Impacts of a novel predator on aquatic invertebrates in fishless lakes: Implications for conservation translocations

by

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ABSTRACT

Fishless mountain lakes hold important ecological and conservation value. As such, managers are establishing conservation goals (e.g., non-native fish removal) to restore the naturalness to many of these lakes. Managers who are recovering native coldwater fish populations threatened by climate change (e.g., Westslope Cutthroat Trout, *Oncorhynchus clarki lewisi* and Bull Trout, *Salvelinus confluentus*) are simultaneously exploring conservation strategies involving the intentional translocation of native fish species to more suitable areas. These areas include unoccupied, or naturally fishless, stream and lake habitat within their native range or favorable habitats outside their native range. This action presents a potential threat for fishless mountain lakes as conservation managers view these as recovery habitat for imperiled native fish species. The purpose of my study was to inform native fish recovery efforts by assessing the potential consequences of translocating native fishes to naturally fishless lakes, thus outside their historic distribution. Forty alpine and sub-alpine lakes in Banff National Park, Alberta and Kootenay National Park, British Columbia were sampled and divided into three lake types, including: 13 naturally fishless lakes, 13 native fish-bearing or native fish-stocked lakes, and 14 non-native fish-stocked lakes historically unoccupied by fish. Littoral invertebrate community composition (presence or absence), density and diversity were examined among lake types to 1) quantify the impacts of introducing non-native fishes into historically fishless lakes, and 2) quantify the differences between native fish lakes and naturally fishless lakes. These comparisons provided context for the scale of impact between two predators of different geographic origins introduced to fishless lakes. Native and non-native fishes similarly altered littoral invertebrate community composition of fishless lakes; however, non-native fishes had the greatest impact on littoral invertebrate density. Although impacts varied between native and non-native predators, the introduction of a novel fish predator to fishless lakes resulted in a negative impact to key littoral macroinvertebrates, such as Gammaridae, Ephemoptera and Plecoptera, and a positive impact to burrowing taxa, such as Oligochaeta, Nemata and Chironomidae. The variation in environmental gradients amoung lake types was controlled for, suggesting fish presence strongly influenced changes to invertebrate community composition and density. While the introduction of non-native fishes has been repeatedly shown to affect invertebrate communities, the translocation of native fishes similarly has the potential to alter the ecology of a naturally fishless lake. With considerations for possible aquatic-terrestrial cross-boundary effects, this study suggests that conservation ecologists consider the entire ecosystem when building resilience for climate change.

PREFACE

This thesis is an original work by Allison L.K. Banting. A version of this thesis is intended for publication. The study was conceived by my co-supervisor, Dr. Mark Taylor, and I led the study design, field data collection, data analysis, and manuscript composition. Dr. Mark Taylor was involved in conceptual and methodological development, field data collection and contributed manuscript revisions and edits. Dr. Mark Poesch served as primary supervisor and assisted with funding. Co-supervisor, Dr. Rolf Vinebrooke, provided feedback on the manuscript draft and data analysis. Dr. Laura Gray-Steinhauer, Dr. Andreas Hamann and Dr. Mark Poesch provided statistical advice. This research was funded by Parks Canada and by Alberta Conservation Association (ACA) Grants in Biodiversity.

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1.0 INTRODUCTION

Fishless mountain lakes hold important ecological and conservation value (Cole and Landres 1996, Knapp et al. 2001a, Schindler 2009). From an ecological perspective, they support unique biological communities by providing habitat conditions free from fish predation (McNaught et al. 1999, Knapp et al. 2005, Schilling et al. 2009a) where downstream physical barriers prevented the natural colonization of fishes (Knapp et al. 2001a). Fishless lakes enhance biodiversity by providing conditions that support the conservation of endemic and genetically unique organisms. For example, cold water refuge for those sensitive to climate change (e.g., meltwater stonefly *Lednia tumana*; Muhlfeld et al. 2011), breeding habitat for anurans (Tiberti and Hardenberg 2012) and waterfowl (Elmberg et al. 2010), or habitat for invertebrates in areas where dispersal is restricted by topographical barriers (Donald et al. 2001). In addition, fishless lakes have been used as reference ecosystems to which altered lakes can be compared. Typically, these comparisons involve the use of aquatic invertebrates as biological indicators of human-mediated disturbances, such as non-native fish introductions (Schilling et al. 2009a).

Despite the unique and important contribution to biodiversity that fishless lakes provide, they have historically been undervalued (Schindler and Parker 2002). Abundant in food resources, fishless lakes were considered opportune habitat to introduce sport fish and create unique recreational angling opportunities (Donald 1987, Bahls 1992, Knapp et al. 2001a). In North America, widespread fish stocking began at the turn of the twentieth century (Donald 1987, Bahls 1992). This includes the Canadian mountain national parks, where fish hatcheries were established for propagation of game fish. In Banff National Park, Alberta, 25% of an estimated 486 lakes have been altered through non-native fish introductions, and of those 84% were historically fishless (Schindler 2000). Non-native salmonids (e.g., Brook Trout, *Salvelinus* *fontinalis*; Rainbow Trout, *Oncorhynchus mykiss*) were the preferred fishery over native salmonids (e.g., Bull Trout, *Salvelinus confluentus;* Westslope Cutthroat Trout*, Oncorhynchus clarki lewisi*) for their exceptional growth and catch rate in mountain lakes (Rawson 1940, Donald et al. 1980). For example, Brook Trout accounted for 57 % of 305 lake introductions over seven Canadian mountain national parks (Banff, Jasper, and Waterton Lakes in Alberta and Yoho, Kootenay, Glacier, and Mount Revelstoke in British Columbia), whereby at least 95% of those lakes were historically fishless (Donald 1987). Native cutthroat (Westslope Cutthroat Trout) from local source populations as well as introduced cutthroat varieties (Coastal Cutthroat, *Oncorhynchus clarkii clarkii*; Yellowstone Cutthroat, *Oncorhynchus clarkii bouvierii)* were also stocked in fishless waters or added to stocks of native Westslope Cutthroat Trout already there (Ward 1974). Rainbow Trout was the second most commonly stocked species, and together with Cutthroat Trout made up 73% of the stocking events in all seven Canadian mountain national parks (Donald 1987). With increasing recognition for the value of native fauna (Donald 1987, Schindler and Parker 2002), the Canadian mountain national parks discontinued their stocking program by the 1980s.

At a global scale, there is sufficient data demonstrating direct and indirect ecological impacts of non-native fish introductions on ecosystem function and declines to native biota abundance and diversity (reviewed in Eby et al. 2006). As trout are opportunistic feeders, initial size-selective predation can reduce common yet vulnerable organisms (Bradford et al.1998, Tiberti et al. 2016a), such as conspicuous benthic macroinvertebrates (Knapp et al. 2001b, Schilling 2009a, Pope and Hannelly 2013), microcrustacean prey (Knapp et al. 2005, Weidman et al. 2011, Tiberti et al. 2014) and terrestrial prey (Baxter et al. 2005, Knight et al. 2005, Pope et al. 2009), disrupting the aquatic and terrestrial food web structure (Donald et al. 2001, Schindler et al. 2001, Sarnelle and Knapp 2005). While direct consumption elicits immediate effects on the food web, introduced fish are also capable of disrupting ecosystem processes indirectly by disrupting nutrient cycling, primary productivity, prey behavior and even physical characteristics (Bryan et al. 2002, Simon and Townsend 2003, Parker and Schindler 2006, Weidman et al. 2011).

Attempts to quantify impacts of fish introductions on invertebrates (e.g. crustacean zooplankton and benthic macroinvertebrates) have focused mostly on fish not native to the region or continent. A meta-analysis found the severity of impact in aquatic ecosystems to be relative to the invaders' geographic origin; the most damage is attributed to genera that do not presently occupy the system (Ricciardi and Atkinson 2004). For example, Brook Trout, native to eastern North America and introduced to western mountain lakes, have been widely studied for their impacts on native biodiversity (Knapp et al. 2001a, Pope and Hannelly 2013). When the introduced predator is not native to the region, the resident invertebrate community appears disproportionally vulnerable because the species lack co-evolutionary adaptations that allow for co-existence (Ricciardi and Atkinson 2004, Cox and Lima 2006, Paolucci et al. 2013). But what if the predator is native to the region yet translocated outside its' natural distribution (i.e. within-drainage translocation to a naturally fishless lake)? Ecosystem function may be disrupted by any species possessing sufficiently novel traits and for these reasons should not preclude the potential impacts of native fish species introduced to a system it had not historically occupied (Paolucci et al. 2013, Ricciardi and MacIsaac 2011, Seddon 2010).

Native faunal resistance in aquatic environments may be relative to how naïve the community is to the introduced predator (Cox and Lima 2006). When the introduced species is native to the region, resistance to fish predation may be higher due to co-evolutionary adaptations (Ricciardi and Atkinson 2004, Paolucci et al. 2013). However, "native" becomes contextual upon the spatial and temporal scale because some lakes lack predators that are still present regionally

(Cox and Lima 2006). The invertebrate community within these fishless lakes are presumably structured by the regional invertebrate species pool. Therefore, regionally native fishes may have a lower impact on invertebrate species with high dispersal rates. Because certain aquatic insects are obligately sexual and lack dormant stages, they are active dispersers as flying adults (Shurin et al. 2009). The actively-dispersing invertebrate species in fishless lakes may therefore be resistant to regionally-native fishes because the regional invertebrate species pool co-evolved with these fishes. To my knowledge, there have been no attempts to investigate the effects of translocating native fish species to naturally fishless lakes (but see Hayes and Banish 2017) even though these lakes are already being implicated in these types of translocations concerning the conservation of imperiled native coldwater fish species (e.g. Galloway et al. 2016).

Increasing water temperatures due to global climate change are altering high-elevation lakes worldwide (Heino et al. 2009, O'Reilly et al. 2015, Roberts et al. 2017). The persistence and adaptability of many freshwater fish species will depend on dispersal to favorable habitat (Root et al. 2003). In mountain environments, a species' range expansion is limited by fragmented landscapes and will respond to warming temperatures by shifting to cooler regions upstream (Chu et al. 2005, Hickling et al. 2006), leading to increasingly isolated populations, losses to genetic diversity (Lavergne et al. 2010, Balint et al. 2011), and even extinction (Rosset and Oertli 2011). Interest is growing for a conservation strategy that manages for a resilient ecosystem (Harris et al. 2006) that favors the persistence of imperiled native coldwater fish species in the face of climate change (e.g., Donlan et al. 2005, Choi 2007, Hoegh-Guldberg et al. 2008).

Conservation translocations are a strategy for the preservation of native fish species threatened by climate change that involves moving a species to areas with habitat conditions predicted to be more suitable for their persistence (IUCN 2013). These areas include unoccupied, or naturally fishless, stream and lake habitat within their native range or favorable habitats in another region outside their native range. The practice of translocating species outside of where they naturally occur remains highly debated (Ricciardi and Simberloff 2009a, Bucharova 2017), despite being guided by decision-making frameworks and threshold criteria that are evaluated by risk and feasibility of the introduction site (McLachlan et al. 2007, Seddon 2010, Schwartz et al. 2012, Abeli et al. 2014, Galloway et al. 2016, Hayes and Banish 2017).

The translocation of imperiled native fish species, particularly those that have range or distribution restrictions, is a new threat to fishless mountain lakes. Some managers and scientists are proponents for immediate conservation translocation programs (e.g., Galloway et al. 2016) to address the imminent threat of climate-driven extinction with only a narrow understanding of resident communities (e.g., McLachlan et al. 2007). The growing interest in translocation for species conservation has highlighted the need for additional research that considers the ecology of moving native fish species outside of where they naturally occur. Without more research on associative impacts to naturally fishless mountain lakes, I am not confident that there are sufficient data to inform risk assessments for conservation translocations.

1.1 Study objectives

The purpose of this study was to assess the consequences of translocating native fishes to fishless lakes outside their natural distribution. I compared the littoral invertebrate community composition, density and diversity among three types of lakes, including: (1) 13 naturally fishless lakes, (2) 13 native fish-bearing or native fish-stocked lakes, and (3) 14 non-native fish-stocked lakes historically unoccupied by fish. My first objective was to quantify the effects of introducing non-native fishes into naturally fishless lakes. Impacts on resident invertebrate communities have been repeatedly documented in the literature but provide context for the scale of impact when introducing regionally native fishes. My second objective was to quantify differences between native fish lakes and fishless lakes. The distinct effects of native fish on structuring invertebrate communities, in relation to introduced non-native fish, are important components in predicting the role of a native fish predator introduced to naturally fishless lakes. Study lakes were selected to minimize differences in environmental factors that influence aquatic insect communities between fishless and fish-bearing lakes. This study provides an important perspective on the impacts of native fish to fishless lake biodiversity which may have implications for conservation translocations.

2.0 METHODS

2.1 Study lakes

For this study, we identified forty mountain lakes in Banff National Park, Alberta and adjacent Kootenay National Park, British Columbia. Based on recorded stocking histories and fish status verified by recent fish surveys (M. Taylor, Parks Canada, unpubl. data and pers. comm.), we divided the study lakes into three lake types: (1) naturally fishless 'reference' lakes ("fishless"; n=13), (2) native fish-bearing or native fish-stocked lakes (mostly cutthroat trout, but also Bull Trout) ("native fish"; n=13), and (3) 14 non-native fish-stocked lakes historically unoccupied by fish (mostly Eastern Brook Trout, but also Rainbow Trout) ("non-native fish"; n=14) (Table 1, Appendix 1).

No other fish species have been reported, or are known to exist, in the study lakes. A 'naturally fishless' lake is one that was never stocked (with the exception of Upper Devon and Upper Fatigue lakes; Appendix 1) and does not presently support fish due to downstream physical barriers that have prevented colonization upstream. Although Upper Devon and Upper

Fatigue have a history of stocking (last stocked in 1964 and 1972, respectively), the fish population in these lakes was not self-sustaining; it is likely that the invertebrate community has returned to pre-stocking conditions (e.g. Donald et al. 2001), enabling Parks Canada to change lake status to 'fishless'. A 'non-native fish-stocked lake', also referred to as 'historically fishless' or 'historically unoccupied by fish', is one that was previously fishless but was stocked at least once and continues to support self-sustaining fish populations as a result of natural reproduction. Study lakes were selected to minimize differences in environmental gradients among lake types, including their spatial distribution (location, elevation) and physical characteristics (maximum depth and lake area).

