

Resilience of Mountain Pond Communities to Extreme Thermal Regime Shifts

by

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Abstract

Elevational gradients are ideal ecological venues for testing how communities respond to environmental changes associated with global warming. Recent warming rates have been shown to increase with elevation, thereby potentially having adverse effects on cold-adapted alpine communities. Additionally, as selective pressures vary along elevational gradients, alpine and montane communities may differ in their adaptive potential to novel thermal regimes. I tested this hypothesis by conducting a replicated two-factor (source × elevation) experiment involving a reciprocal transplant of alpine and montane pond communities across two elevational sites (1390 m versus 2345 m asl). At each elevation, half of the mesocosms were inoculated with zooplankton and sedimentary egg-banks collected from alpine ponds while the other mesocosms were similarly seeded with zooplankton and sedimentary egg-banks collected from montane ponds in 2016. After overwintering, the mesocosms were sampled for temperature and plankton during the ice-free periods of 2017 and 2018. The mesocosms at the low elevation were 8.0 ± 1.2 °C warmer than those at the high elevation. Elevation significantly affected total zooplankton biomass, whereas source effects did not. Elevation effects revealed that the temperature difference between sites affected the phenology of species within the assembled communities, but not their total biomass, and neither assemblage displayed local adaptation to a particular elevation. Functional trait analysis revealed that the warmer environment selected for smaller body size and asexual reproduction as a warmer thermal regime stimulated several small parthenogenetic herbivores while suppressing larger, obligate sexual omnivores.

Nevertheless, thermal regime shifts did not substantially affect the abundance-weighted mean functional identities of either transferred pond community, highlighting ponds as potential sources of functional insurance against expected increasingly extreme climate events.

Preface

The thesis reflects a submitted manuscript prepared in collaboration with fellow researchers. The citation for the study and author contributions are as follows:

A version of Chapter 2 has been submitted for publication in the journal *Aquatic Sciences* as: Johnsen MA, Stuparyk BR, Cook J, Vinebrooke RD (2019) Resilience of pond communities to extreme thermal regime shifts: An alpine-montane reciprocal transplant experiment. I designed the study, conducted the experiment, enumerated zooplankton samples, analyzed the data, and composed the manuscript. Rolf Vinebrooke conceived of the idea, facilitated the study, and assisted with revisions of the manuscript. Blake Stuparyk and Jenna Cook helped conduct the experiment, provided feedback on study design and data analysis, and contributed to manuscript revisions.

Dedication

Nanos gigantum humeris insidentes

Standing on the shoulders of giants

- Bernard of Chartres

I dedicate my pursuit of knowledge to the many restless minds that came before me; the scholars, the naturalists, the intellects, and the merely curious who implored to make sense of the chaos that surrounded them in this vast and mysterious universe.

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Table of contents

List of tables	xi
List of figures	xii
Chapter 1: Introduction	1
Research background and rationale.....	1
<i>Global change in mountain ecosystems</i>	1
<i>Mechanisms of elevation-dependent warming</i>	3
<i>Hydrological implications</i>	3
<i>Ice cover phenology</i>	4
<i>Alpine lake and pond communities</i>	6
<i>Spatial insurance</i>	8
<i>Local adaptation</i>	9
Conclusion	10
Research objectives	11
Literature cited	12
Chapter 2: Resilience of pond communities to extreme thermal regime shifts: An alpine-montane reciprocal transplant experiment	21
Introduction	21

Methods	26
<i>Study area</i>	26
<i>Experimental design and set-up</i>	28
<i>Sampling</i>	29
<i>Analyses</i>	31
Results	36
<i>Temperature</i>	36
<i>Community biomass</i>	41
<i>Species exchange and rank clocks</i>	43
<i>Functional identity and stepwise regression</i>	46
Discussion	50
Conclusions.....	58
Literature Cited.....	59
Chapter 3: Conclusions	72
Synthesis.....	72
Shortcomings	74
Future Research.....	75
Literature cited	79
Complete list of literature cited.....	83
Appendix A: Supplemental information for chapter 2	100

Appendix A-1: Experimental design, species pools, and source water chemistry	100
Appendix A-2: Mesocosm lux	105
Appendix A-3: Pelagic food web structure.....	108
Appendix A-4: Periphyton community assessment	112
Appendix A-5: Species traits and functional analysis	116

