Assisted colonization of a regionally native predator impacts benthic invertebrates in fishless mountain lakes

Allison L. K. Banting1,2 | Mark K. Taylor1,2 | Rolf D. Vinebrooke3 | Chris M. Carli4 | Mark S. Poesch2

1Parks Canada Agency, Banff National Park, Alberta, Canada
2Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada
3Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada
4Fisheries and Oceans Canada, Whitehorse, Yukon, Canada

Correspondence
Mark K. Taylor, Parks Canada Agency, Banff National Park, Alberta, Canada. Email: mark.taylor@canada.ca

Funding information
Alberta Conservation Association, Grant/Award Number: 020-00-90-230; Parks Canada

Abstract
The intentional introduction of native cold-water trout into high-elevation fishless lakes has been considered a tool to build resilience to climate change (i.e., assisted colonization); however, ecological impacts on recipient communities are understudied. The purpose of this study was to inform native cold-water trout recovery managers by assessing potential consequences of translocating a regionally native trout (westslope cutthroat trout; Oncorhynchus clarkii lewisi) into fishless mountain lakes. This study compared littoral benthic invertebrate richness, diversity, community structure and abundance between three groups of lakes (fishless, native trout, nonnative trout) in the Canadian Rocky Mountains. While richness and diversity were preserved across all lake groups, other lines of evidence suggested that the introduction of native westslope cutthroat trout into fishless lakes can alter littoral benthic invertebrate communities in similar ways as nonnative brook trout (Salvelinus fontinalis). The community structure of cutthroat trout lakes resembled brook trout lakes compared to that of fishless lakes. For example, both trout-lake groups contained a lower density of free-swimming ameletid mayflies and a higher density of certain burrowing taxa. Risk assessments for trout-recovery actions should consider the potential for collateral damage to recipient invertebrate communities. Future research should identify possible cascading trophic effects on species subsidized by invertebrate prey.

KEYWORDS
aquatic conservation, assisted colonization, freshwater biodiversity, invasive species, species at risk

1 | INTRODUCTION

Fishes in the Salmonidae family are vulnerable to climate change since they depend on cold water temperatures (Bear, McMahon, & Zale, 2007; Selong, McMahon, Zale, & Barrows, 2001). Climate change has direct effects on salmonids due to their ectothermic physiology. However, climate change also causes indirect effects as other stressors are exasperated by warming water. For example, native inland salmonids of western North America such
as cutthroat trout (*Oncorhynchus clarkii*) are particularly vulnerable to competition from nonnative salmonids that have been broadly introduced outside of their range (Bear et al., 2007; Schindler, 2000). Cutthroat trout have experienced climate-mediated hybridization with rainbow trout (*Oncorhynchus mykiss*; Muhlfeld et al., 2014) and range contraction associated with the occurrence of brook trout (*Salvelinus fontinalis*; Wenger et al., 2011).

The persistence and adaptability of cold-water species may depend on their ability to disperse to colder habitats (Root et al., 2003). However, in mountain environments, a species’ range expansion can be limited by topographic barriers. A recovery action for cold-water fishes could be to move individuals upstream of topographic barriers where stream and lake temperatures are more suitable for their persistence (i.e., assisted colonization; Ricciardi & Simberloff, 2009; IUCN/SSC, 2013). These areas include unoccupied fishless lakes within the fishes’ native range (e.g., Galloway, Muhlfeld, Guy, Downs, & Fredenberg, 2016; Hayes & Banish, 2017).

Assisted-colonization practitioners are conflicted by the need for both rigorous risk assessment and immediate action on species-at-risk recovery (Ricciardi & Simberloff, 2009). Land-management agencies must address the risk of assisted colonization in terms of their own management policies and regulations (McLachlan, Hellman, & Schwartz, 2007). While the introduction of organisms outside of their native range is generally considered high risk (IUCN/SSC, 2013), there is much less understanding of potential impacts of introducing species within their native range but outside of their historical local distribution. This is problematic as there is little evidence to support risk assessments for such recovery actions despite the appetite for translocating native cold-water trout to high-elevation habitats (but see Galloway et al., 2016). The purpose of this study was to contribute to risk assessments for the assisted colonization of native cold-water trout by quantifying the potential consequences of translocating westslope cutthroat trout (*Oncorhynchus clarkii lewisi*; herein WSCT) into fishless mountain lakes in the Canadian Rocky Mountains.

Fishless mountain lakes hold important ecological and conservation value (Cole & Landres, 1996; Knapp, Matthews, & Sarnelle, 2001; Schindler & Parker, 2002) as they support endemic species by providing refuge from fish predation (McNaught et al., 1999; Schilling, Loftin, & Huryn, 2009). Yet, fishless lakes have traditionally been undervalued by land managers (Schindler & Parker, 2002). For example, due to their abundance in food resources, fishless lakes were considered opportune habitat to introduce nonnative sport fishes to create unique recreational angling opportunities (Donald, 1987; Knapp et al., 2001).

There is sufficient data that demonstrates the direct and indirect impacts of nonnative trout introductions on native biodiversity, abundance and ecosystem function in mountain habitats (Eby, Roach, Crowder, & Stanford, 2006). As several salmonids are opportunistic feeders, size-selective predation can reduce common, yet vulnerable, organisms such as conspicuous benthic invertebrates (Bradford et al., 1998; Pope & Hannelly, 2013), microcrustaceans (Tiberti, von Hardenberg, & Bogliani, 2014; Weidman, Schindler, & Vinebrooke, 2011) and even terrestrial invertebrates (Baxter, Fausch, & Saunders, 2005; Pope, Piovella-Scott, & Lawler, 2009). Nonnative trout can also disrupt an entire food web via a trophic cascade (Epanchin, Knapp, & Lawler, 2010; Parker & Schindler, 2006). However, there is considerably less literature on the effects of introducing regionally native trout (herein native trout). These are trout that were introduced to a historically fishless lake within their native range but not within their historic local distribution.

Invertebrate prey communities within lakes are presumably structured by the regional invertebrate species pool as these taxa have strong dispersal mechanisms (Loewen & Vinebrooke, 2016). Therefore, introduced native trout may have a lower impact on recipient invertebrates compared to introduced nonnative trout as they co-evolved with the regional invertebrate species pool (i.e., the distinctiveness hypothesis; Ricciardi & Atkinson, 2004; Cox & Lima, 2006). Indeed, a meta-analysis found that the severity of impacts from the invasion of aquatic species was related to the invaders’ and recipients’ ecological distinctiveness (Ricciardi & Atkinson, 2004). It is assumed that the ecological distinctiveness of behavioral and life-history traits is correlated with taxonomic distinctiveness given that genetic convergence increases with taxonomic relatedness (Thorpe, 1982).