The study lakes are situated in alpine and sub-alpine environments (1981 m to 2453 m; mean 2194 m), they range from 2-32 ha (mean 12.8) in size, and have maximum depths that vary from 3 m to 71 m (mean 21 m) (Table 1, Appendix 2). Lake depths were known prior to the study and measured with a depth finder while lake area, catchment area and elevation were estimated using geographic information systems (GIS).

2.2 Sampling strategy

Depending on the size of the lake, three to seven sample sites were distributed amoung different substrate types in proportion to how common they were (Knapp et al. 2001b, O'Hare et al. 2007). For example, a 10-ha lake would require six sample sites; therefore, a lake with three common substrate types would be allocated two sample sites per substrate type for a total of six sites. This approach ensured each substrate type was sampled and accounted for the spatial heterogeneity of littoral invertebrate taxa among substrate classes (David et al. 1998). Each sample site measured four meters of shore length and extended out to a depth of one meter. Lakes were visited once during the study following ice-off, from June 15th to July 1st, 2015, or June 13th to June 29th, 2016.

2.3 Environmental predictor variables

At each sample site, we measured water temperature as well as dissolved oxygen (DO), pH, and conductivity with a handheld water quality meter (YSI 650 multiparameter meter; YSI Incorporated, Yellow Springs, OH, U.S.A). All point measurements were taken from a depth of 1-m prior to littoral invertebrate sampling to minimize disturbance of readings. 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). The amount of woody debris (WD) and aquatic macrophytes (AM) were categorized as absent, present or abundant; however, neither descriptors were found in abundance therefore these data are interpreted as binary data (0,1). To interpret woody debris and aquatic macrophytes at the lake level, I rounded the mean value to the nearest integer (e.g., <0.5= 0 (absent); >0.5= 1 (present)). Sampling locations were marked on the map with respect to surrounding riparian vegetation type and significant landmarks or other lake features.

2.4 Littoral invertebrate collection

We collected littoral invertebrate samples from each sample site with the travelling-kick-and-sweep method and 400 µm mesh net, similar to Jones et al. (2007). A sample site contained three transects placed perpendicular to shore, spaced two meters apart and extending offshore to 1-m depth. Sampling was standardized over a ten-minute period (David et al. 1998, Jones et al. 2007). We sampled each transect for 3-minutes, and recorded transect length as distance varied depending on the slope of the lake bottom. For an additional minute, we collected missed invertebrates within the sampling area by sweeping the water column, searching under stones/logs and jabbing aquatic macrophyte when present, then pooled these samples with the transect-kick samples (O'Hare et al. 2007). This collection method estimates taxon abundance per unit area (density). We tested a second method in four lakes (from two watersheds) for collecting free-swimming macroinvertebrates using submerged bottle traps containing glow sticks (n= 10/lake), as described by Schilling et al. (2009b). Bottle traps were set 1m from the lake shore and deployed overnight (c. 10 h deployment) to attract free-swimming macroinvertebrates. This method, however, was later discontinued due to physical constraints and the equal detection probability to the travelling-kick-and-sweep method. We then carefully rinsed samples of organic debris and sediment over a 400 µm sieve then fixed them with Formalin. Following field data collection, we transferred samples to 70% ethanol for long-term preservation and transport to the laboratory for processing. In the laboratory, a qualified benthic invertebrate taxonomist, Craig Logan Consulting, processed and sorted the samples using standard quality assurance and quality control procedures. Depending on the density of organisms presumed to be in a sample, the taxonomist took subsamples using a Marchant box (Marchant 1989) and extrapolated this value to the approximate density of the original value. The taxonomist identified the sorted invertebrates to the finest practical taxonomic level, which was typically to species (31%) and genus (59%), but also to family (9%) or phylum (0.4%), then provided the total number of organisms for each taxon per sample site. Taxa were checked against the reference collection of Environment Canada held at the Canada Centre for Inland Waters in Burlington Ontario. For quality assurance and control, randomly chosen specimens were verified by a secondary taxonomist (Biotax Inc).

Rare taxa accounted for 56 % of the taxa identified at the genus level. Unless otherwise stated, rare taxa were removed if found in fewer than four lakes (<10%) to minimize the large influence that rare species (or large number of zeroes) have on analyses (Legendre and Legendre 1998) (Appendix 3). Once I removed rare species, 71% of taxa were limited to one genus per family. With the exception of Nemata, which were identified at the phylum level, all identifications were made to family, a level considered suitable for indicating relatively large between-lake differences, and adopted for data analysis of aquatic biomonitoring programs for rivers in Canada (Hemsley-Flint 2000 in O'Hare 2007, Reynoldson et al. 2001, Jones 2008, McDermott et al. 2014). According to McDermott et al. (2014), Nemata are typically excluded from the samples as they are not adequately sampled using a 400 µm mesh. For this study, we kept Nemata under the assumption that capture probability for larger Nematodes should be roughly equal among all lakes. The Nemata phylum comprise a major part of the diverse littoral invertebrate community of lakes, occupy key positions in soil food webs, and are important bioindicators of disturbance (Bongers and Ferris 1999). Zooplankton, however, were removed because sampling methods were not designed to collect a full representation of the zooplankton community.

Littoral invertebrates were standardized by the sample area (individuals per square meter), then averaged by the number of sample sites per lake to obtain a composite mean density per taxon per lake.

2.5 Statistical analyses

2.5.1 Environmental predictor variables

I used permutational analysis of variance (perANOVA, permutations = 999; Anderson 2001) to ensure community differences among lake types were not strongly influenced by the variation in underlying environmental variables, including lake morphometry, water chemistry and substrate variables. I also conducted contingency tests (Fisher's exact test) on the presence or absence of habitat variables (woody debris and aquatic macrophytes). Prior to testing, I used box and whisker plots to visualize the distribution of environmental variables and checked for normality (Shapiro-Wilk) and equal variance (Levene's test). Morphometry data were $\log_{10}(x)$-transformed and substrate (percent composition) data were arcsine$\sqrt{(x)}$-transformed (McCune and Grace 2002). Environmental variables that met the assumptions before (e.g., water chemistry) and after (e.g., morphometry) transformations were also checked with one-way analysis of variance (ANOVA), producing nearly identical results to the perANOVA.

2.5.2 Littoral invertebrate community structure and differences among lake types

I used non-metric multidimensional scaling (NMDS) to visualize multivariate patterns in two-dimensional space among lake types based on the (dis)similarities in invertebrate assemblages. NMDS is a non-parametric ordination method suited to non-normal and zero-inflated ecological data sets (McCune and Grace 2002). This method allowed for the comparison of insect assemblages amoung lake types based on their projected position, or proximity, in low dimensional ordination space. Two ordinations were created by applying (1) Bray–Curtis dissimilarity to visualize density data (individuals per square meter) by lake, and (2) Jaccard similarity coefficient to visualize community composition in the form of presence or absence

(0,1). Taxa (vectors) were fitted to the ordination by significance of the correlation of each variable with a cut off *p*-value of < 0.05, determined by 999 permutations. NMDS scores among lake types (fishless, native and non-native) were compared using one-way ANOVA or perANOVA and Tukey's Honest Significant Difference (HSD) or Games-Howell post hoc comparison tests depending on how assumptions of each test were met.

I analyzed differences in the littoral invertebrate communities among lake types using permutational multivariate analysis of variance (PERMANOVA, 999 permutations; Anderson, 2001) of Bray-Curtis dissimilarity. In addition, I calculated differences among the occurrence (presence/absence) data by applying the Jaccard similarity coefficient. I tested homogeneity of the multivariate dispersions using group centroids with the PERMDISP procedure, a resemblance-based permutation test that examines changes to the average within-group dispersion and their equivalence among groups (Anderson 2006, Anderson and Walsh 2013). These two tests are capable of distinguishing between the shift in the structure of the invertebrate community among lake types (PERMANOVA; i.e. differences in centroid location), and the degree of within group variability (PERMDISP; i.e. differences in variability from one to the other groups) (Anderson and Walsh 2013). PERMDISP can also be interpreted as beta diversity (Anderson 2006, Anderson et al 2006), the turnover in species composition among a set of lakes, calculated as the mean distance of lakes to the group centroid. I then identified which combination of lake types those differences were most evident using a multilevel pairwise comparison test (Martinez Arbizu 2017), followed by the Holm's (1979) correction to account for multiple comparisons, which present the risk of falsely rejecting a null hypothesis (Type 1 error).

I compared total and taxon-specific density of common littoral invertebrate taxa among lake types using perANOVA. To examine which combination of lake types were most different, I used post-hoc comparison tests, including Tukey's HSD and Games–Howell tests depending on how the assumption of equal variance was met (Levene's test). I also compared the frequency of occurrence of taxon among lake types using Pearson's chi-square tests when expected values were >5 and Fisher's exact tests when expected values were ≤ 5. Pairwise comparisons following a significant result was tested using Fisher's exact test.

In addition, four simple measures of diversity were calculated for each lake: (1) richness or the number of taxon in each group of lakes, (2) Simpson's diversity, (3) Shannon's diversity, and (4) community evenness (Pielou 1966). One-way analysis of variance (ANOVA) were performed to determine if diversity indices were different among lake types, followed by multiple pairwise comparisons (Tukey's HSD). To consider the entire community, I included rare species for the diversity analyses.

Prior to analyses, density values of common littoral invertebrate taxa were $\log_{10}(x + 1)$ transformed to reduce the asymmetry of the species distributions (Legendre and Legendre 2012) and the influence of dominant species and outliers for ordination (McGarigal et al. 2000).

2.5.3 Environmental predictors of variation in the littoral invertebrate community

I used Redundancy Analysis (RDA; Legendre and Legendre 2012) and Variance Partitioning Analysis (VPA; Borcard et al. 1992) to evaluate environmental predictors of variation in the littoral invertebrate community across lakes. A detrended correspondence analysis (DCA; Hill and Gauch, 1980) was initially performed, and based on the gradient length of the dominant axes (1.8 standard deviations for axis 1 and 1.3 for axis 2), linear response models were suitable for analyses (Lepš and Šmilauer 2003).

Prior to analysis, I scaled and centered environmental variables to compare gradient lengths then transformed invertebrate density values using the Hellinger transformation to ensure linearized relationships between the species that contained many zeroes (Legendre and Gallagher

2001). This transformation also comes with the advantage of not strongly weighting rare taxa in the analysis, and allows the use of a Euclidean-based ordination methods such as RDA (Legendre and Gallagher 2001).

Correlated environmental variables (Spearman's rank; r > 0.6) were removed prior to analysis. For example, clay and cobble were negatively correlated (r = - 0.62) (e.g., lakes with abundant clay had little cobble) and boulder and cobble were positively correlated (r = 0.60); therefore, I removed cobble and used the remaining four substrate categories (clay, sand/gravel, pebble, boulder) to describe the littoral substrate. I further evaluated collinearity among variables using variance inflation factor (>10) to reduce the risk of overestimating the significance of correlated variables.

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 in order to proceed with forward selection. As forward-selection based on significance is prone to inflation, I added a double-stopping criterion (Blanchet et al. 2008) to select the most parsimonious set of predictors. The significance of each environmental predictor variable describing the littoral invertebrate community was determined using Monte Carlo permutation tests with 5000 permutations. Subsequent permutation tests determined significance of individual axes and the significance of the overall ordination of the reduced model (Borcard et al. 2011).

Complementary to the RDA, I tested the percent contribution of individual environmental variables in structuring the littoral invertebrate community with variation partitioning analysis (VPA) by decomposing the explained variance into three fractions and selecting the most parsimonious set of predictors, or predictor, from each group of explanatory variable. This procedure used a series of partial RDA's to partition the variation of the morphometric, water chemistry, littoral substrate and habitat variables to further emphasize the environment–taxa interactions by providing a more simplified view of these relationships.

All statistical analyses were performed in R version 3.3.3 (R Core Team, 2017) using the following packages: (1) "vegan" (Oksanen et al. 2012) for PERMANOVA, PERMDISP, RDA, VPA, pairwise permutation tests and diversity measures (2) "pairwiseAdonis" (Martinez Arbizu 2017) for pairwise tests following PERMANOVA, (3) "ecodist" (Goslee and Urban 2017) for the NMDS (4) "adespatial" (Dray et al. 2018) for the forward selection procedure, (5) "lmperm" (Wheeler and Torchiano 2016) for perANOVA, and (6) "Stats" for ANOVA and pairwise tests. The significance criterion used in all data analyses was $p < 0.05$.

3.0 RESULTS

3.1 Environmental predictor variables

Environmental variables, including lake morphometry, water chemistry, littoral substrate and habitat were similar among the lake types. Despite finding no significant dissimilarities (perANOVA; Table 1), certain features were more characteristic of a type of lake. For instance, fishless lakes were on average deeper (maximum depth) and had a larger mean catchment area compared to native and non-native fish lakes (Table 1). The proportion of sand/gravel observed in non-native fish lakes was higher than fishless and native fish lakes, while the proportion of clay was highest in native fish lakes. Each lake type was, on average, mostly characterized by clay, which accounted for 29.7 to 43.3 % of the littoral area that was sampled (Table 1). The most abundant woody debris was observed in native fish lakes but aquatic macrophytes were not reported.

3.2 Taxon-specific analyses

A total of 76,590 specimens from 40 mountain lakes were identified to 231 taxa, whereby 31% were identified to species, 59% to genus, 9% to family and 1% to phylum (Appendix 3). Rare taxa (found in <4 lakes) removed prior to analysis, accounted for 56% of the taxa identified at the genus level and 42% at the family level. The higher taxonomic groups of the common taxa used in analyses, include: Oligochaeta, Arachnida, Collembola, Coleoptera, Diptera, Ephemeroptera, Plecoptera, Trichoptera, Amphipoda, Veneroida, Nemata, Platyhelminthes, and Tardigrada (Table 2).

