measure of flow stability, was similar across all occupancy categories, however it was highest in Bull Trout Only sites (Figure 6). Co-occupancy and Tailed Frog Only sites tended to occur in locations that had not burned as recently as Bull Trout Only sites (Figure 6).

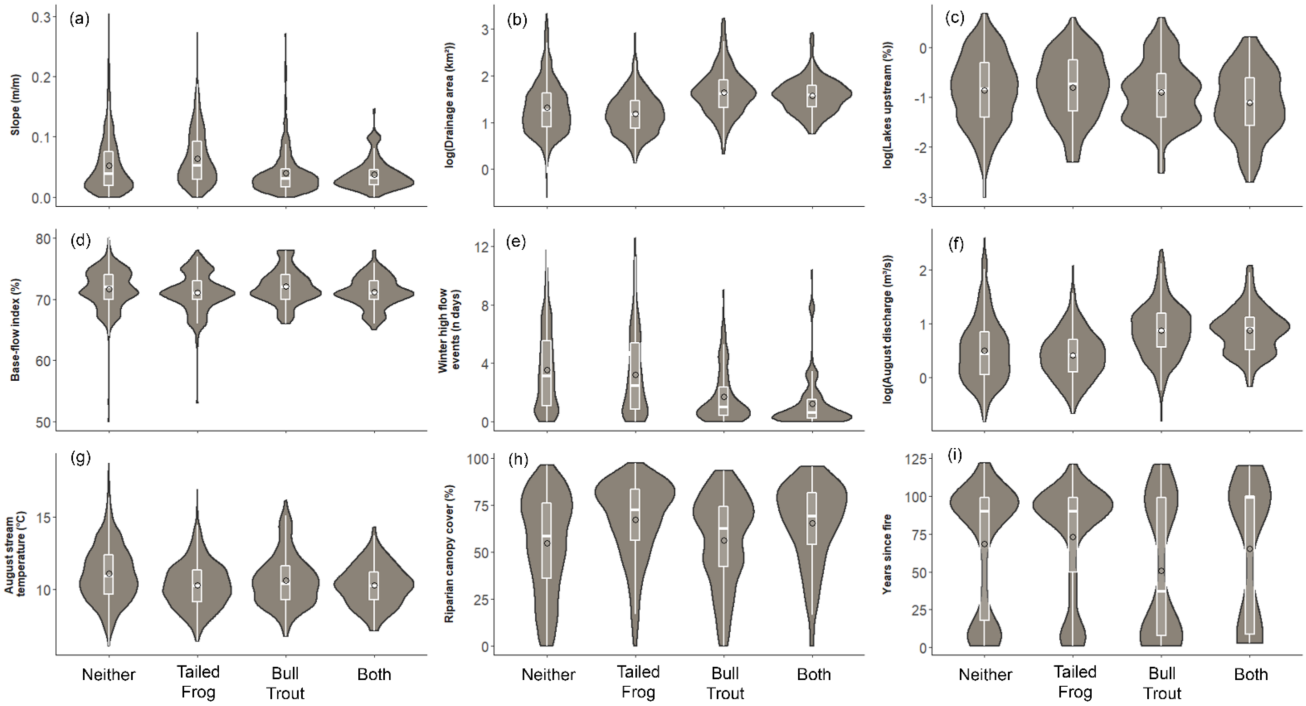

Figure 6. Distribution of stream characteristics (**a**–**i**) across each of four species occupancy categories: Sites where neither tailed frogs nor bull trout were detected (n = 1684 Neither sites), sites occupied by tailed frogs but not bull trout (n = 664 Tailed Frog Only sites); sites occupied by bull trout but not tailed frogs (n = 331 Bull Trout Only sites), and sites occupied by both tailed frogs and bull trout (n = 150 Both sites). The violin plots show a smoothed frequency distribution of all sites across each variable (density plot width), as well as the median (white line), mean (circle), 25th and 75th percentiles (ends of box), and minimum and maximum (white lines depicting 1.5 × the inter-quartile range).