The scale of taxonomic distinctiveness required for one type of salmonid to structure invertebrate prey differently than another type of salmonid is unknown. Ricciardi and Atkinson (2004) found that the highest-impact aquatic invaders are more likely to belong to genera not already present in the system. WSCT have been negatively impacted by introduced nonnative brook trout (i.e., *Salvelinus*) in western North America, but cutthroat trout have also co-occurred with a native *Salvelinus* species (e.g., bull trout; *Salvelinus confluentus*) for at least 12,000 years. However, there is some evidence for species-specific differences in how recipient invertebrate prey respond to fish predators (Anderson, 1980; Carlisle & Hawkins, 1998; Hume & Northcote, 1985). For example, Anderson (1980) reported that brook trout in the Canadian Rockies had the largest impact on zooplankton communities compared to bull trout and cutthroat trout.
Regardless of the taxonomic scale, if the distinctiveness hypothesis applies in the context of introduced salmonids, assisted colonization of a native trout may exert less adverse effects on fishless mountain-lake ecosystems compared to introduced nonnative trout. However, ecosystem function may be disrupted by any species that possess novel traits (Seddon, 2010). It cannot be assumed that an introduced animal will not impact recipient communities solely because of its apparent similarity to a resident species. For this reason, the potential impacts of introducing a native trout to a waterbody that was not historically occupied by trout should not be precluded.

The objective of this study was to compare littoral benthic invertebrate (herein littoral invertebrates) communities between three groups of lakes (fishless, native trout, and nonnative trout). Several response variables (littoral invertebrate richness, diversity, community structure and density) were measured to ensure a comprehensive assessment of the relative impacts of native versus nonnative trout on littoral invertebrate communities in fishless mountain lakes.

2 | METHODS

2.1 | Study-area description

Banff National Park (BNP) in the Rocky Mountains of Alberta, Canada, encompasses 6,641 km² of mountainous terrain, with numerous glaciers and icefields, dense coniferous forest and alpine landscapes. On the eastern side of the Continental Divide, the park has a subarctic climate with cold, snowy winters and mild summers. One lake in this study was on the Continental Divide next to BNP. Kootenay National Park consists of 1,406 km² of montane, sub-alpine and alpine habitats (Figure 1). The hydrology in both parks is dominated by snowmelt runoff in the spring, which produces high flows from April to June that rescind to base flows in the fall and over winter.

2.2 | Brief history on stocking

Between the turn of the century and the 1970s, trout were introduced to 25% of an estimated 486 lakes in BNP.
Of those, 84% were historically fishless (Schindler, 2000). In the beginning, settlers and Canadian Pacific Railway (CPR) workmen moved fish species about in considerable quantities (Ward, 1974). By 1915, a hatchery was built in Banff and early stocking was from locally sourced WSCT trout eggs (Ward, 1974). WSCT are native to the montane and foothill streams of southern Alberta within the Oldman and Bow watersheds and parts of the Missouri and Columbia basins in the intermountain western United States (USA). Egg collection from the wild proved to be difficult and the hatchery did not meet production capacity. In 1928 and 1941, additional hatcheries were built in Waterton and Jasper, respectively. To bolster production, eggs were imported from British Columbia and the USA. Cutthroat trout subspecies, such as Yellowstone cutthroat trout (Oncorhynchus clarkii bouvieri) and coastal cutthroat trout, (Oncorhynchus clarkii clarkii) were stocked in combination with some local WSCT. The stocking records often do not distinguish between subspecies. In some instances, stocking records suggested one species or sub-species of trout were introduced, but contemporary sampling indicated a different species or sub-species now occurs despite a lack of records for their introduction. In other cases, no records existed, but the contemporary presence of a given species suggested it was a stocked source as natural colonization was improbable with such steep geography.

Brook trout is of the genus Salvelinus, which is also endemic to North America, but separated from Oncorhynchus 30–40 million years ago (Behnke, 1992). The historic distribution of brook trout was from: The Atlantic seaboard south to Cape Cod; in the Appalachian Mountains south to Georgia; and in the upper Mississippi and Great Lakes drainages, north to Hudson Bay (Scott & Crossman, 1973). Brook trout have been widely introduced in many parts of the world because of its appeal as a sport fish (Scott & Crossman, 1973). Records for brook trout introductions in BNP started in 1910; however, brook trout were apparently introduced to the Bow River prior to 1900 by CPR workmen (Ward, 1974). Banff and then Jasper and Waterton hatcheries obtained eggs from large-scale suppliers from Eastern Canada and the USA. Brook trout was also chosen because of the exceptional growth and catch rates obtained in mountain lakes in the 1930s (Rawson, 1940). Brook trout were indiscriminately stocked on top of wild and previously stocked cutthroat trout. Brook trout usually out-competed other native and stocked trout and seldom co-exist with other trout (Table S1). By the 1980s, the Canadian mountain national parks discontinued the stocking program based on an increased recognition of the value of native fauna, however, many of these populations have persisted (Donald, 1987).

### 2.3 Lakes

Thirty-six mountain lakes were identified and categorized into three groups based on contemporary occurrence of trout (Table S1): lakes not occupied by fish (fishless; \( n = 13 \)); lakes occupied by WSCT (native trout; \( n = 10 \)); and lakes occupied by nonnative brook trout (nonnative trout; \( n = 13 \)).

Fishless lakes are lakes that were historically fishless and were never stocked (\( n = 10 \)) or were stocked decades ago, but only one generation of fish survived due to a lack of spawning habitat or winter kill (\( n = 2 \); Table S1). It is likely that the littoral invertebrate communities had returned to pre-stocking conditions, given the life span of trout and the resilience of mountain lake ecosystems (Donald, Vinebrooke, Anderson, Syrgiannis, & Graham, 2001; Knapp et al., 2001).