3.2.1 Percent occurrence of common littoral invertebrates

Enchytraeidae, Chironomidae, and Nemata were among the most common (sampled from all 40 study lakes) (Table 2). Limnephilidae was the next most frequent taxa occurring 85 - 93% of the time depending on the lake type. Hygrobatidae and Lumbriculidae were collected more frequently from non-native fish lakes (on average, 45.5% more) and native fish lakes (on average, 34.5 % more) compared to fishless lakes, whereas Ameletidae and Perlodidae were more commonly collected from fishless lakes (on average, 35.5% more). Nemouridae were collected more frequently (35% more, on average) from both fishless and native fish lakes compared to non-native fish lakes (Table 2).

3.2.2 Density of common littoral invertebrates

The most abundant taxa (> 20 to 131 individuals per square meter), including Chironomidae, Nemata and Naididae occurred in greater densities in fish-bearing lakes (non-native and native fish lakes) compared to fishless lakes (Table 3). The conspicuous taxa to fish, however, such as Gammaridae and Ameletidae were significantly more abundant in fishless lakes (Table 3 and Figure 2). Gammaridae density was reduced by the presence of non-native fish, whereas Ameletidae density was reduced by the presence of both native and non-native fish. Taxa that were significantly favored in native fish lakes, include: Lebertiidae, Tipulidae, Limnephilidae, and Sphaeriidae (Table 3 and Figure 2). The density values for other littoral invertebrate groups ranged from 0.002 (Macrobiotidae) to 8.66 (Lebertiidae) individuals per square meter (Table 3). Higher order taxa that were not significantly different among lake types, include Coleoptera, Collembola, Platyhelminthes and Tardigrada. The density of taxa for fishless lakes was 158 individuals per square meter, 245 for native fish lakes and 221 for non-native fish lakes (Table 3; perANOVA, permutations = 999; $p = 0.02$). The differences in total density among lake types reflected those found in taxon-specific differences, such that significant differences between native versus fishless lakes and non-native versus fishless lakes were more likely to be detected than differences found between native and non-native fish lakes (Table 3). When Chironomidae and Nemata are removed, native fish lakes have a greater total density of invertebrates, followed by fishless lakes then non-native fish lakes; however, these results were not significant.

3.3 Richness and diversity amoung lake types

There were no differences between the number of species (richness) and the number of abundant species (Shannon diversity) among lake types (Figure 3, Appendix 4). However, there were significantly more dominant species (Simpson diversity) in native fish lakes compared with non-native and fishless lakes (Figure 3, Appendix 4). Compared to non-native fish lakes, there was greater uniformity in abundances (Pielou's evenness) between taxon in native fish lakes.

3.4 Littoral invertebrate community structure amoung lake types

A non-metric multidimensional scaling (NMDS) plot of dissimilarity (Bray-Curtis) showed a clear separation of communities reflecting fish community types (Figure 4, stress = 0.17). The first two NMDS axes were selected to represent the variation in the littoral invertebrate community. The distribution of lakes indicated a change in the assemblage from non-native (altered) lakes to fishless (pristine) lakes. The NMDS scores associated with the density data for NMDS axis one and two were significantly different among lake types (perANOVA, permutations = 999; $p = 0.01$ (axis 1); $p < 0.001$ (axis 2)). In concordance to the plot, a significant separation exists among most lakes representing each lake type, particularly along NMDS axis two between fish-bearing lakes (native and non-native; top half of the plot) and fishless lakes (bottom half of the plot) (Figure 4, Games-Howell; non-native vs. fishless, $p = 0.006$; native vs. fishless, $p = 0.003$). Native and non-native fish lakes were also significantly separated along the first axis (Games-Howell; non-native vs. native, $p < 0.001$).

The NMDS plot representing the degree of similarity in taxonomic composition (Jaccard's similarity coefficient) displayed greater resemblances between fish-bearing communities (Figure 5, stress = 0.26). NMDS scores associated with axis one were not significantly different (ANOVA; $F_{2,37} = 1.12$, $p = 0.337$). NMDS scores associated with axis two were, however, significantly separately among lake types (ANOVA; $F_{2,37} = 12.67$, $p < 0.001$), and is further revealed between fish-bearing (native and non-native) and fishless lakes (Figure 5) (Tukey HSD; non-native vs. fishless, $p < 0.001$; native vs. fishless, $p = 0.003$). An important distinction between the two ordinations becomes evident when density values are converted to occurrence values (Figure 5), whereby compositional differences between native fish lakes and non-native fish lakes are no longer significant.

The first NMDS axis corresponded to higher densities of Gammaridae (Gamm) and Ameletidae (Amel), which were also associated with fishless lakes (Figure 4 and Table 4). Meanwhile, higher densities of Chironomidae (Chir), Naididae (Naid), Nemata (Nema), and Enchytraeidae (Ench) were strongly correlated to NMDS axis two, where the majority of non-native fish lakes are positioned. Likewise, greater occurrence of Chironomidae (Chir) and Naididae (Naid) were found in non-native fish lakes and associated with axis one (Figure 5 and Table 4). The correlations of the remaining taxa for both axes were $|r| < 0.60$ (Table 4).

3.5 Differences in littoral invertebrate communities among lake types

PERMANOVA confirmed significant differences among lake types in the density and occurrence of littoral invertebrate assemblages ($p < 0.001$; Table 5), consistent with the perANOVA test results on NMDS scores. Pairwise comparisons revealed which combination of lake types were responsible for the observed differences (Table 5). Consistent with the NMDS ordinations, native fish lakes differed in their taxonomic assemblages from non-native fish lakes only when density values were calculated.

The littoral invertebrate community within fishless lakes had larger average within group distances using group centroids (PERMDISP; $\mu_{\text{Fishless}} = 0.41$) compared with native ($\mu_{\text{Native}} = 0.19$ and non-native fish lakes ($\mu_{\text{Non-native}} = 0.23$). Differences among group centroids were only detected when comparing fish-bearing (native and non-native) lakes to fishless lakes (Table 5). For these pairs, significant differences detected using PERMDISP and PERMANOVA indicates both a shift in the structure of the invertebrate community (difference in group centroids) and a turnover in species composition among a set of lakes, also known as beta diversity. There was, however, no turnover in species composition (PERMDISP) among native and non-native fish lakes (Table 5). There was also no indication of species turnover in the form of occurrence among any lake type combinations (Table 5).

3.6 Relationship between littoral invertebrate community and environmental variables

The reduced Redundancy Analysis (RDA) model axes 1 and 2 accounted for 6.6% and 2.7%, respectively, of the total variation in the littoral invertebrate community explained by two significant environmental variables for all 40 study lakes (Figure 6). Forward selection procedure identified lake temperature and elevation as the most significant environmental variables in explaining a portion of the variation in the littoral invertebrate density data (Table 6). Compared to the global model (R^2adj = 12.4%) that included all 13 environmental variables, forward selection adequately reduced the model while capturing most of the variance explained with only two environmental variables (R^2adj = 9.2%). The first RDA axis was significant ($F_{1,37} = 4.23$, $p = 0.003$), as well as the ordination ($F_{1,37} = 2.98$, $p < 0.001$).

Sphaeriidae and Naididae dominate lakes that are warmer in temperature (Figure 6a) and are strongly correlated with RDA axis 1, compared with Ameletidae and Enchytraeidae, which were found to prefer colder lakes. Chironomidae were typically found in greater densities at lower elevations, compared to Capniidae (Fig 6a), which are associated with higher elevation lakes and are strongly negatively correlated with RDA axis 2. It is evident in Figure 6b there is no pattern of separation among the lakes based on fish community type, indicating that neither a change in water temperature nor elevation were associated with a particular lake type.

The environmental variables selected for the variation partitioning analysis (VPA) were the same that were chosen under the reduced RDA model (Figure 7). Elevation explained 6.7% of the variance, water temperature explained 3.1 %, and 2.1% was explained by their interaction. Compare this result to the 88.1% of unexplained variance (Figure 7), which would constitute a portion of the explained variance by the fish community if fish density data were available for this analysis.

4.0 DISCUSSION

4.1 Environmental variables among lake types

My approach to minimize environmental variability among lake types isolated possible fish effects from confounding environmental variables that may otherwise influence the invertebrate community. Invertebrate communities have been found to be more vulnerable to fish predation when systems have simple habitat structure (i.e. without submergent vegetation), typically found at higher elevations (Carlisle and Hawkins 1998, Schilling et al. 2009a, Nasmith et al. 2012). Other studies have demonstrated how lake origin or physiography do not always mediate the effects of fish predation on invertebrate communities (Carlisle and Hawkins 1998, Schilling et al. 2009b, Ricciardi and MacIsaac 2011).

Most factors known to influence invertebrate communities were measured. After fish predation, water temperature and elevation were shown to be the most important variables in structuring the invertebrate community among lake types, yet the variation explained in the community by these two variables was only 9.3% (RDA). In addition, when following Holm's correction for multiple comparisons in the RDA model, these variables were no longer significant.

4.2 Community response to non-native fish introductions in historically fishless lakes

Non-native fish introductions have caused significant changes to the density and composition in the littoral invertebrate community of historically fishless lakes. Comparative adverse effects have been corroborated by other studies in this region (Donald et al. 2001, Schindler and Parker 2002, Weidman et al. 2011, Messner et al. 2013, MacLennan and Vinebrooke 2016), as well as in many other mountainous areas in North America (Anderson 1980, Bradford et al. 1998, Carlisle and Hawkins 1998, Knapp et al. 2001b, Knapp et al. 2005, Schilling 2009a, Epanchin et al. 2010, Pope and Hannelly 2013) and in Europe (Tiberti et al. 2014, Tiberti et al. 2016b, Milardi et al. 2016). Of the larger, more active and conspicuous taxa that characterize fishless lakes, Ameletidae, Plecoptera (Nemouridae and Perlodidae), and Gammaridae were the most negatively affected by non-native fish introductions. This may suggest that non-native fish predation was initially a function of invertebrate size, mobility and/or conspicuousness (Meissner and Muotka 2006). Non-native fish presumably specialized on a specific prey disproportionately until it became scarce, at which point they switched to new prey (Bryan and Larkin 1972). Consequently, taxa with these characteristics are reduced or eliminated soon after stocking occurs (Schilling et al. 2009a). For example, in a study examining the macroinvertebrate community three-years following fish stocking in formerly fishless lakes, five free-swimming macroinvertebrates were eliminated and the abundances of other taxa were greatly reduced (Schilling et al. 2009a). Further, when non-native fish predation reduces the density of biphasic invertebrates (i.e. Ameletidae), these effects can translate into reduced biomass for terrestrial consumers (Finlay and Vredenburg 2007, Pope et al. 2009, Epanchin et al. 2010).

The littoral invertebrate community may be affected by direct predation (as described above) or by indirect predation. Our results suggest that when non-native fish are present, there is an increase in burrowing taxa, such as Oligochaeta and Nemata. Carlisle and Hawkins (1998) and Knapp et al. (2001b) also found evidence for this in mountain lakes. Various mechanisms by which non-native fish can indirectly increase burrowing taxa density have been suggested, such as the release of Gammaridae predation pressure on Chironomidae (Weidman et al. 2011), changes to Gammaridae behaviour (e.g. hiding in the sediment to resist predation; Luecke 1986, McNaught et al. 1999), and/or an increase in nutrient flow generated by fish in the form of fish feces (Leavitt et al. 1994, Carlisle and Hawkins 1998, Knapp et al. 2001b). Determining which mechanism is most responsible for changes to burrowing taxa density may provide important cues into other taxon-specific responses and interactions in these systems (Carlisle and Hawkins 1998).

The high density of burrowing taxa is responsible for the greater total invertebrate density found in non-native fish lakes in relation to the other lake types. If Chironomidae and Nemata (the two most abundant taxa in all lakes) are not included, the total number of invertebrates found in fishless lakes would be greater than non-native fish lakes by 12.8%. In this scenario, Ameletidae and Gammaridae make up 31% of the population of invertebrates in fishless lakes and only 0.2% of the population in non-native fish lakes.

I was, however, expecting a greater abundance of free-swimming macroinvertebrate communities in fishless lakes. Families in the orders Hemiptera (Corixidae) and Coleoptera (Dytiscidae, Gyrinidae, Ptilodactylidae) were underrepresented in our kick samples (occurring at only one fishless lake each), which may be suggestive of the collection method used. Highly mobile species can easily evade capture from the kick-net method used, making passive capture methods more effective (Schilling et al. 2009b). Bottle traps set overnight with a glowstick (as described by Schilling et al. 2009b), for example, collect free-swimming macroinvertebrates that are more active at night (Hampton and Duggan, 2003). With this collection method, Schilling et al. (2009b) found six free-swimming macroinvertebrate species unique to fishless lakes. Although samples were taken from Eastern North America (Maine) where lake physiography may result in greater occurrences of free-swimming macroinvertebrates. The pilot work conducted for my study compared invertebrate samples from bottle traps and kick sweeps yielding similar results; both methods either simultaneously detected few or abundant free-swimming macroinvertebrates. In addition, it became unfeasible to carry the additional capture equipment due to the physical constraints and remote locations of these lakes. However, additional test lakes would provide greater statistical power in our prediction that both methods can have equal detection probabilities, which is why future studies could benefit from either incorporating or testing both techniques.

Although invertebrate community evenness and diversity indices were not different between non-native and fishless lakes, these results may primarily be attributable to the complex effects that dominant predators have on the trophic structure of the benthos. It is suggested that, because fish and large predaceous benthic species share a common prey (i.e. herbivorous insects), predation pressure by fish is compensated by large predaceous benthic organism in a fishless environment (Harvey 1993), such as Gammaridae and Ameletidae that dominate fishless lakes in this study. This result is consistent with a previous study on the compensatory effects of adding or removing fish predators which can induce changes in community composition, or species identity, without compromising the predator to prey richness ratio (Donald and Anderson 2003). Thus, predation pressure on shared food resources is maintained.

4.3 Littoral invertebrate community of native fish lakes

Native fish lakes support the most diverse (Simpson diversity) littoral invertebrate community among lake types, characterized by conspicuous and active littoral invertebrates (Gammaridae, Limnephilidae), molluscs (Sphaeriidae) and burrowing taxa (Tipulidae, Oligochaeta, Nemata and Chironomidae). There was also a greater uniformity in abundance between taxa (evenness) indicating community stability in predator/prey relations, which has been observed when fish predators specialize on prey in proportion to their availability and detection probability (Bryan and Larkin 1972). This pattern is particularly different from non-native fish lakes, where individual taxa in the community are inequitably impacted by predation pressure. The introduction of non-native fishes likely led to the rapid collapse of their preferred prey and eventually the establishment of a stable but uneven community comprised of sub-optimal prey (Tiberti et al. 2016a).