3.6. What Are the Wildfire Trends across Occupancy and Co-Occupancy Categories?

Overall fire history patterns are similar across occupancy categories, as a high proportion of sites in all four categories experienced wildfire in the Big Burn of 1910 and again in the early 2000's (Figure 7). However, in 1910, Tailed Frog Only sites burned at a much larger proportion than the other three site types (i.e., more than twice the proportion of Bull Trout Only sites). This trend of high fire activity continued into the late 1910s and early 1920s, with sites we classified as Tailed Frog Only or Neither burning in larger proportion than the sites recently classified as Bull Trout Only or Both. In the 1920s and 1930s, relatively few sites of any type had wildfire within their watersheds according to GIS data. During the 1940s–1960s, there was a small increase in wildfire activity, especially in Tailed Frog Only sites, with as many as 3% of these 664 sites burning in each decade. Sites recently classified as Neither burned the next most frequently during this period. From the 1970s to the 1990s, there was again very little wildfire in any of these watersheds. Only 47 of the 2829 survey sites had any mapped fire within these three decades and only 4 of those occurred during the 1990s. There was a large increase in wildfire activity during the 2000s, especially at locations recently classified as Bull Trout Only or as Both. Nearly 20% of the 331 survey sites classified as Bull Trout Only burned during this time span, as did 14% of the 150 Both sites. Although the number of sites with wildfire in their watershed diminished somewhat in the 2010s, it was still larger than any pre-2000 decade since the 1910s. The 2010s continued the recent trend of proportionately more wildfire in locations where bull trout were recently detected (i.e., Both and Bull Trout Only sites) than in Neither or Tailed Frog Only locations (Figure 7).

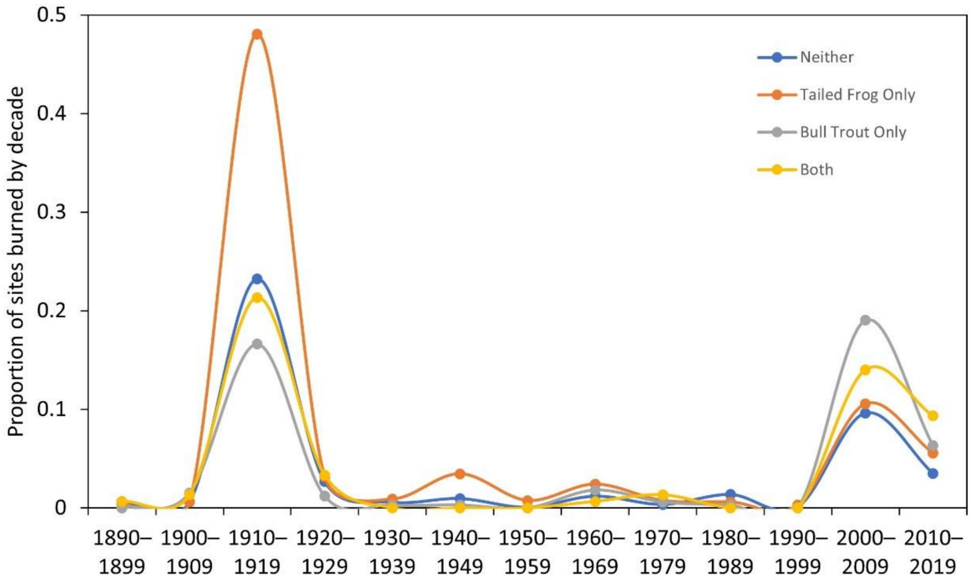

Figure 7. Proportion of sites with recorded wildfire in the watershed each decade, from 1890 to 2019, categorized by recent (2006–2011) occupancy combinations of tailed frogs and bull trout from 2829 electrofishing surveys. Fire events from 1878 and 1889 were excluded due to a single year of fire data present in each of the respective decades.