Native trout lakes were lakes that were stocked with native WSCT. These lakes may have been stocked with other species more than four decades ago, but contemporary sampling confirmed the sole occurrence of pure WSCT (\( n = 4 \); Table S1). Given there were not a lot of historically fishless lakes stocked with WSCT, lakes that were historically occupied by WSCT were also included in this study group. These lakes were either never stocked or were stocked but, based on contemporary sampling, the native genotype prevailed (\( n = 6 \)). Lakes that were historically occupied by WSCT were grouped with lakes stocked with WSCT. This decision assumed that stocking happened long enough ago (mean number of years since last stocking was 68 years) that stocked lakes with self-sustaining populations of WSCT had a littoral invertebrate community that had converged to that of historically occupied WSCT lakes (Donald et al., 2001; Knapp et al., 2001).

Nonnative trout lakes are sites that were historically fishless but were stocked at least once with nonnative brook trout (\( n = 10 \)). Nonnative trout lakes also included two lakes, one with both brook trout and WSCT, and the other with brook trout and rainbow trout. Anderson (1980) showed brook trout had a disproportionately larger effect on zooplankton communities compared to cutthroat trout, so these mixed lakes were considered nonnative trout lakes in the analyses.

### 2.4 Spatial sampling design

Study lakes were systematically selected to minimize differences in environmental gradients between lake groups (i.e., fishless, native trout, nonnative trout). The study lakes were situated at sub-alpine and alpine elevations (1,981–2,453 m), ranged in size from 2 to 35 ha and had maximum depths that vary from 3 to 71 m, with
catchment areas ranging from 39 to 3,743 ha (Table S2). Water temperature and dissolved oxygen at the time of sampling ranged from 4.2 to 14.9°C and 8.2 to 12.4 mg/L, respectively, but the time of day was not standardized (Table S3). Conductivity ranged from 32 to 336 μS/cm and pH ranged from 6.6 to 9.3. The substrate was most often equal parts clay, cobble and boulder with some outliers. A marginal amount of woody debris was found in most lakes. Macrophytes were rare in sub-alpine and alpine lakes in the Canadian Rockies. With the exception of catchment area (perANOVA, 999 permutations; \( p = .01 \)), there were no significant differences in lake morphometry, water chemistry, littoral substrate or habitat between the lake groups (perANOVA, \( p > .05 \); Table S3).

### 2.5 Sampling sites

Three to seven littoral invertebrate sample sites were allocated per lake depending on lake size: three samples for 0–2 ha lakes; four samples for 2.1–4 ha lakes; five samples for 4.1–8 ha lakes; six samples for 8.1–16 ha lakes; and seven samples for 16.1–35 ha lakes. Within lakes, sites were proportionally allocated between different substrate types (Knapp et al., 2001). For example, if a lake required six sample sites and there were three equally common substrate types, then two sites were allocated per substrate type. Lakes were visited once following ice-off, from 15 June to 1 July 2015, or 13 June to 29 June 2016.

### 2.6 Environmental predictor variables

At each sample site, measurements were taken of water temperature, dissolved oxygen (DO), pH and conductivity with a YSI 650 multiparameter meter (YSI Incorporated, Yellow Springs, OH). Calibrations were made before each trip. All measurements were taken from a depth of 1 m prior to sampling littoral invertebrates. To determine substrate composition, we visually estimated percent cover of each substrate category then standardized to sample area. Substrates were categorized as clay (<0.1 cm), sand/gravel (0.1–1.6 cm), pebble (1.7–6.4 cm), cobble (6.5–25.6) and boulder (>25.6 cm). Woody debris and aquatic macrophytes were categorized as absent or present. A third category of abundant was also in the protocol, but woody debris and aquatic macrophytes were never abundant in the study lakes.

### 2.7 Littoral invertebrate collection

Littoral invertebrates were collected from each site with the travelling kick-and-sweep method (400 μm mesh), similar to Jones, Somers, Craig, and Reynoldson (2007). At each site, three transects were established perpendicular to shore, spaced 2 m apart and extending into the lake to a depth of 1 m. Sampling was standardized over a 10-min period (David, Somers, Reid, Hall, & Girard, 1998; Jones et al., 2007). Each transect was sampled for 3 min and the length of the transect was recorded, as distance varied depending on the slope of the lake bottom. For an additional minute, missed littoral invertebrates were collected within the sampling area by sweeping the water column and searching under stones/logs (O’Hare et al., 2007). This collection method estimates taxon abundance per unit area (density).

Samples were rinsed over a 400-μm mesh-sized sieve to remove organic debris and fine sediment, and fixed with formalin. Samples were transferred to 70% ethanol for long-term preservation and transport. A certified benthic invertebrate taxonomist processed and sorted the samples. The taxonomist enumerated 300 organisms from a subsample of cells using a Marchant box (Marchant, 1989). The data were then extrapolated to the total number of cells. The taxonomist identified the sample of littoral invertebrates to the genus level, but the analysis was done at the family level (see below—Statistical Analyses). One exception was Nematoda, which were identified at the phylum level (Table S4). Taxa were checked against the reference collection of Environment and Climate Change Canada, held at the Canada Centre for Inland Waters in Burlington, Ontario, Canada. For quality assurance and control, randomly chosen samples were verified by a secondary taxonomist to achieve 95% sorting and identification efficiency.

### 2.8 Statistical analyses

Littoral invertebrates were standardized by the sample area (individuals per square metre), then averaged by the number of sample sites per lake to obtain a composite mean density per taxon per lake. All analyses were performed at the family level. Many studies have shown that taxonomic detail has little influence on multivariate descriptions of benthic communities, and the family level provides sufficient resolution for bioassessments (e.g., Bowman & Bailey, 1997). Secondly, collapsing the data at the family level reduced the number of zeros and helped normalize residual variances (Norris & Georges, 1993). With the exception of littoral invertebrate richness and diversity analysis, rare taxa were excluded at the genus level for each analysis if the taxa were found in fewer than four lakes (<10%; Table S4) to minimize the large influence that rare taxa have on analyses (Legendre & Legendre, 2012). Once rare species were
removed, 71% of the taxa were limited to one genera per family. Zooplankton were also removed because sampling methods were not designed to collect a full representation of the zooplankton community.

2.9 Littoral invertebrate richness and diversity between lake groups

Richness and Shannon's diversity were compared between lake groups, using a one-way analysis of variance (ANOVA). To consider the entire community, rare species were included for the diversity analysis. Prior to analysis, density values of littoral invertebrates were log_{10} (x + 1) transformed to reduce the asymmetry of the species distributions (Legendre & Legendre, 2012) and the influence of dominant species and outliers for ordination (McGarigal, Cushman, & Stafford, 2000).