Native fish lakes maintain a community of certain taxa that frequent both fishless and non-native fish lakes. Similar to non-native fish lakes, there was a low percent occurrence of Ameletidae and a high density of burrowing taxa (Oligochaeta, Nemata and Chironomidae), indicating that fish presence, and not strictly non-native fish presence, directly and indirectly affect specific prey species. Despite these similarities between non-native and native fish lakes, the native fish are able to co-exist with certain large, active, and conspicuous taxa such as Plecoptera and Gammaridae generally found in fishless lakes. Wilhelm et al. (1999) similarly found large invertebrate prey to co-exist with native Bull Trout. These resemblances may be reflected in the co-evolutionary adaptation that large invertebrate prey have for the presence of native fish species (Cox and Lima 2006, Paolucci et al. 2013). In laboratory trials, Luecke (1986) demonstrated how the addition of native cutthroat trout caused native *Hyalella azteca* (Amphipoda) to burrow in the sediment to avoid predation, while *Callibaetis sp.* (Ephemoptera) did not, resulting in higher predation rates on *Callibaetis sp*. This behavioural adaptation could explain why Gammaridae (Amphipoda) are able to persist in moderation with native fish but not with non-native fishes. The physical inability of *Callibaetis sp.* (Ephemoptera) to burrow into soft sediments, may explain why Ameletidae (Ephemoptera) from this study did poorly in the presence of both groups of fish.

Even with the co-evolved predator-prey interactions that permit the co-existence of certain taxa in native fish lakes, native and fishless lake invertebrate communities remain highly distinct in their assemblages. These comparisons are important components in distinguishing between native and non-native fish species and predicting the role of these predators in invaded ecosystems.

4.4 How native and non-native predators structure littoral invertebrate communities

Native and non-native fishes produce similarly altered invertebrate community composition (which taxon occur and which do not) relative to fishless lakes, likely because both systems share a common top-level predator from the same family (Salmonidae) (Bryan and Larkin 1972). With evidence for a shared level of impact between the native and non-native fishes, it is not surprising that I found considerable variation in invertebrate density and composition between native fish lakes and fishless lakes. However, when I compare invertebrate density in non-native and native fish lakes to fishless lakes, it becomes evident that the impact on the community is magnified by non-native fishes. Therefore, my results suggest that impacts indeed vary depending on the invaders' origin and becomes more predictable when the characteristics of both the invader and the resident community is considered, a pattern that is in agreement with past meta-analyses (Ricciardi and Atkinson 2004, Paolucci et al. 2013).

Prey naiveté could be the principal reason for the variation in effects between non-native and native fish lakes on fishless lakes (Cox and Lima 2006). This result is consistent with Anderson (1980) past surveys of mountain lakes in the Canadian Rockies, who found Brook Trout to have the greatest effect on zooplankton assemblage, followed by Rainbow Trout, Dolly Varden (*Salvelinus malma*), and cutthroat trout. In my study, I observed how fishless lake communities are acutely sensitive to non-native fishes, presumably because they do not recognize or respond appropriately towards a novel fish predator (Cox and Lima 2006); the non-native fish species being more novel than native fish species. The lack of co-evolved anti-predator defenses play a role in how quickly prey become scarce in non-native fish lakes (Cox and Lima 2006, Paolucci et al. 2013). For example, McIntosh and Townsend (1995) found invertebrates to alter their behavior based on their exposure to predation strategies that they are were most familiar with. The most common non-native fish species in this study (Brook Trout) may be more efficient at exploiting benthic prey than the most common native fish species (cutthroat trout*)* (Hume and Northcote 1985). However, Carlisle et al. (1998) found only subtle differences in the feeding behavior between introduced cutthroat and Brook Trout in mountain lakes in Utah. Alternatively, a stronger impact may be detected if there was a higher density, thus biomass, of non-native fishes than native fishes, which translates into a higher prey consumption rate to accommodate the increased nutrient and energy demand (Simon and Townsend 2003).

Sampling only in spring as opposed to both spring and fall limited my ability to capture seasonal variation in the invertebrate community. Greater statistical power with replication of seasons could make more robust conclusions, but was not possible given the magnitude of this study and difficulty in accessing the lakes. Knapp et al. (2001b) made the argument that fluctuations in abundances between seasons are a source of noise, rather than bias. If future studies were to examine both seasons, however, any community differences influenced by spawning activity would be discounted with greater confidence. For example, Anderson (1980) suggested that differences in abundances between native and non-native fish lakes may be influenced by spring and fall feeding pressure related to the spawning period of native fish (i.e. cutthroat trout that spawn in the spring) and non-native fish (i.e. Brook Trout that spawn in the fall). Nevertheless, if spawning pressure is indeed responsible for seasonal variation in invertebrate density, then it was not enough to have had an effect on the difference in community composition between native and non-native fish lakes, otherwise certain taxa would have already been eliminated provided the extended period the non-native fish have been introduced for. It is intriguing, however, that there can be a coexistence of large invertebrate prey with fall-spawning native Bull Trout, as demonstrated by Wilhelm et al. (1999) in a study on the seasonal food habits of Bull Trout from Harrison lake (a native lake used in this study). In addition, three native fish lakes and four non-native fish lakes in this study support populations of fish species that spawn in opposing seasons. Anderson's (1980) past surveys had also shown that invertebrate communities in mountain lakes supporting native cutthroat and Bull Trout populations (with opposing spawning seasons) more closely resembled the community of fishless lakes than that of non-native fish lakes. Therefore, these findings suggest that the regional species pool of invertebrates was responding more strongly to the prior (evolutionary) experience with the type of predator (native vs. non-native) rather than the seasonal variation in spawning habits. These factors, among others, play an important role in how the community of fishless lakes will respond to translocating native fish predators outside their natural distribution for conservation purposes.

4.5 Potential impacts of conservation translocations on littoral invertebrates

The observed effects that introduced non-native fishes have on community composition of historically fishless lakes provides context for potential impacts when translocating native fishes. Although native fishes co-exist with large littoral invertebrate prey species commonly found in fishless lakes (Gammaridae and Plecoptera), this does not suggest fishless lakes are suitable for potential establishment of native fish populations, which was suggested by Wilhelm et al. (1999) for Bull Trout in this area. More importantly, the littoral invertebrate community in native fish lakes is more similar to the composition of the community in non-native fish lakes than to fishless lakes, thus any introduction would result in a community composed of similar taxa to non-native fish lakes. However, the variation in impact becomes more quantifiable when measuring invertebrate density, and may depend on the lineages (species') prior evolutionary experience to the predator.

Fishless lakes may be topographically isolated from fish immigration, but are not isolated from invertebrates with dispersal abilities, which differ by species. Therefore, the evolutionary adaptation of the invertebrate communities, even in fishless lakes, may be directly related to their dispersal abilities from the regional species pool originating from both native fish lakes and naturally fishless streams and lakes. Consequently, I would expect to see greater impact on taxa with poor dispersal abilities than on taxa with high dispersal abilities (e.g., Ameletidae). Some species with high dispersal abilities, however, could have been isolated between lakes by topographic barriers (Donald et al. 2001), which means they will not be able to maintain certain populations in historically fishless lakes with translocated native fish species. This becomes a concern for the recovery of Ameletidae populations as native fish lakes already support less individuals than fishless lakes. Further, Ameletidae are particularly important and highly regarded in the literature for their contribution to terrestrial consumers in sub-alpine and alpine environments (e.g., Knapp et al. 2001b, Finlay and Vredenburg 2007, Epanchin et al. 2010).

For a system that lacks the adaptation towards a novel fish predator, even those that are native to the region, immediate changes to invertebrate density is expected followed by changes to community composition. The change to community structure may not be as detrimental in all situations if the translocations do not interfere with the evolutionary significance of the recipient community (i.e. within-drainage translocations) (Ricciardi and Simberloff 2009b). However, despite invertebrate dispersal abilities and thus evolutionary experience with the translocated species, it becomes difficult to forecast unforeseen cascading trophic impacts to aquatic ecosystems, and just as notable, impacts across the aquatic-terrestrial interface where some terrestrial species rely on invertebrates for their persistence (reviewed in Eby et al. 2006).

5.0 CONCLUSION

To my knowledge, there have been no attempts to quantify community level impacts of translocating native fish species to naturally fishless lakes (but see Galloway et al. 2016 and Hayes and Banish 2017), while few studies have compared prey responses between native and non-native predators in aquatic ecosystems (e.g., but see Carlisle and Hawkins 1998, Huryn 1998, Biggs et al. 2000, Donald et al. 2001, Benjamin et al. 2011, and for meta-analyses see Ricciardi and Atkinson 2004 and Paolucci et al. 2013). If native and non-native fish similarly shape community composition, as my results suggest, then the invertebrate community of fishless lakes will suffer significant changes even when native predators are considered for translocation. This study clearly demonstrates that fishless lakes support a unique littoral invertebrate community that is vulnerable to loss or reductions associated with translocating native fish species outside their natural distribution.

Those proposing conservation translocations might argue that the benefits of recolonizing imperiled native fish species may outweigh the risks (Hoegh-Guldberg et al. 2008). Yet proposed risk assessments for conservation translocations have had little consideration for the full extent of the invader's impacts at multiple ecological levels (e.g., individual, population, community, ecosystem; Townsend 2003). For example, when evaluating the risk and feasibility of the introduction site, the absence of "threatened, endangered, or sensitive native aquatic species" as highly suitable habitat in a risk assessment (e.g., Galloway et al. 2016) may be naïve and ignoring important considerations for rapid declines to an otherwise stable community. Considerations have been made to introduce native fishes to restored fishless lakes formerly occupied by non-native fishes, with the idea that native fish species can beneficially fill vacancies created by non-native fish species (e.g., Galloway et al. 2016). But if native fishes are just as likely to alter community composition, then the replacement of non-native predators with native fishes will continue to impact the invertebrate community. Further, this strategy inhibits and diverts resources from conservation efforts to restore historically fishless lakes impacted by non-native fish introductions.

That conservation translocations are already being undertaken (e.g., McLachlan et al. 2007), emphasizes the urgency to develop a predictive understanding of the consequences at the ecosystem level (Simon and Townsend 2003, Ricciardi and Simberloff 2009a) and the time lags associated with those effects. At present, our best predictor are the impacts associated with non-native fish introductions to historically fishless lakes. Further, by incorporating the ecological characteristics of native fish predators in addition to the knowledge of trophic relations of different lake types, we have a greater ability to predict a pattern of impact.

Quantifying the impacts between fish predators offers a broader understanding of the mechanisms that influence invertebrate communities in fishless lakes. This study contrasts impacts on littoral invertebrate communities of top-level fish predators evolved from the same family (Salmonidae) but originate from different regions. In turn, this strengthens our ability to predict the outcome of native fish translocations as a future conservation scheme. The results of this study suggest that conservation translocations proposed for imperiled native fish species may negatively impact the littoral invertebrate community of naturally fishless lakes.

TABLES

Table 1. Summary of fish status and lake characteristics of 40 mountain lakes sampled in spring 2015 and 2016 in Kootenay National Park, B.C. and Banff National Park, Alberta, categorized by lake type.

Lake Characteristics	Fishless (n = 13)	Native (n = 13)	Non-native (n = 14)	*p*-value
Fish Status				
Fish species (n^a)	——	BLTR (3); CTTR (11)	BKTR (13); CTTR (2); RBTR (2)	
Morphometry				
Elevation (m)	2221 (39)	2132 (25)	2224 (36)	$p = 0.14$
Maximum depth (m)	27 (4.9)	17 (3.1)	18 (2.2)	$p = 0.20$
Lake area (ha)	13.7 (2.5)	11 (2.4)	13.5 (3.0)	$p = 0.58$
Catchment Area (ha)	872 (312)	324 (101)	296 (73)	$p = 0.06$
Water Chemistry				
Water Temperature (ºC)	7.7 (0.54)	9.8 (0.61)	8.5 (0.67)	$p = 0.09$
Dissolved Oxygen (mg/L)	10.4 (0.26)	10.4 (0.26)	9.7 (0.27)	$p = 0.09$
Conductivity (µS/cm)	193 (15)	189 (23)	159 (14)	$p = 0.22$
pH	8.1 (0.16)	7.6 (0.14)	7.8 (0.20)	$p = 0.10$
Substrate (% composition)				
Clay	29.7 (6.9)	43.3 (6.9)	31.3 (5.8)	$p = 0.23$
Sand/Gravel	13.3 (3.1)	10.6 (1.6)	20.5 (6.4)	$p = 0.18$
Pebble	22.0 (3.9)	15.3 (2.4)	19.4 (3.5)	$p = 0.38$
Cobble	25.6 (3.4)	23.5 (4.1)	19.6 (4.0)	$p = 0.55$
Boulder	9.4 (3.0)	7.2 (2.6)	9.2 (2.6)	$p = 0.89$
Habitat (% occurrence)				
Woody Debris	7.7	46.2	28.6	$p = 0.10$
Aquatic Macrophytes	7.7	0	28.6	$p = 0.11$

Note: Environmental variables and their mean (SE) are provided from spring 2015 and 2016. Substrate variables were calculated as percent mean composition (SE) standardized by sample area. Habitat variables were recorded as present or absent and presented here as percent occurrence by lake type. Differences among lake types in topography and water chemistry variables were compared by permutational analysis of variance (perANOVA) at the $p < 0.05$ level. Binomial habitat variables were tested using Fisher's Exact Test ($p < 0.05$). BLTR, Bull Trout (*Salvelinus confluentus)*; CTTR, Cutthroat Trout *(Oncorhynchus clarki)*; BKTR, Brook Trout *(Salvelinus fontinalis)*; RBTR, Rainbow Trout *(Oncorhynchus mykiss)*.
n^a = number of lakes where species is present.

Table 2. Percent occurrence of common littoral invertebrate taxa (present in >10 % of lakes), categorized by lake type.