4. Discussion

4.1. Species Occupancy and Co-Occupancy Habitat Models

We found support for our hypothesis that bull trout and tailed frogs occupy the coldest streams, but tailed frogs are found at higher elevations and steeper gradients compared with bull trout. Our analyses suggest that Rocky Mountain tailed frogs and bull trout share similar habitats, but we also observed subtle differences in habitat associations that show each species may partition their space use into different reaches of headwater sites. Despite these differences, both tailed frogs and bull trout clearly need colder water temperatures and may be vulnerable to stream warming and changes in stream conditions associated with wildfire. Indeed, August stream temperature was one of the strongest predictors of species occupancy and co-occupancy in our datasets. This is consistent with previous studies. Isaak et al. [42] reported that 10–12 °C was an upper threshold for bull trout because occupancy probabilities in warmer stream temperatures were low. Studies of tailed frog occurrence suggest that 10–11 °C is optimal [42,56]. However, like bull trout, there is evidence that Rocky Mountain tailed frogs may adapt to slightly warmer waters [45] and have short-term tolerance of very warm (up to 21.0–26.6 °C) waters [27,43]. Isaak et al. [42] were not able to identify a lower temperature threshold because both bull trout and tailed frogs had their highest occupancy probabilities in the coldest available streams. A recent study at the northern edge of the range of Rocky Mountain tailed frogs, however, suggests that maximum weekly average stream temperatures may need to be >8 °C to support tailed frog reproduction [56]. Bull trout have among the lowest upper thermal limits and growth optima (around 13 °C) of North American salmonids, although this optimum depends on other influences such as consumption and interactions with other species [57,58].

Besides temperature, flow was the next most important variable explaining tailed frog and bull trout occupancy. Based on previous findings [42], we expected August discharge to be the most important predictive flow variable for these species; instead, August discharge was not selected in a single model and winter high flow was one of the top variables in all our models. Occupancy of both species was highest in streams that had fewer winter high flow events, although tailed frogs were quite tolerant of streams with winter high flow events, when other conditions were met. This variable may have represented more limiting conditions than August discharge, especially for bull trout, as both occupancy and co-occupancy with tailed frogs was reduced substantially in locations with greater high winter flow events. Winter is a particularly stressful (although understudied) season. Overwintering ecology of stream-dwelling salmonids, including bull trout, is perhaps the least understood aspect of their life history [59]. The winter high flow events variable captured the influence of flow regime in combination with climate-drive effects on winter, such as more frequent winter warming leading to rapid snowmelt or rain-on-snow events. Incubating eggs of bull trout and other fall spawners are likely to be at high risk in snow-melt basins where climate warming increases the amount of rainfall, thereby increasing the frequency and magnitude of winter flood events and enhanced scour of the substrate [18]. Similarly, mortality of young-of-year tailed frog tadpoles, which hatch in June and July [60], may increase with winter scour. This could explain why 1-year-old tadpoles are at lower abundance in recently disturbed streams [25,61]. However, the several attributes of tailed frogs and the streams they inhabit may make them more tolerant of winter high flow events, including having the ability to latch on to substrates using their suctorial mouth parts, moving down into substrates and interstitial spaces, having multiple larval cohorts present at any given time, and inhabiting smaller, steeper headwater streams. Base-flow index was also important for tailed frog occupancy and for co-occupancy with bull trout. Tailed frog occupancy was lowest at the highest base-flow index, indicating that tailed frogs may prefer somewhat smaller streams that have more seasonal variation in flow. The base-flow index is a measure of the proportion of streamflow that can be attributed to groundwater discharge into a stream (i.e., calculated as base flow to total flow) and thus, the higher the base-flow index, the more sustained a stream's flow throughout the year.

In addition to stream temperature and flow regime, we had hypothesized that both species would be negatively affected by recent wildfires, but this effect would diminish with time since fire. We found support for this hypothesis in that riparian canopy cover and time since fire were important predictors of tailed frog occupancy, slope was important for bull trout, and time since fire was important for co-occupancy of both species. Along with the cooling effect of riparian cover on streams, which is often lost in higher severity wildfires [25], post-metamorphic life stages of tailed frog are known to prefer denser riparian canopies, often measured as low levels of ambient light [62]. Terrestrial gene flow between streams may also be affected by canopy loss from fire [63]. Fire is known to have negative effects on the youngest life stages of tailed frogs, particularly in the first year (embryos, young-of-year tadpoles, and 1-year-old tadpoles; [61]). Abundance of tailed frog tadpoles, however, has been observed to return to pre-fire levels within 12 years of wildfire, suggesting that either frogs are colonizing streams from nearby refugia or long-lived adults are surviving and reproducing successfully in post-fire environments, perhaps once stream conditions stabilize [64]. Channel slope is another variable that likely captures several interacting factors, including the prevalence of certain microhabitat types (e.g., riffles, runs, and pools), width, gradient, and flow. We found that bull trout occupied lower gradient stream reaches compared to higher gradient streams occupied by tailed frogs. Our results were consistent with analysis of >100 streams in western Montana that reported bull trout occurrence was negatively associated with channel gradient, usually in combination with width, woody debris, and brook trout presence [65].