2.10 Littoral invertebrate community structure between lake groups

Nonmetric multidimensional scaling (NMDS) was used to visualize multivariate patterns between lake groups in two-dimensional space based on the similarities in littoral invertebrate assemblages. Jaccard’s similarity coefficient was used to visualize community composition in the form of presence or absence. Taxa (vectors) were fitted to the ordination by significance of the correlation of each variable with a cut-off p-value of <.05, determined by 999 permutations. NMDS scores between lake groups were compared using permutational analysis of variance (perANOVA, 999 permutations) and Tukey’s Honest Significant Difference (Tukey HSD) post-hoc comparison test.

Permutational multivariate analysis of variance (PERMANOVA, 999 permutations; Anderson, 2001) was also used, based on Jaccard’s similarity coefficient to examine differences in littoral invertebrate communities between lake groups. Since PERMANOVA is sensitive to differences in the within-group dispersion, an analysis for homogeneity of multivariate dispersion was performed using PERMDISP (Anderson, 2006; Anderson, Ellingsen, & McArdle, 2006; Anderson & Walsh, 2013). This test compares the within-group variability between groups of individual points and their average distance to the group centroid. PERMDISP was completed in conjunction with PERMANOVA to ensure significant differences are the result of different mean values between group centroids (PERMANOVA; multivariate location) rather than dispersion (PERMDISP; within-group variability) from the centroids (Anderson, 2006; Anderson & Walsh, 2013).

2.11 Littoral invertebrate densities between lake groups

Taxon-specific density of common littoral invertebrate taxa was compared between lake groups, using perANOVA (999 permutations). To examine which lake group combination were most different, post-hoc comparison tests were used, including Tukey’s HSD and Games–Howell, depending on how the assumption of equal variance was met (Levene’s test).

2.12 Environmental predictors of variation in littoral invertebrate communities

Redundancy Analysis (RDA; Legendre & Legendre, 2012) was used to evaluate environmental predictors of taxonomic variation in the littoral invertebrate community between lake groups. A detrended correspondence analysis (DCA; Hill & Gauch, 1980) was initially performed, and based on the gradient length of the dominant axes (1.8 standard deviations for axis one and 1.3 for axis two), linear response models were suitable for analyses (Lepš & Šmilauer, 2003).

Environmental variables were scaled and centered to compare gradient lengths. Then, littoral invertebrate densities were transformed using the Hellinger transformation to ensure linearized relationships between the taxa that contained many zeroes (Legendre & Gallagher, 2001). Collinearity among variables was evaluated using variance inflation factor (>10) to reduce the risk of overestimating the significance of correlated variables. Correlated environmental variables were removed prior to analysis (Spearman’s rank; r > .6).

Measured environmental variables used for the initial model included elevation, maximum depth, lake area, water temperature, dissolved oxygen (DO), conductivity, pH, clay, sand/gravel, pebble, boulder, habitat, woody debris and aquatic macrophytes. The significance of the global model was tested with the complete set of predictors to proceed with forward selection. A double-stopping criterion (Blanchet, Legendre, & Borcard, 2008) was added to select the most parsimonious set of predictors. The significance of each environmental predictor variable was determined using Monte Carlo permutation tests with 4,999 permutations. Subsequent permutation tests determined significance of individual axes and the significance of the overall ordination of the reduced model (Borcard, Gillet, & Legendre, 2011).

All statistical analyses were performed in R version 4.0.1 (R Core Team, 2020) using the following packages: (a) vegan (Oksanen et al., 2012) for NMDS, PERMANOVA, PERMDISP, RDA, pairwise permutation tests and diversity measures; (b) pairwiseAdonis (Martinez-Arbizu, 2017) for pairwise tests following PERMANOVA; (c) adespatial (Dray et al., 2018) for the forward selection procedure;
(d) `lmperm` (Wheeler & Torchiano, 2016) for perANOVA; and (e) Stats for ANOVA and pairwise tests. The significance criterion used in all data analyses was $p < .05$. The R code used for this analysis is available from https://doi.org/10.5061/dryad.ffbg79csg.

3 | RESULTS

3.1 | Littoral invertebrate richness and diversity between lake groups

There were no differences in species richness (ANOVA; $F_{2,33} = 0.57, p = .57$) and Shannon diversity (ANOVA; $F_{2,33} = 2.57, p = .09$) between lake groups.

3.2 | Littoral invertebrate community structure between lake groups

The NMDS plot that represents the degree of similarity in taxonomic composition (Jaccard's similarity coefficient) displayed greater resemblances between native and non-native trout lakes compared to fishless lakes (Figure 2; stress = 0.20). NMDS scores associated with axis one were significantly separated between two of the three lake groups (perANOVA, $p < .01$; Figure 2) (Tukey HSD; nonnative vs. fishless, $p = .004$; native vs. fishless, $p = .005$; nonnative vs. native, $p = .99$). NMDS scores along axis two were not significantly different between lake groups (perANOVA, $p = .66$).

Consistent with the perANOVA test results on NMDS scores, PERMANOVA of Jaccard's coefficient confirmed significant differences between lake groups (Table 1). Pairwise comparisons revealed native and nonnative trout lakes were significantly different from fishless lakes, but not from each other (Table 1). There was no difference in dispersion between lake groups, which suggests that significant differences in PERMANOVA results were attributed to a difference in location (average community composition) rather than within-group variability (PERMDISP; Table 1).

3.3 | Littoral invertebrate densities between lake groups

Both native and nonnative trout lakes contained the highest density of taxa compared to fishless lakes (264, 232 and 157 individuals per square meter, respectively; Table 2; $p = .04$ and $p = .04$, respectively). However, the density of littoral invertebrates did not differ between native and nonnative trout lakes (Table 2; $p = .97$).