Higher Taxa	Family	Code	Percent (%) Occurrence				Post-hoc comparisons		
			Fishless	Native	Non-native	*p*-value	Native vs. Fishless	Non-native vs. Fishless	Native vs. Non-native
Oligochaeta	Enchytraeidae	Ench	100	100	100	1			
	Lumbriculidae	Lumb	23	77	79	<0.01	0.02	<0.01	1
	Naididae	Naid	77	100	100	0.06			
Arachnida	Hydrozetidae	Hydr	8	31	21	0.38			
	Malaconothridae	Mala	15	23	21	1			
	Trhypochthoniidae	Trhy	8	0	29	0.11			
	Hygrobatidae	Hygr	0	15	36	0.05	0.48	0.04	0.38
	Lebertiidae	Lebe	77	92	79	0.66			
	Oxidae	Oxid	15	31	29	0.73			
Collembola	Bourletiellidae	Bour	15	15	0	0.37			
	Isotomidae	Isot	62	31	21	0.10			
Coleoptera	Dytiscidae	Dyti	54	62	64	0.85			
Diptera	Ceratopogonidae	Cera	15	23	36	0.54			
	Chironomidae	Chir	100	100	100	1			
	Tipulidae	Tipu	23	62	50	0.15			
Ephemeroptera	Ameletidae	Amel	85	38	43	0.04	0.04	0.05	1
Plecoptera	Capniidae	Capn	23	0	7	0.20			
	Chloroperlidae	Chlo	38	15	29	0.46			
	Nemouridae	Nemo	46	38	7	0.05	1	0.03	0.08
	Perlodidae	Perl	31	8	0	0.04	0.32	0.04	0.48
Trichoptera	Limnephilidae	Limn	85	92	93	0.83			
Amphipoda	Gammaridae	Gamm	46	62	21	0.12			
Veneroida	Sphaeriidae	Spha	77	100	93	0.20			
Nemata	Nemata	Nema	100	100	100	1			
Platyhelminthes	Planariidae	Plan	46	46	50	0.97			
Tardigrada	Macrobiotidae	Macr	15	8	7	0.83			

Note: Significant results (highlighted in grey) determined by Fisher's exact tests or Pearson's chi-square tests ($p < 0.05$). Only significant post-hoc comparisons are presented, determined by Fisher's exact tests.

Table 3. Density (individuals·m^2) of common littoral invertebrate taxa (present in >10 % of lakes), categorized by lake type.

Higher Taxa	Family	Mean Density (individuals·m^2)				Post-hoc comparisons		
		Fishless mean (SE)	Native mean (SE)	Non-native mean (SE)	*p*-value	Native vs. Fishless	Non-native vs. Fishless	Native vs. Non-native
Oligochaeta	Enchytraeidae	13.32 (3.49)	8.89 (2.72)	22.04 (4.61)	0.13			
	Lumbriculidae	0.09 (0.06)	1.21 (0.28)	1.75 (0.58)	0.02	0.02	0.03	0.98
	Naididae	14.79 (5.15)	20.26 (4.53)	30.85 (5.85)	0.02	0.04	0.04	0.99
Arachnida	Hydrozetidae	0.07 (0.07)	0.08 (0.03)	0.12 (0.10)	0.54			
	Malaconothridae	0.0009 (0.0007)	0.08 (0.07)	0.04 (0.03)	0.53			
	Trhypochthoniidae	0.004 (0.003)	0	0.05 (0.03)	0.03	0.99	0.17	0.14
	Hygrobatidae	0	0.28 (0.13)	0.16 (0.13)	0.53			
	Lebertiidae	3.80 (1.45)	8.66 (1.37)	2.10 (0.42)	0.01	0.04	0.98	0.02
	Oxidae	0.37 (0.17)	0.08 (0.03)	0.66 (0.22)	0.31			
Collembola	Bourletiellidae	0.04 (0.03)	0.01 (0.01)	0	0.22			
	Isotomidae	0.12 (0.08)	0.02 (0.01)	0.04 (0.02)	0.44			
Coleoptera	Dytiscidae	0.97 (0.25)	2.68 (0.80)	1.01 (0.36)	0.60			
Diptera	Ceratopogonidae	0.01 (0.01)	0.15 (0.07)	0.50 (0.37)	0.40			
	Chironomidae	66.68 (15.57)	131.81 (16.84)	99.74 (12.22)	<0.01	0.02	0.06	0.50
	Tipulidae	0.04 (0.02)	0.63 (0.17)	0.20 (0.07)	0.01	0.02	0.42	0.20
Ephemeroptera	Ameletidae	5.87 (2.21)	0.68 (0.34)	0.19 (0.06)	<0.01	<0.01	<0.01	0.88
Plecoptera	Capniidae	1.39 (0.80)	0	0.01 (0.01)	0.03	0.18	0.19	0.99
	Chloroperlidae	0.22 (0.11)	0.05 (0.04)	0.25 (0.09)	0.44			
	Nemouridae	0.54 (0.22)	0.26 (0.15)	0.02 (0.01)	0.08			
	Perlodidae	0.11 (0.06)	0.06 (0.03)	0	0.16			
Trichoptera	Limnephilidae	0.67 (0.21)	4.66 (0.82)	2.08 (0.85)	<0.01	<0.01	0.43	0.02
Amphipoda	Gammaridae	24.96 (9.40)	10.87 (2.64)	0.04 (0.02)	0.02	0.98	0.04	0.03
Veneroida	Sphaeriidae	10.51 (2.97)	26.16 (4.03)	7.22 (1.40)	<0.01	<0.01	0.94	0.01
Nemata	Nemata	12.67 (3.11)	27.56 (4.77)	52.36 (10.02)	0.01	0.04	0.01	0.69
Platyhelminthes	Planariidae	0.38 (0.17)	0.10 (0.04)	0.05 (0.02)	0.11			
Tardigrada	Macrobiotidae	0.002 (0.001)	0.01 (0.01)	0.02 (0.01)	1.00			
Total		157.64 (27.96)	245.24 (23.50)	221.48 (21.26)	0.02	0.01	0.03	0.90

Note: Significant results (highlighted in grey) determined by permutational analysis of variance (perANOVA; $p < 0.05$). Post-hoc comparisons were made using Tukey LSD or Games–Howell. Density values were $\log_{10}$ (x+1) transformed prior to analysis.

Table 4. Eigenvectors for littoral invertebrate taxa with non-metric multidimensional scaling (NMDS) axes 1 & 2.

Taxon	Mean Density		Presence / Absence	
	Axis 1	Axis 2	Axis 1	Axis 2
Bour	0.10	-0.06	-0.01	-0.38
Capn	-0.40	-0.51	-0.50	-0.13
Macr	-0.04	0.07	0.16	-0.04
Trhy	-0.27	0.18	0.12	0.29
Perl	0.31	0.07	0.15	-0.46
Hygr	-0.03	0.16	0.09	0.13
Hydr	0.14	0.04	0.24	-0.16
Mala	-0.07	0.30	0.16	0.15
Oxid	0.05	0.33	0.29	0.07
Cera	-0.01	0.26	0.28	0.14
Chlo	-0.11	-0.08	-0.21	-0.03
Nemo	0.29	-0.02	0.12	-0.59
Isot	0.14	-0.12	-0.23	-0.53
Gamm	0.68	0.05	0.18	-0.58
Tipu	0.31	0.33	0.45	-0.25
Plan	0.18	-0.17	-0.14	-0.09
Amel	0.57	-0.38	-0.29	-0.53
Lumb	-0.06	0.41	0.38	0.29
Dyti	0.26	0.31	0.09	-0.09
Lebe	0.56	0.38	0.29	-0.36
Limn	0.41	0.41	0.32	-0.21
Spha	0.46	0.61	0.51	-0.15
Naid	0.07	0.81	0.63	0.07
Ench	-0.14	0.64	0.25	0.01
Chir	0.14	0.84	0.65	0.03
Nema	-0.27	0.69	0.48	0.25

Note: Correlations with $r^2 > 0.14$ ($p < 0.05$) are highlighted in grey. Refer to table 2 for family codes.

Table 5. PERMANOVA analysis (999 permutations) comparing differences in community composition of a) $\log_{10}(x+1)$ transformed density values (individuals·m^2) and b) occurrence data (0,1), among lake types using (a) Bray-Curtis and (b) Jaccard as their respective (dis)similarity measures. PERMDISP probabilities for multivariate homogeneity of dispersions using group centroids are also shown. Summary of pairwise permutation tests for lake type combinations are presented with Holm's corrected *p*-values.

	PERMANOVA						PERMDISP
a) Density (Bray-Curtis)	*Df*	*SS*	*MS*	*pseudo-F*	R^2	*p(perm)*	*p-value*
Treatment	2	1.00	0.50	4.93	0.21	<0.001	<0.001
Residuals	37	3.77	0.10		0.79		
Pairs				*F*	R^2	*p.adj*	*p.adj*
Fishless vs. Native				5.58	0.19	<0.001	<0.001
Fishless vs. Non-native				4.57	0.15	<0.001	<0.001
Native vs. Non-native				4.33	0.15	<0.001	0.12
b) Occurrence (Jaccard)	*Df*	*SS*	*MS*	*pseudo-F*	R^2	*p(perm)*	*p-value*
Treatment	2	0.53	0.26	2.26	0.11	<0.001	0.14
Residuals	37	4.32	0.12		0.89		
Pairs				*F*	R^2	*p.adj*	*p.adj*
Fishless vs. Native				2.64	0.10	0.01	0.07
Fishless vs. Non-native				3.17	0.11	<0.001	0.24
Native vs. Non-native				0.73	0.03	0.67	0.49

Note: Significant values ($p < 0.05$) are highlighted in grey.

Table 6. Results of the forward selection procedure in order of significance for the associations between environmental variables and variation in littoral invertebrate density (individuals·m^2).

Variable	*Adjusted R^2 Cum*	*F*	*P*-value
Water Temperature (ºC)	0.05	3.13	<0.01
Elevation (m)	0.09	2.70	<0.01
Maximum depth (m)	0.12	2.12	0.07
Sand/Gravel	0.14	1.88	0.08
Aquatic Macrophyte	0.16	1.74	0.11
Woody Debris	0.17	1.61	0.13
Pebble	0.17	0.94	0.44
Lake area (ha)	0.17	0.88	0.51
pH	0.18	1.29	0.23
Conductivity (µS/cm)	0.16	0.61	0.74
Clay	0.15	0.63	0.70
Dissolved Oxygen (mg/L)	0.14	0.54	0.80
Boulder	0.12	0.51	0.81

Note: Significant values ($p < 0.05$) are highlighted in grey.

FIGURES

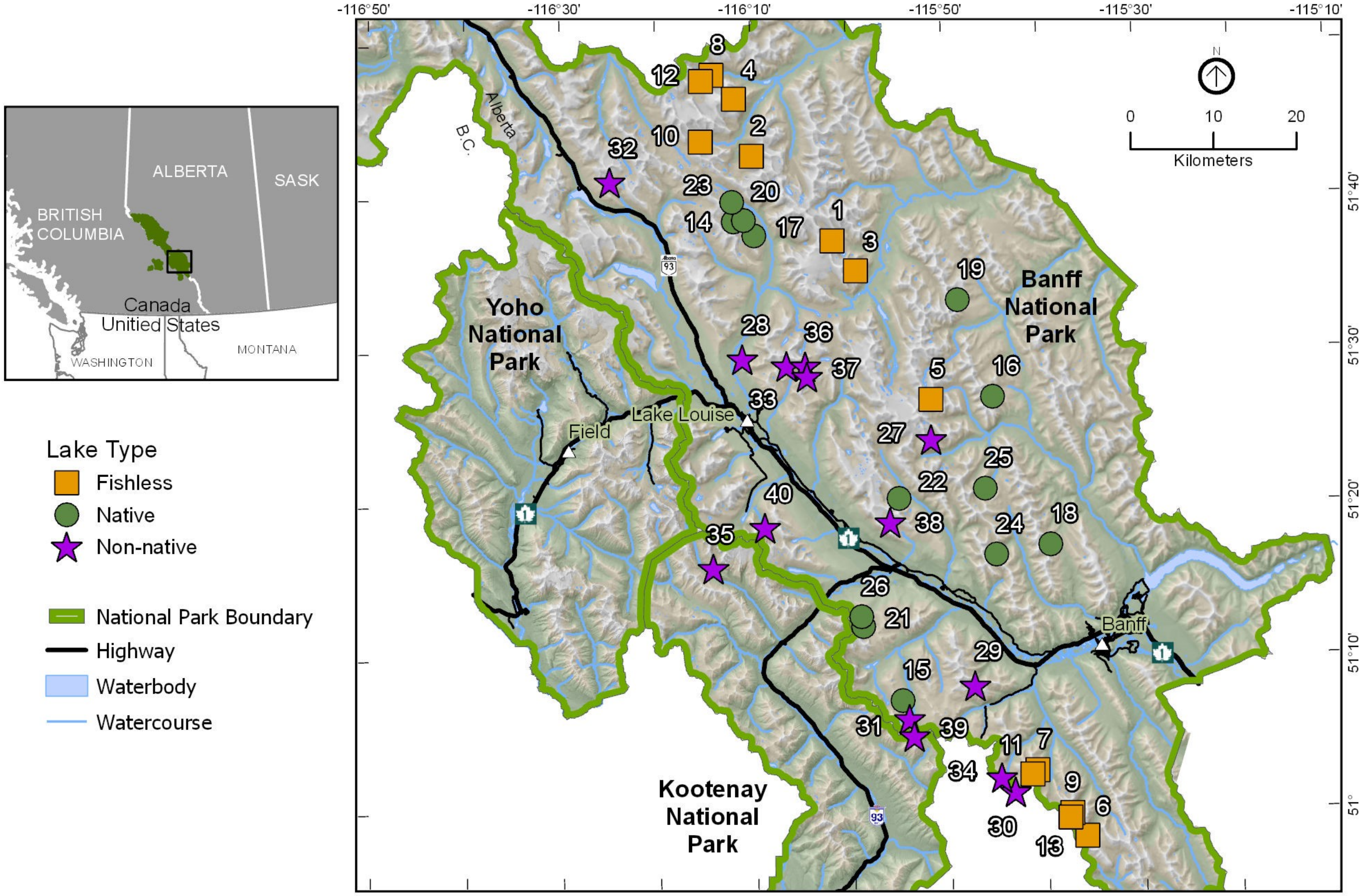

Figure 1. Map of the 40 study lakes sampled for littoral invertebrates in spring 2015 and 2016 in Kootenay National Park, B.C. and Banff National Park, Alberta, illustrated by lake type. Refer to table A2 for lake names associated with lake number.