We also found that interactions with other aquatic species were important for both tailed frogs and bull trout, which could have implications for conservation planning if species distributions shift with environmental change [38,66,67]. Although cutthroat trout were the most abundant of the salmonids examined (Figure S5), tailed frog occupancy was not negatively associated with any salmonid except bull trout (see Table 2), and that was only true of our smaller, methodological test dataset. All salmonids are potential predators of tailed frogs which can alter tadpole behaviors, such as shifting to nocturnal feeding to avoid predation [55]. Bull trout, in contrast, were negatively associated with total salmonid abundance and positively associated with cutthroat trout. Among salmonids in the northern Rocky Mountains, cutthroat trout are known to occupy the coldest thermal niches along with bull trout and tailed frogs [42]. Differences in foraging tactics and foraging microhabitats may lead to resource partitioning and dietary segregation of cutthroat trout and bull trout, potentially important mechanisms allowing coexistence of these two salmonids [68]. We suspect that cutthroat and bull trout are sympatric along stream temperature gradients, until the highest and coldest headwater stream reaches, where only bull trout tend to persist. Continuing upstream, eventually even bull trout drop out, whereas tailed frogs are capable of occupying the highest and steepest reaches of the headwaters. These highest parts of the watershed are not too cold for bull trout, but rather get too shallow or too steep to be accessible by bull trout.

We found support for our hypothesis that co-occupancy does occur fairly frequently (but less so than allotopic occupancy, at least at the scale of a study reach) and under environmental conditions that are intermediate to those where one species occurs without the other. To our knowledge, this is the first paper to assess the conditions under which tailed frogs and bull trout co-occupy stream reaches across the northern Rocky Mountains. Understanding species co-occurrence patterns is critical for informing conservation strategies, especially when one species is formally protected (e.g., ESA-listed bull trout) and another species potentially benefits from that protection. Co-occupancy analyses have also been useful for understanding biotic interactions and niche partitioning between native species (e.g., bull trout and cutthroat trout, [68]; Columbia spotted frogs and salmonids, [69]) or between native and non-native species (e.g., bull trout and brook trout, [70]; Columbia spotted frogs and introduced salmonids, [71,72]). Like all salmonids, bull trout are predators of tailed frogs and thus co-occupancy, or the lack thereof, may also be influenced by predator-prey relationships. Besides interactions with other salmonids, flow regimes (i.e., winter high flow events, base-flow index), and time since fire also explained patterns of tailed frog and bull trout co-occupancy. These relationships were similar but often intermediate to those discussed for each species previously.

4.2. Methodological Comparisons

Electrofishing provided a reliable method for detection of Rocky Mountain tailed frogs, even when sampling was focused on and equipment was calibrated to target bull trout [47]. Tadpoles were the most common tailed frog life stage detected in stream surveys, likely because they are strictly aquatic and overwinter for 3–4 years before reaching metamorphosis [73]. Our results demonstrated that night is preferable to day snorkeling for tadpole detection, possibly as a result of tadpole predator avoidance behavior [55]. Tadpoles attach to smooth, cobble-sized, submerged rocks during the day for concealment and move to upper rock surfaces at night to feed on algae and other components of the periphyton or biofilm. Hence, they are most readily observable using night snorkeling. Our methodological analysis of 106 sites also confirmed that electrofishing was a reliable method for species detection, only slightly (10.8% of the time) underestimating occupancy compared with night snorkeling. This result justified our use of a larger (2829 sites) dataset where only electrofishing surveys were conducted and to rely on naïve estimates of occupancy (i.e., not corrected for detection) for modeling habitat associations. We did not assess kick-netting (also called rubble rousing), another common method for sampling tailed frog tadpoles, but another study found that the detection rate for kick netting for Rocky Mountain tailed frogs was 0.56 versus 0.79 (95% CI = 0.63–0.88) for electrofishing [50]. Although electrofishing does not have perfect detection even for bull trout, with enough effort and proper technique it has been shown to be a reliable method [47].