![Figure 2](image-url)  
**FIGURE 2** NMDS ordination of littoral benthic invertebrate community data, based on Jaccard’s similarity coefficient, colored by lake group (fishless, native trout, nonnative trout). Ellipses enclosing 60% of lakes for each lake group are presented in corresponding colors (stress = 0.20). Red vectors represent intrinsic taxa variables after correlation analysis with a cut-off $p$-value of .05.

|   | Df | SS  | MS  | Pseudo-$F$ | $R^2$ | $p$(perm) |
|---|----|-----|-----|------------|------|-----------|
| **PERMANOVA** |    |     |     |            |      |           |
| Treatment | 2  | 0.54| 0.27| 2.43       | 0.13 | <0.01     |
| Residuals | 33 | 3.66| 0.12| 0.87       |      |           |
| **Pairs** |    |     |     |            |      |           |
| Native vs. fishless | | 2.35| 0.10| 0.04       |      |           |
| Nonnative vs. fishless | | 3.41| 0.12| <0.01      |      |           |
| Nonnative vs. native  | | 1.17| 0.05| 0.31       |      |           |
| **PERMDISP** |    |     |     |            |      |           |
| Treatment | 2, 33 | 2.33| 0.11|           |      |           |

Note: Results are based on Jaccard's similarity coefficient and generated from littoral benthic invertebrate occurrence data (0,1). Pairwise comparison results are presented using Holm's correction method. Significant values ($p < .05$) are highlighted in bold.
**Table 2** Mean density of littoral benthic invertebrates (individuals m\(^{-2}\)), standard error of the mean (in parentheses) and results for permutational ANOVA (perANOVA; \(p < .05\)) of common taxa (present in >10% of lakes), categorized by lake group (fishless, native trout, nonnative trout).

| Higher taxa | Family | Mean density (individuals m\(^{-2}\)) | Per ANOVA | Post-hoc comparisons |
|-------------|--------|-------------------------------------|-----------|---------------------|
|             |        | Fishless mean (SE) | Native mean (SE) | Nonnative mean (SE) | p-value | Native vs. fishless | Nonnative vs. fishless | Nonnative vs. Native |
| Oligochaeta | Enchytraeidae | 13.32 (3.49) | 9.68 (3.41) | 23.22 (4.83) | 0.09 |  |  |  |
|             | Lumbriculidae | 0.09 (0.06) | 1.43 (0.36) | 1.85 (0.61) | 0.02 | 0.05 | 0.06 | 0.98 |
|             | Naididae | 14.79 (5.15) | 22.52 (5.77) | 32.41 (6.12) | 0.02 | 0.06 | 0.03 | 0.99 |
| Arachnida   | Hydrozetidae | 0.07 (0.07) | 0.10 (0.04) | 0.13 (0.10) | 0.40 |  |  |  |
|             | Malaconothridae | 0.002 (0.002) | 0.10 (0.09) | 0.04 (0.03) | 0.34 |  |  |  |
|             | Trhypochthoniidae | 0.004 (0.003) | 0 | 0.05 (0.03) | 0.06 |  |  |  |
|             | Hygrobatidae | 0 | 0.36 (0.16) | 0.17 (0.14) | 0.24 |  |  |  |
|             | Lebertiidae | 3.80 (1.45) | 9.86 (1.72) | 2.21 (0.44) | 0.02 | 0.03 | 0.99 | 0.03 |
| Coleoptera  | Oxidae | 0.37 (0.17) | 0.07 (0.03) | 0.70 (0.23) | 0.57 |  |  |  |
|             | Isotomidae | 0.12 (0.08) | 0.02 (0.01) | 0.04 (0.02) | 0.40 |  |  |  |
|             | Dytiscidae | 0.97 (0.25) | 3.43 (1.01) | 1.07 (0.37) | 0.31 |  |  |  |
| Diptera     | Ceratopogonidae | 0.01 (0.01) | 0.19 (0.09) | 0.52 (0.40) | 0.31 |  |  |  |
|             | Chironomidae | 66.68 (15.57) | 147.64 (20.94) | 104.22 (12.68) | <0.01 | 0.01 | 0.04 | 0.57 |
|             | Tipulidae | 0.04 (0.02) | 0.61 (0.17) | 0.21 (0.08) | 0.01 | 0.03 | 0.40 | 0.20 |
| Ephemeroptera | Ameletidae | 5.87 (2.21) | 0.87 (0.43) | 0.20 (0.06) | <0.01 | <0.02 | <0.01 | 0.77 |
| Plecoptera  | Capniidae | 1.39 (0.80) | 0 | 0.01 (0.01) | 0.26 |  |  |  |
|             | Chloroperlidae | 0.22 (0.11) | 0.05 (0.05) | 0.27 (0.09) | 0.29 |  |  |  |
|             | Nemouridae | 0.54 (0.22) | 0.34 (0.20) | 0.02 (0.01) | 0.15 |  |  |  |
|             | Perlodidae | 0.11 (0.06) | 0.07 (0.04) | 0 | 0.21 |  |  |  |
| Trichoptera | Limnephilidae | 0.67 (0.21) | 4.24 (0.71) | 2.19 (0.90) | <0.01 | 0.01 | 0.34 | 0.07 |
| Amphipoda   | Gammaridae | 24.96 (9.40) | 12.42 (3.27) | 0.02 (0.02) | 0.03 | 0.99 | 0.07 | 0.07 |
| Veneroida   | Sphaeriidae | 10.51 (2.97) | 31.09 (4.96) | 7.55 (1.46) | <0.01 | <0.01 | 0.89 | <0.01 |
| Nematoda    | Nematoda | 12.67 (3.11) | 18.62 (3.16) | 55.04 (10.48) | <0.01 | 0.25 | <0.01 | 0.18 |
| Platychelminthes | Planariidae | 0.38 (0.17) | 0.13 (0.08) | 0.05 (0.02) | 0.14 |  |  |  |
| Total       | 157.64 (27.96) | 264.24 (28.92) | 232.19 (21.74) | <0.01 | 0.04 | 0.04 | 0.97 |

*Note:* Post-hoc comparisons were made using Tukey HSD or Games–Howell. Significant values (\(p < .05\)) are highlighted in bold. Density values were log\(_{10}\) (\(x + 1\)) transformed prior to perANOVA analysis.
The density of individual littoral invertebrate taxa in native trout lakes was more likely to be similar to non-native trout lakes compared to fishless lakes. For example, both trout-lake groups had reduced densities of the free-swimming and conspicuous Ameletidae compared to fishless lakes (Table 2 and Figure 3). Furthermore, Chironomidae were found at significantly higher densities in both trout-lake groups compared to fishless lakes. There were some key differences between native and nonnative trout lakes. Native trout lakes contained higher densities of certain taxa compared to both fishless and nonnative trout lakes. For example, Lebertiidae and Sphaeriidae were found at significantly higher densities in both trout-lake groups compared to fishless lakes.