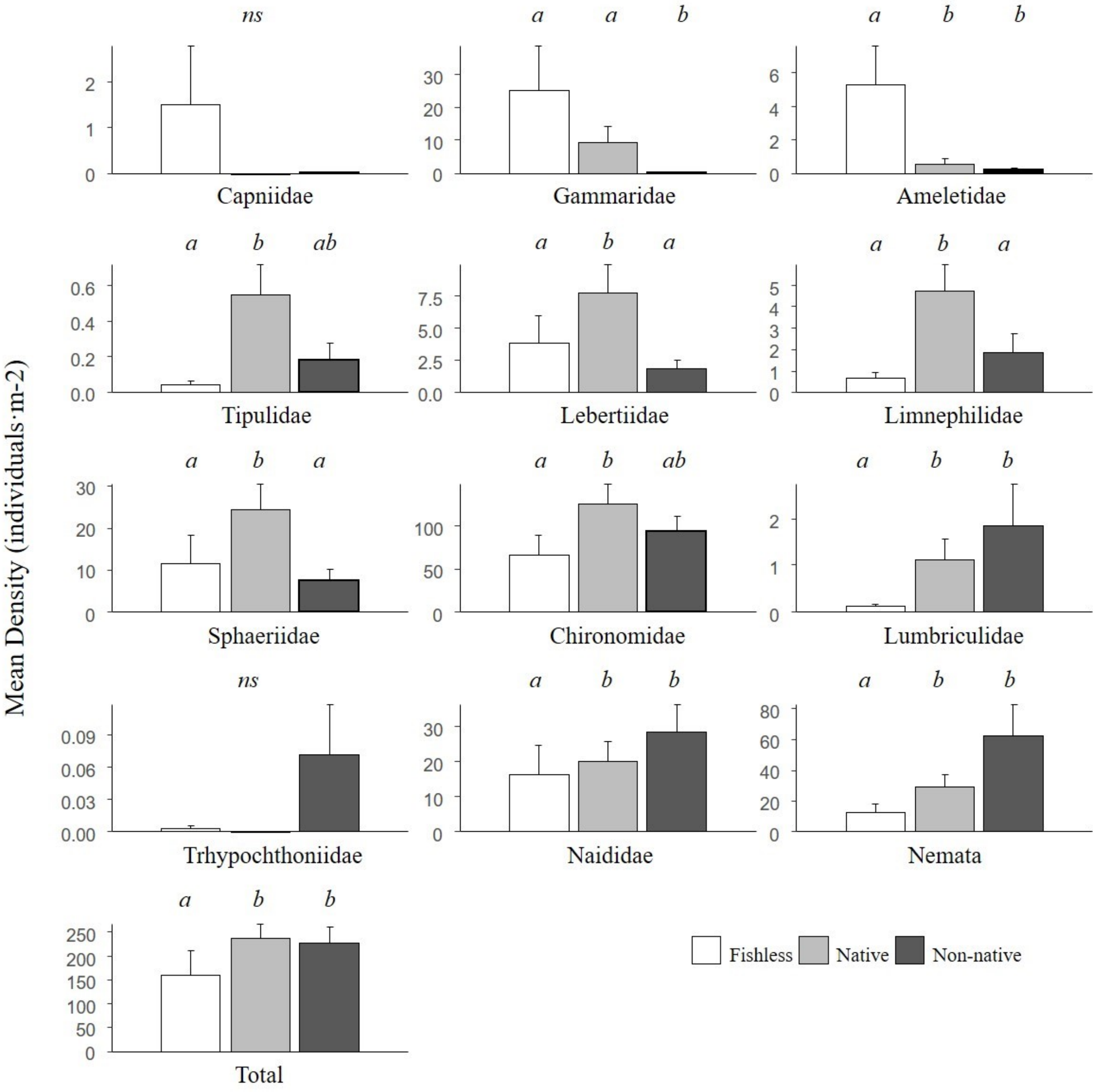

Figure 2. Density (individuals·m^2) of littoral invertebrate taxa, categorized by lake type. Only significant littoral invertebrate taxa are shown, determined by permutational analysis of variance (perANOVA; $p < 0.05$). Bars indicate standard error of the mean. Letters above bars denote Tukey HSD and Games-Howell post hoc test results. 'NS' indicates non-significant post-hoc pairwise comparison results.

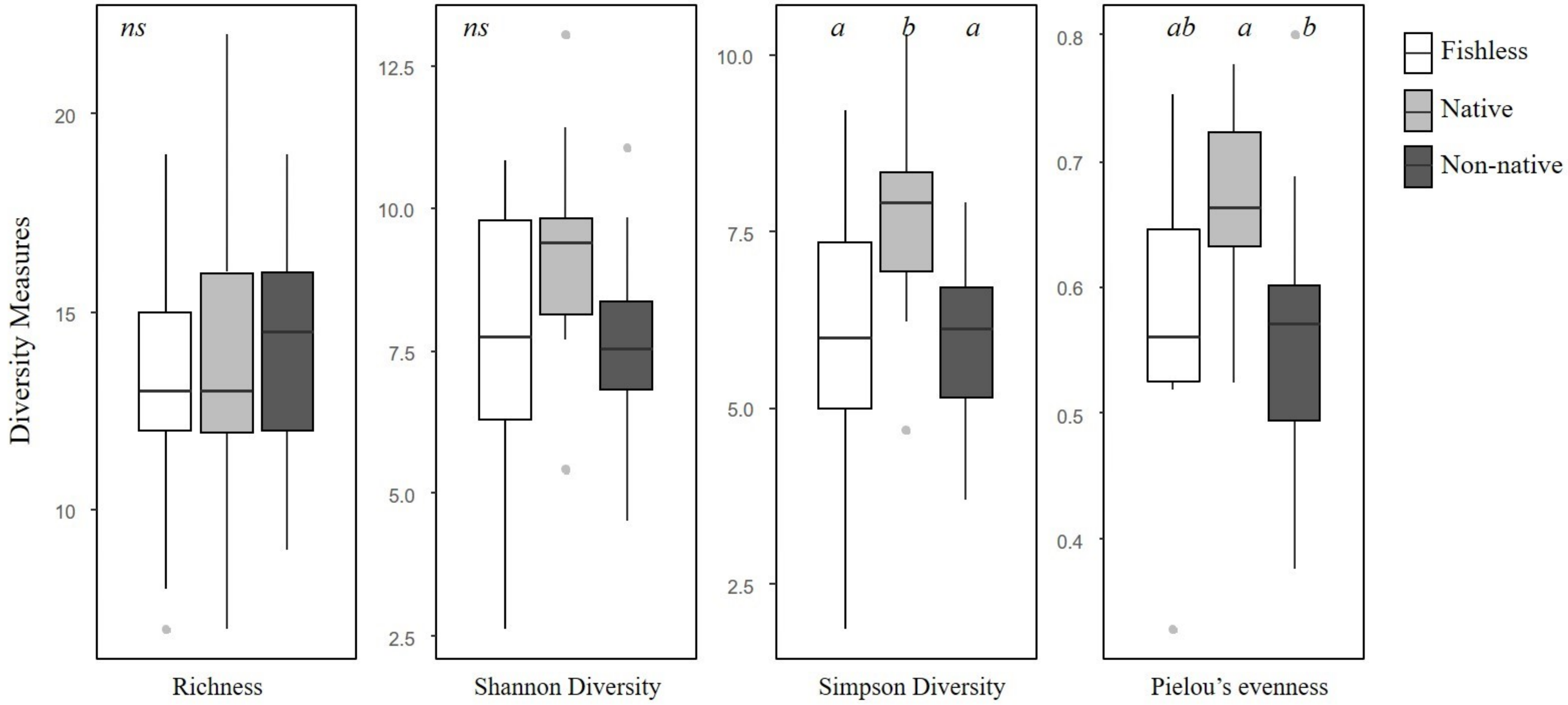

Figure 3. Box plots of Richness, Shannon diversity, Simpson diversity, and Pielou's evenness indices, categorized by lake type. The line within each box marks the median, the bottom and top of each box indicate the 25th and 75th percentiles, the whiskers below and above each box represent the error, and the points above the whiskers indicate any outliers. Differences were compared by analysis of variance (ANOVA; $p < 0.05$). Letters above bars denote Tukey HSD post hoc test results. 'NS' indicates non-significant post-hoc pairwise comparison results.

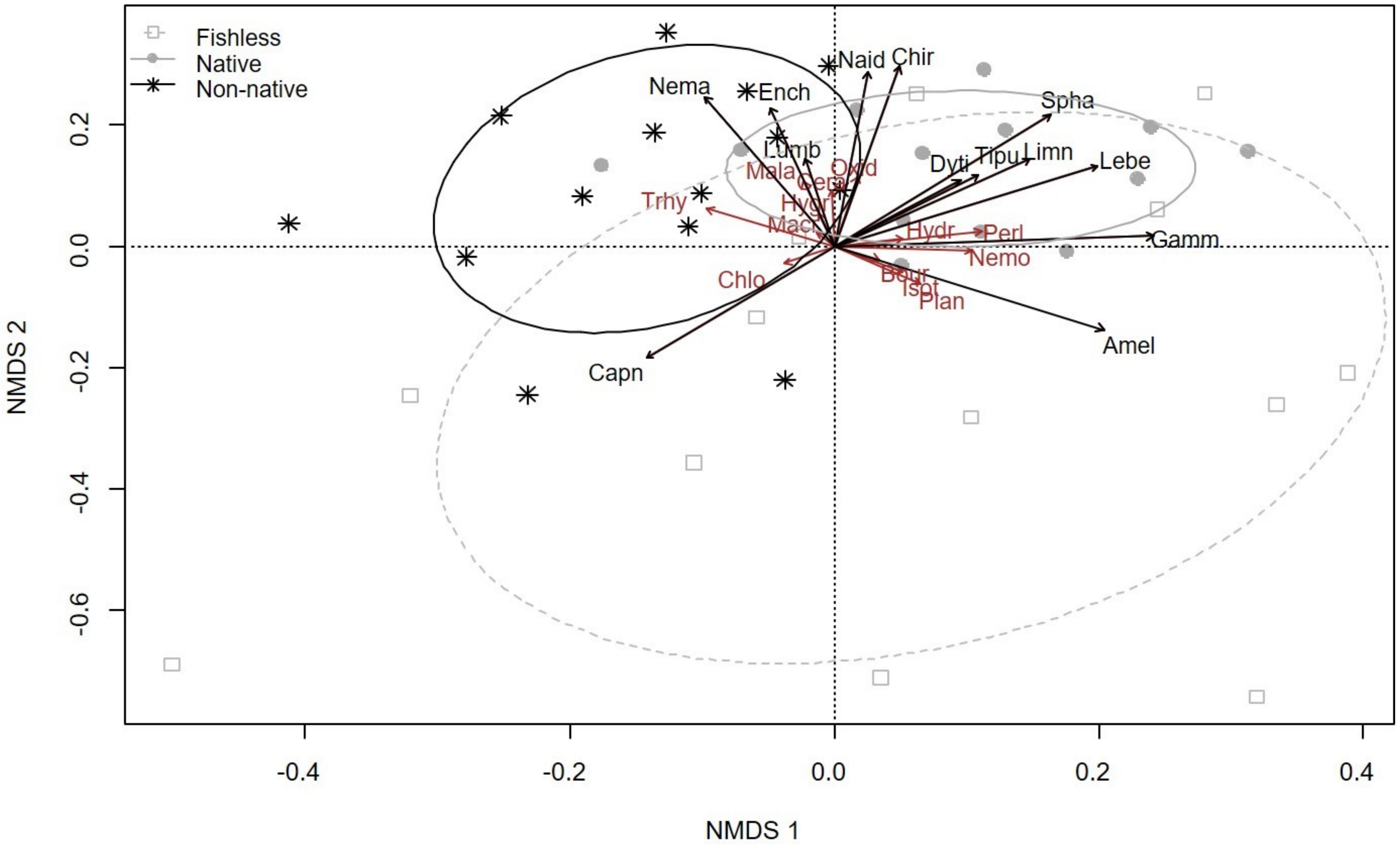

Figure 4. Non-metric multidimensional scaling (NMDS) ordination of Bray-Curtis dissimilarity among density vectors (26 common littoral invertebrate taxa) (stress = 0.17; density values were $\log_{10}$ (x+1) transformed prior to analysis). Bolded taxa (vectors) represent significant taxa after correlation analysis with a cut off *p*-value of 0.05. Taxa showing significant associations with NMDS axes are given in table 4. Confidence ellipses enclose the majority of lakes representing each lake type. Refer to table 2 for family codes.