We were also concerned that a lack of field-measured habitat characteristics might limit our inference for habitat associations when using the larger GIS-only dataset. Contrary to expectations, we found that few of the field-measured variables proved to be important, relative to GIS-derived predictors, when both were allowed to compete for inclusion in occupancy models for each species. Only percent undercut bank was selected for tailed frogs and it had relatively weak predictive power compared with the GIS-derived variables, especially compared to August stream temperature and winter high flow events. These same GIS-derived variables were the top predictors of bull trout occupancy, with the addition of riparian canopy cover. The lack of predictive power from the field-measured variables could be attributed to the spatial-scale at which they were measured. The 100-m reach-scale may be too large to provide predictive capacity for species that might be more strongly associated with microhabitats (pools or runs in the case of bull trout and riffles in the case of tailed frogs), which may or may not be present in different numbers in each reach. At any rate, these preliminary results allowed us to move forward with analysis of the larger dataset that solely relied on GIS-derived habitat and environmental variables.

4.3. Implications for Climate Change

There remains considerable uncertainty about the amount and rate of climate-associated stream warming [74] and possible interactive effects with other environmental changes, such as wildfire [75,76]). Both bull trout and tailed frogs live in stream networks that have considerable spatio-temporal variation in temperature because of diverse ground water sources, riparian cover, flow patterns, and a large latitudinal span. They also exhibit population-level adaptation [45,77] and are adept at exploiting microhabitats, such as thermal refuges, when water temperatures become elevated. Provided thermal refuges persist [42], it is possible both species could benefit from warming that increases food production and growth during some periods of the year [78]. Nonetheless, strong associations between environmental factors affected by climate and the occurrence of these species implies future vulnerability to ongoing changes. A logical next step is the development of predictive distribution models that are applied beyond survey sites geographically and combined with future hydroclimatic scenarios to estimate long-term risks throughout the species' ranges. This has been attempted for bull trout [15] but using scenarios which ignored the stochastic disturbances and enhanced warming that wildfires will provide in the future [79], but see [75]. Also lacking from those and most other future scenarios are biological interactions [80], which will be an important factor for distributions of a species like the Rocky Mountain tailed frog that is sometimes preyed upon by bull trout and other salmonids. Emerging from the next generation of more realistic future projections, however, could be an enhanced ability to identify the subsets of streams that are most likely to serve as long-term climate refuges and populations that are most vulnerable to local extirpations. Given the degree of niche overlap and co-occurrence between bull trout and tailed frogs, it could also be possible to identify areas of overlap where both species may persist and then work to protect these streams and associated basins based on more holistic approaches to biodiversity in forested headwater basins.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/w14071162/s1, Figure S1: Distribution of elevation and precipitation across each of four species occupancy categories at 2829 sites in the northern Rocky Mountains; Figure S2: NPMR modeled relationships between tailed frog tadpole occupancy and important predictor variables using 96 study sites where both field-measured and GIS-derived variables were available; Figure S3: Bi-variate plots of NPMR modeled relationships between tailed frog tadpole occupancy rate and important predictor variables in relation to bull trout presence using 96 study sites where both field-measured and GIS-derived variables were available; Figure S4: NPMR modeled relationships between bull trout occupancy and important predictor variables using 96 study sites where both field-measured and GIS-derived variables were available; Figure S5: Distribution of fish species abundance from electrofishing surveys across each of four species occupancy categories at 2829 sites in the northern Rocky Mountains; Table S1: Habitat characteristics of sample sites included in the field methods comparison; Table S2: Detection rates of Rocky Mountain tailed frogs using three methods.

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Institutional Review Board Statement: This study was carried out in strict accordance with the Guidelines for the Use of Fishes in Field Research (ASIH/AFS/AIFRB 1987, 1988) and the Principles for the Utilization and Care of Vertebrate Animals Used in Testing, Research, and Training (United States Interagency Research Animal Committee, Federal Register. 1985; 50(97): 20864–20865). We conducted this research prior to the existence of the USDA Forest Service Research and Development Institutional Animal Care and Use Committee (IACUC). Prior to 2015, there was no formal IACUC policy or ethics review. In 2015, United States Department of Agriculture Research and Development adopted the policy to form an IACUC and became an officially registered federal research institution. As a result, this sampling prior to 2015 is exempt from IACUC because it complied with the 1987 Guidelines and 1985 Principles cited above and was completed prior to more recent IACUC requirements for approval.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data associated with the Isaak et al. [42] paper were deposited in a Dryad digital repository https://doi.org/10.5061/dryad.d0s7k (accessed on 15 May 2021).

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