There were some key differences between native and nonnative trout lakes. Native trout lakes contained higher densities of certain taxa compared to both fishless and nonnative trout lakes. For example, Lebertiidae and Sphaeriidae were found at the highest densities in native trout lakes compared to other lake groups. Nonnative trout and fishless lakes did not differ for these taxa (Table 2 and Figure 3). Native trout lakes also had the highest densities of Tipulidae and Limnephilidae, followed by nonnative trout and fishless lakes (Table 2 and Figure 3). Native trout exerted an intermediate effect on certain littoral invertebrates compared to nonnative trout. For example, Naididae and Nematoda were at the highest densities in nonnative trout, followed by native trout and fishless lakes (Table 2 and Figure 3). Lumbriculidae also followed this pattern, but post-hoc comparisons were not statistically significant (Table 2 and Figure 3). Gammaridae were almost completely absent from nonnative trout lakes, but at intermediate densities in native trout lakes compared to fishless lakes (Table 2 and Figure 3).

The following taxa were not statistically different between lake groups in the perANOVA comparison: Enchytraeidae, Hydrozetidae, Malaconothridae, Trhypochthoniidae, Hygrobatidae, Malaconothridae, Trhypochthoniidae,

**Figure 3** Density (individuals·m⁻²) of littoral benthic invertebrate taxa, categorized by lake group (fishless, native trout, nonnative trout). Only significant taxa are shown, determined by permutational analysis of variance (perANOVA, 999 permutations; *p* < .05). Bars indicate standard error of the mean. Letters above bars denote Tukey HSD and Games-Howell post-hoc test results. “NS” indicates nonsignificant post-hoc comparison results.
Hygrobatidae, Oxidae, Isotomidae, Dytiscidae, Ceratopogonidae, Chloroperlidae, Nemouridae, Perlodidae, and Planariidae (Table 2).

3.4 Environmental predictors of variation in the littoral invertebrates

The RDA model axes one and two accounted for 6.4% and 3.0% of the total taxonomic variance, respectively. Two environmental variables—elevation and water temperature—were statistically significant predictors of the invertebrate communities. Compared to the global model ($R^2_{adj} = 12.3\%$), forward selection reduced the model while capturing most of the variance explained with only two environmental variables—lake temperature and elevation ($R^2_{adj} = 9.4\%$; Table S5; Figure S1a). The first RDA axis was significant ($F_{1,33} = 3.81, p = .004$), as was the ordination ($F_{1,33} = 2.81, p < .001$). There was no pattern of separation between the lakes based on lake groups (Figure S1b). Elevation and water temperature showed very little correlation. Warmer lakes contained greater densities of Sphaeriidae and Naididae, and Ameletidae and Enchytraeidae were better represented in colder lakes (Figure S1a). Higher densities of Chironomidae were associated with lower montane lakes, whereas Capniidae were associated with alpine and subalpine lakes (Figure S1a).

4 DISCUSSION

This study revealed several lines of evidence that suggested stocking native WSCT into fishless lakes can alter littoral invertebrates in similar ways as nonnative brook trout. For example, littoral invertebrate community structure was indistinguishable between native and nonnative trout lakes when compared to fishless lakes. Both trout-lake groups contained a lower density of free-swimming ameletid mayflies and higher densities of burrowing taxa such as Naididae, Nematoda and Chironomidae. Aggregate properties of the invertebrate community, such as species richness and diversity, were similar between all lake groups. Nevertheless, the finer-scale taxonomic differences between the lake groups highlight the potential ecological consequences of cold-water trout-conservation efforts for mountain-lake ecosystems.

The direct effect of predation is the most likely explanation for the observed differences in littoral invertebrate communities between fishless lakes and lakes occupied by trout (Carlisle & Hawkins, 1998; Knapp et al., 2001). These conspicuous invertebrates do not have behavioral mechanisms to persist when they co-occur with fish predators (Luecke, 1986). For example, Luecke (1986) demonstrated how the addition of native cutthroat trout caused *Hyalella azteca* (Amphipoda) to burrow into the sediment to avoid predation, while *Callibaetis* sp. (Ephemoptera) did not, resulting in higher predation rates on *Callibaetis* sp. The physical inability of *Callibaetis* sp. to burrow into soft sediments may also explain why Ameletidae were at such low densities in all trout lakes in this study.

Higher densities of certain burrowing taxa in the presence of either nonnative or native trout may be attributed to the indirect effects of predation. Weidman et al. (2011) suggested that trout predation on gammarids releases sediment-dwelling invertebrates from competition or predation by these amphipods. Another hypothesized indirect positive effect of introduced trout on burrowing invertebrates was based on an expected increase in nutrient recycling from fish fecal matter (Carlisle & Hawkins, 1998; Leavitt, Schindler, Paul, Hardie, & Schindler, 1994).

The effects of trout introductions on the community structure and abundance of benthic invertebrates in fishless lakes has been well-documented. However, studies have only examined the effects of nonnative trout (e.g., Tiberti et al., 2014) or a mix of native and nonnative trout without distinguishing between the two (e.g., Bradford et al., 1998; Knapp et al., 2001). For example, Bradford et al. (1998) found that stocked native and nonnative trout reduced or eliminated large, mobile epibenthic or limnetic taxa, such as Baetidae, Siphlonuridae, Notonectidae, Corixidae, Limnephilidae and Dytiscidae, compared to fishless lakes. Knapp et al. (2001) found that five of six clinger/swimmer taxa occurred less frequently, or at reduced densities, in stocked trout lakes compared to fishless lakes. Furthermore, clinger/swimming taxa were virtually absent from mountain lakes stocked with nonnative brook trout in the Italian Alps (Tiberti et al., 2014).

Functional (e.g., scrapers, collectors, shredders and predators) and habitat groups (e.g., swimmers, burrowers, sprawlers, and clingers) were compared between lake groups to provide a broader understanding of how native trout may impact the functioning of the littoral invertebrate community. These analyses provided less clarity since some taxa of the same grouping had opposite effects. For example, Ameletidae and Gammaridae were both grouped as swimmers but were not similarly affected by native and nonnative trout. One explanation is that some taxa within the same functional group have different secondary functions (Hooper et al., 2002). Secondary functions may contribute to a taxon’s response to trout stocking. In this study, *Gammarus lacustris* were classified as swimmers but have also been observed burrowing in sediment, presumably to resist trout predation (Luecke, 1986; McNaught et al., 1999). A second difficulty with comparing habitat and functional
groups across environmental gradients is the high diversity of organism functions that exist within a taxonomic rank, especially at the family level (e.g., Chironomidae; Cummins, 1973).