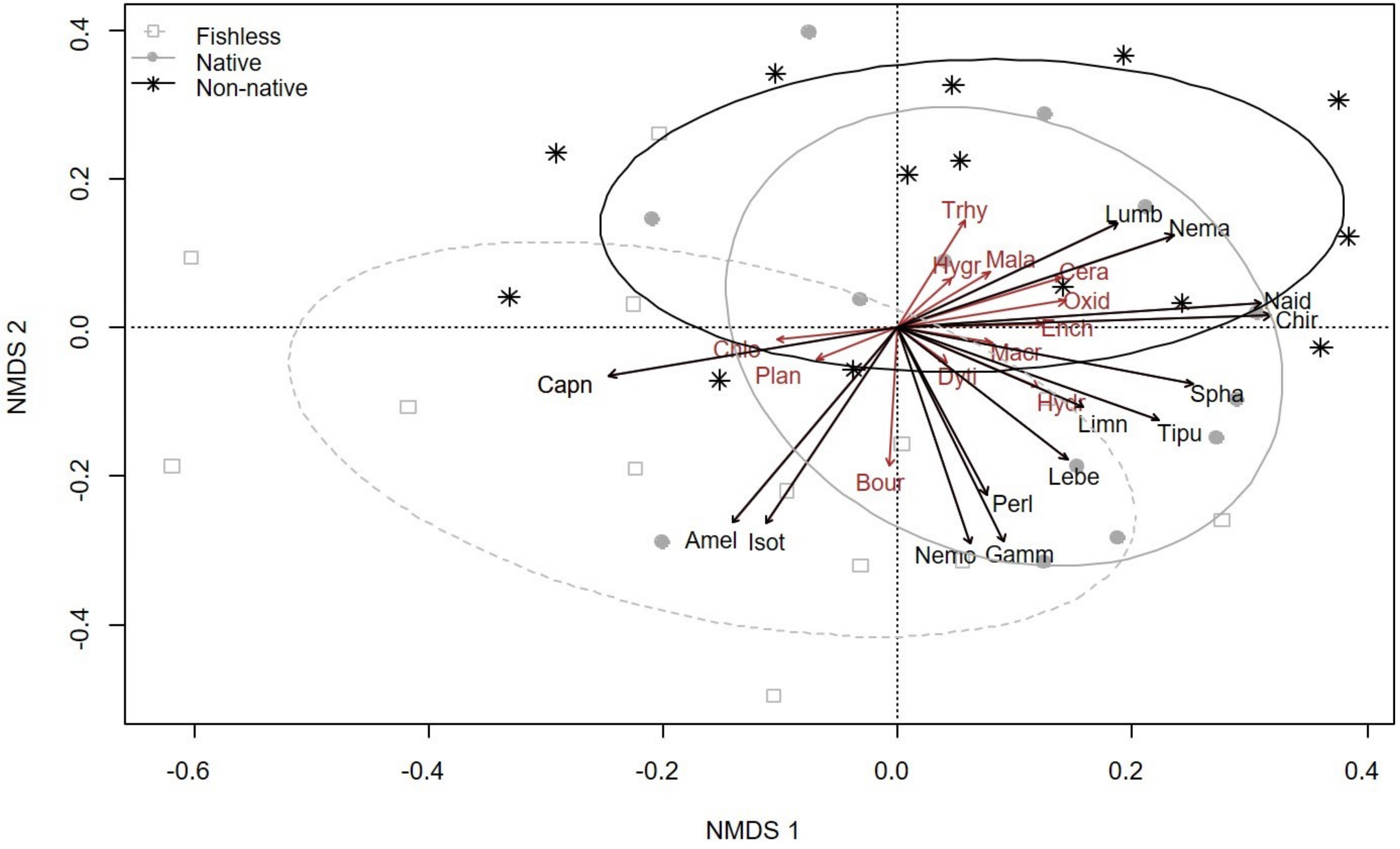

Figure 5. Non-metric multidimensional scaling (NMDS) ordination of Jaccard similarity among composition (0,1) vectors (26 common littoral invertebrate taxa) (stress = 0.27). Bolded taxa (vectors) represent significant taxa after correlation analysis with a cut off *p*-value of 0.05. Taxa showing significant associations with NMDS axes are given in table 4. Confidence ellipses enclose the majority of lakes representing each lake type. Refer to table 2 for family codes.

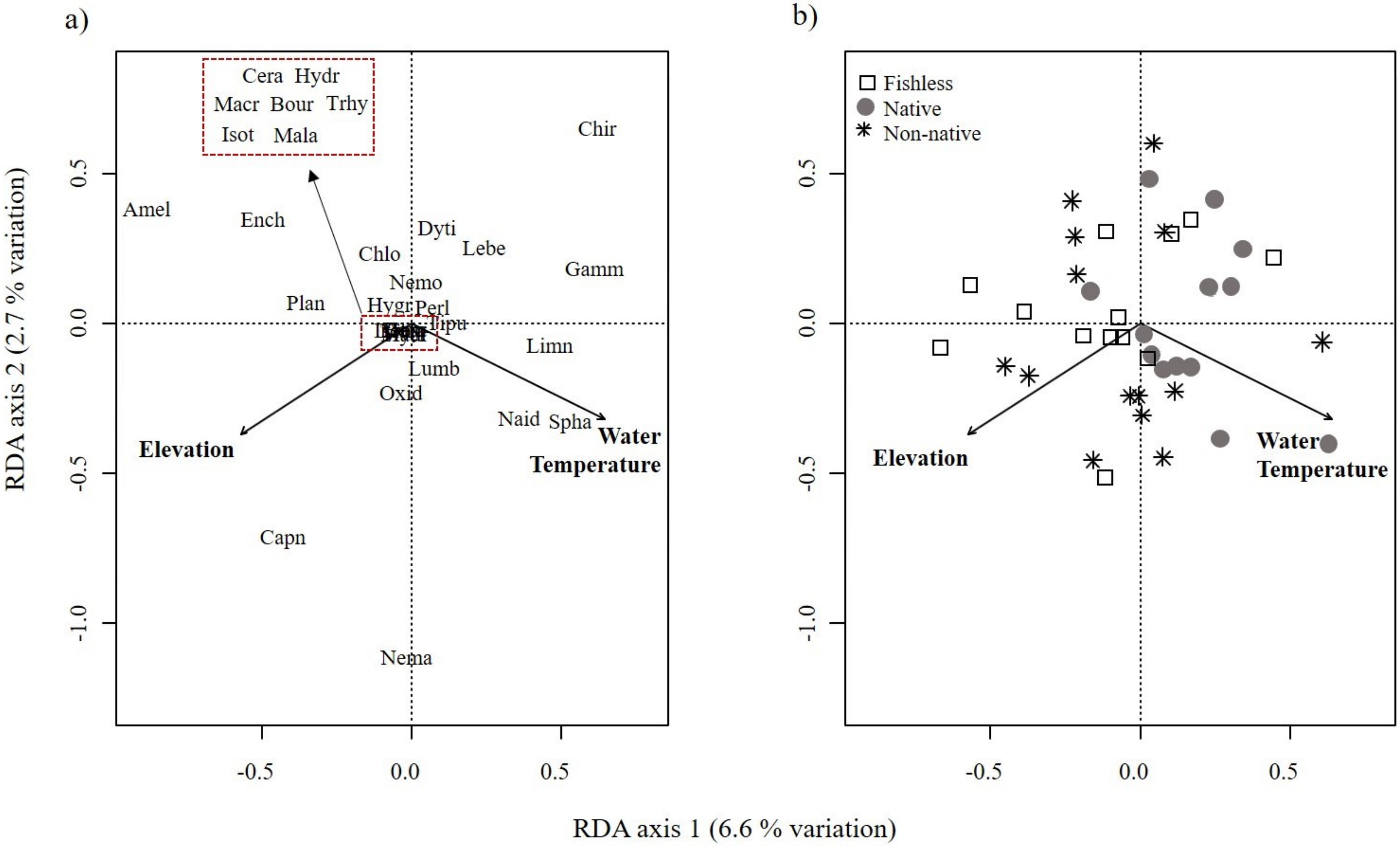

Figure 6. Transformation-based Redundancy Analysis (tb-RDA) with forward selection revealed 9.3 % of total variance explained by two significant ($p < 0.05$) environmental variables in a) 26 common littoral invertebrate taxa (present in $\geq$ 10% of lakes) and b) lakes symbolized by lake type. The first two canonical axes explain together 9.3% of the total variance of the data (RDA 1= 6.6 %, p = 0.004); RDA 2= 2.7 %, p = 0.12). Invertebrate density data were Hellinger transformed and environmental variables were scaled and centered for comparison. Refer to table 2 for family codes.

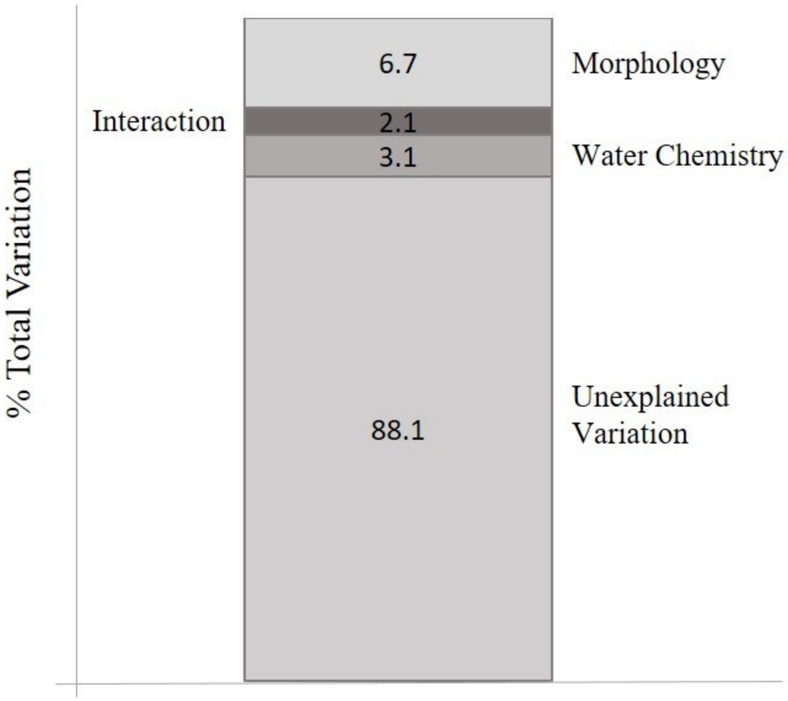

Figure 7. Partition of the variation in the littoral invertebrate community between two parsimonious subsets of explanatory variables (based on forward selection), including water chemistry (water temperature) and lake morphometry (elevation). Littoral substrate and habitat variables were removed from the model by forward selection. The total variation represents 100% of the variation in the community, and the intersection is the joint variation explained by the two explanatory variables.

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APPENDICES

Appendix 1. Stocking history of 40 mountain lakes in Kootenay National Park, B.C. and Banff National Park, Alberta, categorized by lake type.

Lake	Current fish species	Historically	First stocking	Last stocking	Historically stocked in lake	References
Fishless						
259	no fish	fishless				
355	no fish	fishless				
Drummond	no fish	fishless				
Eli (B642)	no fish	fishless				
Goat	no fish	fishless				
Grace	no fish	fishless				
Lower Fatigue	no fish	fishless				4
Lower Martin	no fish	fishless				1
Lower Nasswald	no fish	fishless				10
Upper Devon[1]	no fish	fishless		1964	CTTR	8; 10
Upper Fatigue[1]	no fish	fishless	1961	1972	RBTR	4; 5; 10
Upper Martin	no fish	fishless				1
Upper Nasswald	no fish	fishless				
Native						
Big Fish	CTTR	native				4; 7; 10
Black Rock	CTTR	fishless	1947	1967	CTTR	2; 4; 10
Cutthead	BLTR	native	1963	1972	ATS, CTTR	3; 4; 5
Deer/Pipestone	CTTR	native		1966	RBTR	4; 10
Elk	CTTR	native		1972	CTTR	4; 5; 7; 10
Harrison	BLTR	native		after 1977 if at all	CTTR, BLTR	3; 4; 5; 10
Little fish	CTTR	native				4; 7; 10
Lower Twin	CTTR	fishless		1953	CTTR	11; 10; 4; 5
Luellen	CTTR	fishless	1934	1972	CTTR	4; 5; 9; 10

Moose	CTTR	fishless	Unk.		BKTR	
Mystic	CTTR/BLTR	native				2; 7; 9; 10
Sawback	CTTR	native		Unk.	CTTR	9; 10
Upper Twin	CTTR	fishless		1953	CTTR	4; 7; 8; 10; 11
Non-native						
Badger	BKTR	fishless	1964	1972?	BKTR	4; 5; 10
Baker	BKTR	fishless	1931	1969	CTTR, BKTR	2; 4; 5; 9
Bourgeau	BKTR	fishless	1960		BKTR	2; 4; 10
Citadel	RBTR	fishless		Unk.	RBTR?	
Egypt	BKTR/ CTTR	fishless	1930	1965	CTTR, BKTR	2; 4; 10
Helen	BKTR	fishless	1965		BKTR, RBTR?	2; 4; 10
Hidden	BKTR	fishless	1933	1966	CTTR	2; 4; 6; 9; 10
Howard Douglas	BKTR	fishless	1964	1967	CTTR, BKTR	4; 10
Kaufmann	BKTR	fishless	1960	1967	GLTR, BKTR	10
Ptarmigan	BKTR	fishless	1931	1967	BKTR, LKTR?, CTTR	4; 6; 9; 10
Redoubt	BKTR	fishless	1932	1972	CTTR, BKTR	2; 4; 6; 9; 10
Rockbound	BKTR/ RBTR	fishless	1955	1972?	BKTR, CTTR, RBTR	4; 5; 2; 10
Talc	BKTR	fishless	1957	1967	CTTR, BKTR	10
U. Consolation	BKTR/ CTTR	fishless	1922	1964 or 1981?	BKTR, CTTR (lower lake)	2; 4; 6; 10; 12; 13

Note: BLTR, Bull Trout (*Salvelinus confluentus*); CTTR, Cuttroat Trout (*Oncorhynchus clarki*); BKTR, Brook Trout (*Salvelinus fontinalis*); RBTR, Rainbow Trout (*Oncorhynchus mykiss*); ATS, Atlantic Salmon (*Salmo salar*); GLTR, Golden Trout (*Oncorhynchus mykiss aguabonita*); LKTR, Lake Trout (*Salvelinus namaycush*). The details regarding historically stocked fish species and first/last stocking years should be interpreted with caution due to incomplete stocking records and some discrepancies between records and references. [1]Lake status changed to fishless by Parks Canada. Although Upper Fatigue and Upper Devon have a history of stocking, these populations were not self-sustaining and it is likely that the community has returned to pre-stocking conditions (e.g. Donald et al. 2001).

1 Achuff et al. 1986
2 Anderson 1969a, Anderson 1969b, Anderson 1969c
3 Anderson and Donald 1978
4 Banff National Park Stocking Records
5 Horning 1981
6 Mayhood et al. 1976
7 McAllister et al. 1981
8 Paul and Schindler 1994
9 Rawson 1939
10 Ward 1974
11 Mayhood 1995
12 Vick 1913
13 Paetz and Nelson 1970

Appendix 2. Lake characteristics, including sample year, and lake morphometry of 40 mountain lakes sampled in spring 2015 and 2016 in Kootenay National Park, B.C. and Banff National Park, Alberta, categorized by lake type.