List of tables

Table 1 Linear mixed-effects model on total zooplankton biomass.....	41
Table 2 Richness (SER_r) and biomass-based (SER_b) species exchange ratios.	44
Table A-1.1 Ponds sampled to construct the regional species pools.....	102
Table A-1.2 Zooplankton regional species pools.	103
Table A-1.3 Mean concentrations of chemical variables of the source water	104
Table A-3.1 Linear mixed-effects model on the pelagic consumer : producer biomass ratio	109
Table A-4.1 Linear models on periphyton chlorophyll a.....	113
Table A-5.1 Species traits included in the functional analysis.	116
Table A-5.2 Stepwise regression on species scores along each axis of the principal coordinate analysis.....	117

List of figures

Fig 1 Map of the study area.	27
Fig 2 Ice-cover in the mesocosms.	38
Fig 3 Mean water temperature in the mesocosms during each sampling event	39
Fig 4 Mean (0.5-m depth) water temperature in the mesocosms.....	40
Fig 5 Mean zooplankton biomass ($\mu\text{g/L}$).	42
Fig 6 Rank clock plots for zooplankton communities	45
Fig 7 Functional identity structure of alpine pond zooplankton communities.	47
Fig 8 Functional identity structure of montane pond zooplankton communities.	49
Fig A-1.1 Schematic of the two-factor crossed experimental design	100
Fig A-1.2 Images of the experimental mesocosms	101
Fig A-2.1 Mean maximum daytime lux at 0.5 m depth in the mesocosms.	106
Fig A-3.1 Pelagic food web structure.	110
Fig A-4.1 Mean periphyton chlorophyll a	114

Chapter 1: Introduction

Research background and rationale

Global change in mountain ecosystems

Mountain ecosystems are experiencing disproportionately faster rates of climatic warming, particularly at higher elevations (Pepin et al. 2015). Consequently, these relatively small ecosystems are currently showing declines in winter snowpack formation (Mote et al. 2005), likely resulting in a complete loss of glacial ice cover within a few centuries if air temperatures continue to rise at current rates (Huss et al. 2017). Water releases from the alpine cryosphere are essential for maintaining baseflow, sediment and nutrient transport, and ecosystem structure and function in mountain waterbodies (Klein et al. 2019; Huss et al. 2017). However, some mountain ecosystems are buffered against environmental drivers of change by the complex topography that can create microclimate refugia, thereby decoupling alpine organisms from atmospheric conditions and resulting in a mosaic of thermal microhabitats at a given elevation (Scherrer and Körner 2010). Regardless, the future reduction and loss of meltwater flow is predicted to diminish landscape-scale environmental heterogeneity and species turnover (Jacobsen et al. 2012; Cauvy-Fraunié et al. 2015), and cause the loss of cold-adapted aquatic species from regional species pools (Jacobsen et al. 2012; Redmond et al. 2018). These potentially cascading effects highlight the need to understand how these interconnected systems will respond to climate warming and the functional consequences of species loss (e.g., impact on ecosystem functions).

Alpine lakes and ponds have been identified as 'sentinels of change' as they integrate climatic effects across their entire catchments, are not confounded by local anthropogenic disturbance (e.g., land-use change), and are especially sensitive to projected environmental change due to several characteristics (Hauer et al. 1997; Williamson et al. 2009). Processes in the catchment (e.g., dissolved organic carbon input) and within the waterbody itself (e.g., plankton composition) affect water transparency, which alters the light and heat environment (Adrian et al. 2009; Wetzel and Likens 2013). Water levels reflect the balance of water input (e.g., precipitation, runoff) and water loss (e.g., evaporation). The temperature regime of a lake or pond is highly correlated with regional-scale air temperatures and responds directly and rapidly to changing air temperatures (Adrian et al. 2009). Air temperature is also the dominant driving factor affecting ice phenology (Williams and Stefan 2006), such as the duration of winter ice-cover and the date of ice-off in the spring (Adrian et al. 2009). Physical changes in ice-cover and water temperature have consequences for nutrient and oxygen concentrations and can affect the distribution of biota in the habitat. The community structure (including composition changes), the frequency/duration of algal blooms, and secondary productivity are affected by environmental conditions, and planktonic organisms respond rapidly to subtle thermal changes due to short generation times (Adrian et al. 2009). These measurable metrics reflect direct influence of climate on the waterbody and indirect effects of climate on the catchment (Adrian et al. 2009) making alpine lakes and ponds particularly useful for studying the effects of climate warming on aquatic ecosystems.

Mechanisms of elevation-dependent warming

Increased warming at higher elevations is driven primarily by an increase in ambient air temperature due to increased trapping of solar radiation within the atmosphere.