Despite evidence for similar impacts of native and nonnative trout on littoral invertebrate communities, certain taxon-specific differences emerged between native and nonnative trout lakes. Compared to fishless lakes, the densities of Lebertiidae and Sphaeriidae were significantly higher in native but not in nonnative trout lakes. While the behavioral adaptation of burrowing could explain why Lebertiidae and Sphaeriidae are able to persist in the presence of native trout, it does not explain why densities of Lebertiidae and Sphaeriidae were not as high in nonnative trout compared to native trout lakes. This differential effect of native versus nonnative trout on invertebrate prey has been demonstrated previously (Anderson, 1980; Cox & Lima, 2006; Paolucci, MacIsaac, & Ricciardi, 2013) without a clear understanding of the causal mechanisms. For example, in the mountain lakes of the Canadian Rockies, brook trout had the greatest effect on zooplankton assemblage, followed by rainbow trout, Dolly Varden (Salvelinus malma) and cutthroat trout (Anderson, 1980).

Prey naiveté may be another interpretation of the observed differences between the effects of native and nonnative trout on littoral invertebrate communities (e.g., Cox & Lima, 2006). For example, brook trout may be behaviorally more efficient at exploiting benthic prey than the native trout species (e.g., cutthroat trout; Hume & Northcote, 1985; Carlisle & Hawkins, 1998). While invertebrates would presumably be naïve to any species of trout introduced into a historically fishless lake, these results suggest that littoral invertebrates may be more naïve towards predators that were not native to the region. Indeed, stocked brook trout have only been exerting selection pressures on the regional species pool of littoral invertebrates for approximately 100 years compared to at least 12,000 years of selection pressure for WSCT (Behnke, 1992).

Another potential explanation of the observed difference between the effects of native and nonnative trout on littoral invertebrates is the density dependence of predation pressure. Nonnative trout may be found at higher abundances than native trout, causing greater prey consumption at nonnative trout lakes (e.g., Benjamin, Faust, & Baxter, 2011; Simon & Townsend, 2003). While brook trout were selected for their excellent growth rates in mountain lakes (Donald, 1987), data on relative densities of native versus nonnative trout were not available.

The final consideration for the observed differences in littoral invertebrate densities was partially influenced by the physical habitat of each lake group. Lakes were selected in each group that reduced potential confounding effects of the physical environment. Most environmental variables such as mean elevation, water depth and lake area, were successfully controlled. However, the mean catchment of fishless lakes was more than twice as large as the other groups. Although not statistically different, native trout lakes contained more woody debris than the other two groups. Shoreline structure has been shown to moderate the effects of stocked fish (Nasmith, Tonn, Paszkowski, & Scrimgeour, 2012). However, very little woody debris was found in any given lake, and woody debris was not a significant contributor to the RDA analysis.

### 4.1 Conservation implications

Natural resource agencies are tasked with preserving biodiversity and species at risk. As stewards of publically owned land, agencies are responsible for developing plans to accomplish these goals (e.g., Fisheries and Oceans Canada, 2014). However, these plans often lack policy about new species that might be introduced for conservation purposes (McLachlan et al., 2007). Given the absence of literature on the effects of native cold-water trout on recipient ecosystems, this study argues that conservation practitioners do not have the evidence needed to evaluate the risk of conservation introductions (but see Galloway et al., 2016). Therefore, a liberal policy on assisted colonization could cause broad irreversible damage.

Risk assessments would help guide policy development for assisted colonization. Risk assessments should require evidence of imminent threat to the donor species and a quantitative model of predicted outcomes related to all recipient taxa (see Galloway et al., 2016; Hayes & Banish, 2017). This study shows that the assisted colonization of native cutthroat trout would result in a recipient littoral invertebrate community structured similar to nonnative trout lakes. These data can directly inform local risk assessments and policy. However, the effect of introducing native cold-water trout on other recipient species should also be evaluated. For example, impacts to aquatic invertebrates, such as Ameletidae, might reduce prey for a passerine bird (Epanchin et al., 2010). Given that natural resource agencies have an ethical obligation to avoid collateral harm to other species or ecosystems (IUCN/SSC 2016), a cautious approach is needed for the assisted colonization of native trout.

### ACKNOWLEDGMENTS

We are thankful to Craig Logan for sharing his expertise in invertebrate life history and taxonomy, Dr. Laura
Gray-Steinhauer and Dr. Andreas Hamann for providing statistical advice. A special thank you to the following field assistants for their hard work in field data collection: Hedin Nelson-Chorney, Troy Malish, Fonya Irvine, Brian Merry, Sean O’Donovan, Madeleine Wrazej, Colby Whelan, Kayla Eykelboom, Sarah Fassina and Brenna Stanford. This research was funded by Parks Canada and by Alberta Conservation Association Grants in Biodiversity.

CONFLICT OF INTEREST
The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS
The concept and study design of the project was conceived by Mark Taylor, Mark Poesch, and Rolf Vinebrooke. Allison Banting and Mark Taylor developed and evaluated field collection methods. Chris Carli arranged field logistics, trained and led the field crews. The analysis and interpretation was performed by Allison Banting with guidance from Mark Poesch and Rolf Vinebrooke. The manuscript was written by Allison Banting and Mark Taylor. All authors reviewed, edited and approved the final manuscript.

DATA AVAILABILITY STATEMENT
All data and code required to repeat analyses are available at: https://doi.org/10.5061/dryad.ffbg79csg.

ETHICS STATEMENT
The authors have followed the journal editorial policies and ethical considerations. This research was regulated by Parks Canada Research and Collection Permit #25559.

ORCID
Mark K. Taylor https://orcid.org/0000-0003-0655-4197
Mark S. Poesch https://orcid.org/0000-0001-7452-8180