Lake no.	Lake	Sample year	UTM (E)	UTM (N)	Elevation (m)	Max. Depth (m)	Lake Area (ha)	Catchment area (ha)
Fishless (n=13)								
1	259	2016	567361	5719277	2235	17	11	674
2	355	2016	557640	5729475	2340	44	14	308
3	Drummond	2016	570177	5715661	2220	33	14	312
4	Eli (B642)	2015	555477	5736355	2410	22	11	325
5	Goat	2015	579274	5700161	2453	71	29	181
6	Grace	2015	598196	5647600	2211	15	5	435
7	Lower Fatigue	2015	592185	5655511	2063	3	2	407
8	Lower Martin	2015	552766	5739236	1984	14	12	3743
9	Lower Nasswald	2015	596388	5650327	2224	21	6	441
10	Upper Devon	2016	551472	5731173	2310	32	28	874
11	Upper Fatigue	2015	591573	5654984	2131	12	4	249
12	Upper Martin	2015	551499	5738483	2030	39	27	2947
13	Upper Nasswald	2015	596158	5649800	2265	34	15	441
Native (n=13)								
14	Big Fish	2016	555460	5721556	2215	44	16	576
15	Black rock	2016	575923	5663837	2212	23	5	64
16	Cutthead	2015	586700	5700538	2212	4	3	145
17	Deer	2016	557934	5719868	2186	24	9	160
18	Elk	2015	593728	5682739	2123	7	4	119
19	Harrison	2015	582451	5712184	2232	11	5	167
20	Little Fish	2016	556677	5721716	2200	6	3	58
21	Lower Twin	2015	571171	5672759	2029	32	20	256
22	Luellen	2016	575441	5688212	1981	16	32	1312

23	Moose	2016	555264	5723907	2197	10	7	140
24	Mystic	2016	587201	5681511	2004	15	9	246
25	Sawback	2015	585830	5689449	2055	21	19	810
26	Upper Twin	2015	570947	5673949	2080	16	11	159
Non-native (n=14)								
27	Badger	2015	579309	5695322	2394	18	3	39
28	Baker	2016	556551	5704944	2228	12	35	827
29	Bourgeau	2015	584648	5665621	2131	28	5	265
30	Citadel	2015	589528	5652828	2284	13	3	16
31	Egypt	2015	576746	5661573	2020	32	23	517
32	Helen	2016	540554	5726279	2403	12	2	54
33	Hidden	2016	561879	5704121	2292	32	11	251
34	H. Douglas	2015	587872	5654557	2274	8	2	51
35	Kauffman	2016	553088	5679692	2067	10	11	584
36	Ptarmigan	2016	564134	5704093	2317	21	27	195
37	Redoubt	2016	564349	5702851	2378	11	20	73
38	Rockbound	2016	574390	5685298	2206	16	29	510
39	Talc	2016	577324	5659495	2166	27	9	87
40	U. Consolation	2016	559306	5684633	1988	16	10	680

Appendix 3. Littoral invertebrate taxa collected from 40 mountain lakes in Kootenay National Park, B.C. and Banff National Park, Alberta (spring 2015 and 2016).

Higher Taxon	Family	Genus
Hirudinea	**Erpobdellidae**	**Erpobdella**
	Glossiphoniidae	**Abloglossiphonia**
Oligochaeta	Enchytraeidae	Enchytraeus
		Mesenchytraeus
	Lumbriculidae	Eclipidrilus
		Eiseniella
		Kincaidiana
		Limbriculus
		Stylodrilus
		Unknown specimen
	Naididae	Chaetogaster
		Dero
		Ilyodrilus
		Limnodrilus
		Nais
		Pristina
		Rhyacodrilus
		Tubifex
		Tubificinae
		Uncinais
Arachnida	Hydrozetidae	Hydrozetes
	Malaconothridae	Unknown specimen
	Trhypochthoniidae	Unknown specimen
	Aturidae	**Aturus**
	Feltriidae	**Feltria**
	Halacaridae	**Unknown specimen**
	Hygrobatidae	Hygrobates
	Lebertiidae	Lebertia
	Limnesiidae	**Limnesia**
	Oxidae	Oxus
	Pionidae	**Neotiphys**
		Piona
		Unknown specimen
	Sperchontidae	**Sperchonopsis**
Collembola	Bourletiellidae	Bourletiella
	Hypogastruridae	**Unknown specimen**
	Isotomidae	Unknown specimen
Coleoptera	Dytiscidae	Agabus
		Hydroporus
		Ilybius
		Oreodytes
		Sanfilippodytes

		Stictotarsus
		Unknown specimen
	Gyrinidae	**Gyrinus**
	Hydrophilidae	**Helophorus**
	Ptilodactylidae	**Anchytarsus**
Diptera	Ceratopogonidae	**Atrichopogon**
		Bezzia/Palpomyia
		Ceratopogon
		Culicoides
		Palpomyia
		Stilobezzia
		Unknown specimen
	Chironomidae	Ablabesmyia
		Acalcarella
		Arctopelopia
		Brillia
		Chaetocladius
		Chironominae
		Chironomus
		Cladotanytarsus
		Conchapelopia
		Constempellina
		Corynoneura
		Cricotopus
		Cryptochironomus
		Diamesa
		Diamesinae
		Dicrotendipes
		Diplocladius
		Eukiefferiella
		Harnischia
		Heterotrissocladius
		Hudsonimyia
		Hydrobaenus
		Hydrosmittia
		Krenosmittia
		Larsia
		Limnophyes
		Mesocricotopus
		Metriocnemus
		Micropsectra
		Microtendipes
		Monodimesa
		Odontomesa
		Orthocladiinae

	Orthocladius
	Pagastia
	Paracladius
	Paracladopelma
	Parakiefferiella
	Paramerina
	Parametriocnemus
	Paraphaenocladius
	Paratanytarsus
	Paratrichocladius
	Parorthocladius
	Phaenopsectra
	Polypedilum
	Potthastia
	Procladius
	Prodiamesa
	Protanypus
	Psectrocladius
	Pseudodiamesa
	Pseudosmittia
	Radotanypus
	Rheocricotopus
	Rheopelopia
	Rheotanytarsus
	Sergentia
	Stempellina
	Stempellinella
	Stictochironomus
	Stilocladius
	Syndiamesa
	Synorthocladius
	Tanypodinae
	Tanypus
	Tanytarsus
	Telopelopia
	Thienemanniella
	Thienemannimyia
	Tokunagaia
	Tribelos
	Tvetenia
	Unknown specimen
	Zavrelimyia
Culicidae	**Aedes**
Dolichopodidae	**Unknown specimen**
Empididae	**Clinocera**

		Weidemannia
	Psychodidae	**Psychoda**
	Tipulidae	Dicranota
		Erioptera
		Limnophila
		Limonia
		Ormosia
		Tipula
		Unknown pupa
Ephemeroptera	Ameletidae	Ameletus
	Baetidae	**Calibaetis**
		Diphetor
		Unknown specimens
	Siphlonuridae	**Siphlonurus**
Hemiptera	**Corixidae**	**Sigara**
Megaloptera	**Sialidae**	**Sialis**
Plecoptera	Capniidae	**Bolshecapnia**
		Mesocapnia
		Unknown specimen
		Utacapnia
	Chloroperlidae	**Suwallia**
		Sweltsa
		Unknown specimen
	Leuctridae	**Paraleuctra**
	Nemouridae	Zapada
	Perlodidae	Isoperla
		Megarcys
		Unknown specimen
Trichoptera	**Apataniidae**	**Apatania**
	Leptoceridae	**Mystacides**
	Limnephilidae	**Ecclisomyia**
		Hesperophylax
		Hydatophylax
		Lenarchus
		Limnephilus
		Onocosmoecus
		Psychoglypha
		Pycnopsyche
		Unknown specimen
	Rhyacophilidae	**Rhyacophila**
Amphipoda	Gammaridae	Gammarus
Mysida	**Mysidae**	**Neomysis**
Bivalvia	Sphaeriidae	**Musculium**
		Pisidium
		Unknown specimen

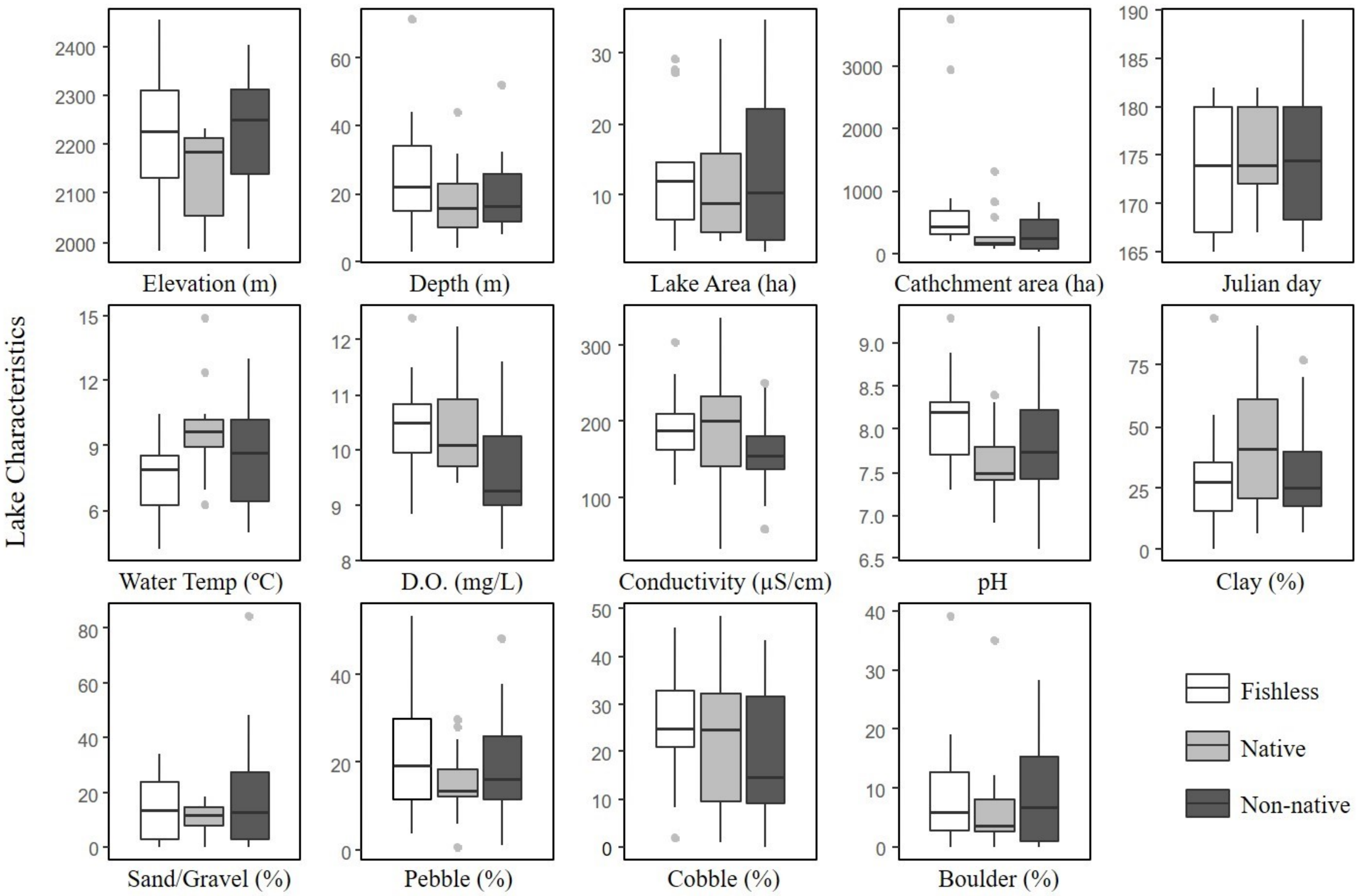
Gastropoda	**Lymnaeidae**	**Galba**
		Lymnaea
		Unknown specimen
Tardigrada	**Hypsibiidae**	**Unknown specimen**
	Macrobiotidae	Unknown specimen
Not considered as part of the macroinvertebrate community		
Platyhelminthes	Planariidae	Polycelis
Nemata	Nemata	Unknown specimen
Cladocera	Daphniidae	Daphnia
		Unknown specimen
Podocopida	Candonidae	Candona
		Unknown specimen
	Cyprididae	Cyclocypris
		Cypria
	Cytherideidae	**Cytherissa**
	Limnocytheridae	Limnocythere
	Llyocyprididae	**Ilyocypris**
Calanoida	Unknown specimen	Unknown specimen
Harpacticoida	Unknown specimen	Unknown specimen
Cyclopoida	Cyclopidae	Unknown specimen

Note: Rare taxa found in fewer than four lakes (<10%) are bolded. Taxa highlighted in grey are significant between lake types, determined by permutational analysis of variance (perANOVA; $p < 0.05$) and evaluated for each taxonomic resolution.

Appendix 4. One-way Analysis of variance (ANOVA) and post-hoc comparison (Tukey's HSD) results for differences ($p < 0.05$; highlighted in grey) in diversity indices among lake types.

Diversity Measures	Fishless mean (SE)	Native mean (SE)	Non-native mean (SE)	*p*-value	Post-hoc comparisons		
					Native vs. Fishless	Non-native vs. Fishless	Native vs. Non-native
Richness	12.85 (0.92)	14 (0.98)	14 (0.79)	0.58			
Shannon Diversity	7.63 (0.70)	9.22 (0.51)	7.65 (0.45)	0.09			
Simpson diversity	6.02 (0.59)	7.65 (0.39)	5.98 (0.32)	0.02	0.037	0.99	0.029
Pielou evenness	0.58 (0.03)	0.67 (0.02)	0.56 (0.03)	0.01	0.077	0.74	0.012

Note: Rare taxa were included in the analysis.



Appendix 5. Box plots showing environmental variables (prior to transformation) collected for each lake and categorized by lake type. The line within each box marks the median, the bottom and top of each box indicate the 25th and 75th percentiles, the whiskers below and above each box represent the error, and the points above the whiskers indicate any outliers. The variables listed do not differ significantly among lake types. Differences were compared by permutational analysis of variance (perANOVA; $p < 0.05$).