REFERENCES
Anderson, M. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 32–46.
Anderson, M. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62, 245–253.
Anderson, M., Ellingsen, M. K., & McAriddle, B. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9, 683–693.
Anderson, M. J., & Walsh, D. C. I. (2013). PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs*, 83, 557–574.
Anderson, R. S. (1980). Relationships between trout and invertebrate species as predators and the structure of the crustacean and rotiferan plankton in mountain lakes. In W. C. Kerfoot (Ed.), *Evolution and ecology of zooplankton communities* (pp. 635–641). Hanover, NH: University Press of New England.
Baxter, C., Fausch, K., & Saunders, W. (2005). Tangled webs: Reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology*, 50, 201–220.
Bear, E. A., McMahom, T. E., & Zale, A. V. (2007). Comparative thermal requirements of westslope cutthroat trout and rainbow trout: Implications for species interactions and development of thermal protection standards. *Transactions of the American Fisheries Society*, 136, 1113–1121.
Behnke, R. J. (1992). Native trout of Western North America. American fisheries society monograph 6, Bethesda, MD. p. 13. https://doi.org/10.1007/BF00042892
Benjamin, J. R., Fausch, K. D., & Baxter, C. V. (2011). Species replacement by a nonnative salmonid alters ecosystem function by reducing prey subsidies that support riparian spiders. *Oecologia*, 167, 503–512.
Blanchet, F., Legendre, P., & Borcard, D. (2008). Forward selection of explanatory variables. *Ecology Letters*, 89, 2623–2632.
Borcard, D., Gillet, F., & Legendre, P. (2011). Numerical ecology with R. New York, NY: Springer International Publishing.
Bowman, M. F., & Bailey, R. C. (1997). Does taxonomic resolution affect the multivariate description of the structure of freshwater benthic macroinvertebrate communities? *Canadian Journal of Fisheries and Aquatic Science*, 54, 1802–1807.
Bradford, D. F., Cooper, S. D., Jenkins, T. M., Kratz, K., Sarnelle, O., & Brown, A. D. (1998). Influences of natural acidity and introduced fish on faunal assemblages in California alpine lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 2478–2491.
Carlisle, D., & Hawkins, C. (1998). Relationships between invertebrate assemblage structure, two trout species, and habitat structure in Utah mountain lakes. *Journal of North American Benthological Society*, 17, 286–300.
Cole, D., & Landres, P. (1996). Threats to wilderness ecosystems: Impacts and research needs. *Ecological Applications*, 6, 168–184.
Cox, J. G., & Lima, S. L. (2006). Naivete and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology and Evolution*, 21, 674–680.
Cummins, K. W. (1973). Trophic relations of aquatic insects. *Annual Review of Entomological*, 18, 183–206.
David, S. M., Somers, K. M., Reid, R. A., Hall, R. J., & Girard, R. E. (1998). Sampling protocols for the rapid bioassessment of streams and lakes using benthic macroinvertebrates (2nd ed.). Toronto, Canada: Ontario Ministry of Environment, Queens Printer for Ontario. Retrieved from: https://atrium.lib.uoguelph.ca/xmlui/handle/10214/15579
Donald, D. B. (1987). Assessment of the outcome of eight decades of trout stocking in the mountain national parks, Canada. *North American Journal of Fisheries Management*, 7, 545–553.
Donald, D. B., Vinebrooke, R. D., Anderson, R. S., Syrgiannis, J., & Graham, M. D. (2001). Recovery of zooplankton assemblages in mountain lakes from the effects of introduced sport fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 1822–1830.
Dray, S., Blanchet, G. F., Borcard, D., Clapeau, S., Guenard, G., Jombart, T., Larouque, G., Legendre, P., Madi, N. & Wagner, H. (2018). Adespatial: Multivariate multiscale spatial analysis. *R package version 0.1-1. Retrieved from: https://cran.r-project.org/web/packages/adespatial/index.htm
Eby, L. A., Roach, W. J., Crowder, L. B., & Stanford, J. A. (2006). Effects of stocking-up freshwater food webs. *Trends in Ecology and Evolution*, 21, 576–584.
Rawson, D. S. (1940). The eastern brook trout in the Maligne River system, Jasper National Park. *Transactions of the American Fisheries Society*, 70, 221–235.

Ricciardi, A., & Atkinson, S. (2004). Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecological Applications*, 7, 781–784.

Ricciardi, A., & Simberloff, D. (2009). Assisted colonisation is not a viable conservation strategy. *Trends in Ecology and Evolution*, 24, 248–253.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, 421, 57–60.

Schindler, D. (2000). Aquatic problems caused by human activities in Banff National Park, Alberta, Canada. *Ambio*, 29, 401–407.

Schindler, D., & Parker, B. (2002). Biological pollutants: Alien fishes in mountain lakes. *Water Air Soil Pollution: Focus*, 2, 379–397.

Scott, W. B., & Crossman, E. J. (1973). *Freshwater fishes of Canada*. Bulletin 184. Ottawa, ON: Fisheries Research Board of Canada 966 pp.

Seddon, P. J. (2010). From reintroduction to assisted colonization: Moving along the conservation translocation spectrum. *Restoration Ecology*, 18, 796–802.

Seleng, J. H., McMahon, T. E., Zale, A. V., & Barrows, F. T. (2001). Effect of temperature on growth and survival of bulltrout with application of an improved method for determining thermal tolerances in fishes. *Transactions of the American Fisheries Society*, 130, 1026–1037.

Simon, K., & Townsend, C. (2003). Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. *Freshwater Biology*, 48, 982–994.

Thorpe, J. P. (1982). The molecular clock hypothesis: Biochemical evolution, genetic differentiation, and systematics. *Annual Reviews of Ecology, Evolution, and Systematics*, 13, 139–168.

Tiberti, R., von Hardenberg, A., & Bogliani, G. (2014). Ecological impact of introduced fish in high altitude lakes: A case of study from the European Alps. *Hydrobiologia*, 724, 1–19.

Ward, J. C. (1974). The *Fishes and their Distribution in the Mountain National Parks*. Report prepared by the Canadian Wildlife Service. Calgary, AB. 41 pp + App. http://friendsofkootenay.ca/fishes-and-their-distribution-mountain-national-parks-canada

Weidman, R. P., Schindler, D. W., & Vinebrooke, R. D. (2011). Pelagic food web interactions among benthic invertebrates and trout in mountain lakes. *Freshwater Biology*, 56, 1081–1094.

Wenger, S. J., Isaak, D. J., Dunham, J. B., Fausch, K. D., Luce, D. H., & Neville, H. M. (2011). Role of climate and invasive species in structuring trout distributions in the interior Columbia River Basin, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 988–1008.

Wheeler, B. & Torchiano, M. (2016). *lmperm: Permutation tests for Linear Models*, R Package Version 2.0.1. Retrieved from: https://cran.r-project.org/web/packages/lmPerm/index.html.

**SUPPORTING INFORMATION**

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

---

**How to cite this article:** Banting ALK, Taylor MK, Vinebrooke RD, Carli CM, Poesch MS. Assisted colonization of a regionally native predator impacts benthic invertebrates in fishless mountain lakes. *Conservation Science and Practice*. 2021;3:e344. [https://doi.org/10.1111/csp2.344](https://doi.org/10.1111/csp2.344)