Enhanced warming occurs in minimum temperatures at higher altitudes, at night, and in the winter due to near-surface water-vapour radiative feedbacks (Pepin et al. 2015).

Downward longwave radiation interacts with increased near-surface water vapour, and the cooler the land surface is, the less outward radiation is shed. Cooler alpine surfaces retain more of the radiative heat they have gained in the form of outward longwave radiation resulting in enhanced warming with elevation (Pepin et al. 2015).

Hydrological implications

Although mountain temperature measurements are complicated by extreme local variability due to the high degree of heterogeneity in topography, slope, aspect and exposure, general warming trends can still be detected (Pepin et al. 2015). Minimum temperatures show a strong degree of warming compared to maximum temperatures causing distinct effects, particularly in the winter and spring months (Pepin et al. 2015; Rood et al. 2016). Winter warming is leading to an increased proportion of winter rain relative to snowfall, which is contributing to the decline of snowpacks (Mote et al. 2005). As minimum temperature warming continues into the spring, particularly at night, the freeze-thaw dynamics of spring snowpacks are being dominated by thawing, which is

increasing the spring snowmelt to a greater extent at an earlier date (Rood et al. 2016). Consequently, there is a shift in the flow seasonality peaking at an earlier date and a pronounced longer duration of low summer baseflow (Rood et al. 2016). Reduced summer baseflow and future predictions of an increased frequency and intensity of drought (Rood et al. 2016) will both contribute to a reduction in water input to lakes and ponds. With a decreased input of water, there is an increase in the residence time of water within a lake, increasing the importance of within-lake processes (Preston et al. 2016). Additionally, smaller lakes are predicted to become more 'pond-like' (Parker et al. 2008; Bradley et al. 2004), and there is an increased potential for ponds to dry completely.

Ice cover phenology

Warming has direct effects on the duration of ice-cover and the date at which lakes and ponds become ice-free. The ice-off date is controlled primarily by snowfall, rainfall, and air temperature (Preston et al. 2016). The extent of the winter snow accumulation influences the onset of ice-off with dry years experiencing advanced snowmelt and ice-off in comparison to years with greater snowpack (Sadro et al. 2018). However, the advancing date of ice-off is most strongly influenced by the increased proportion of winter rain relative to snowfall (Sadro et al. 2018; Mote et al. 2005). Both of these effects are expected to increase in a warmer, drier future climate (IPCC 2014; Rood et al. 2016).

The date of lake ice-off has already advanced in high elevation lakes in the Rocky Mountains of the United States (Preston et al. 2016; Sadro et al. 2018), and is predicted to continue increasing into the future (Roberts et al. 2017). An earlier ice-off date results in elevated surface water temperatures and an increase of 4 °C has been recorded in high elevation lakes of Colorado, USA when compared to late ice-off years (Preston et al. 2016). Additionally, dry years with earlier ice-off reduce the flushing of lake water, resulting in increases in particulate carbon and nitrogen concentrations (Sadro et al. 2018). Increased particulate concentrations may reduce water clarity and release phytoplankton from UV-B induced photoinhibition further stimulating primary productivity (Williamson et al. 2010). The interactions of a longer ice-free season, higher surface water temperatures, and increased nutrient availability may synergistically affect phytoplankton phenology and support greater primary production (Sadro et al. 2018). Consequently, the bottom-up effects of climate change have the potential cascade to higher trophic levels (e.g., benthic and pelagic invertebrates), the implications of which are not fully understood (Parker et al. 2008; Roberts et al. 2017).

Alpine lake and pond communities

Alpine communities are often considered to be at greater risk than lower montane communities under a rapidly changing climate because the former is relatively species-poor (Lyons and Vinebrooke 2016) with a lower probability of containing species that are tolerant of higher temperatures (Strecker et al. 2004; Hozapfel and Vinebrooke 2005; Williamson et al. 2009). Alpine lake communities are characterized by only a few coldwater stenothermic zooplankton species, especially sensitive to warming (Vinebrooke and Leavitt 2005). Due to the low alpha diversity, alpine communities hypothetically contain low functional insurance according to the insurance hypothesis (Yachi and Loreau 1999). Previous studies have identified that moderate warming can stimulate large-bodied cladocerans (i.e., *Daphnia* spp.; Weidman et al. 2014) while suppressing large-bodied copepods (i.e., *Hesperodiaptomus* spp.; Fischer et al. 2011; Thompson et al. 2008). However, more substantial warming has negative impacts on both large grazers (Strecker et al. 2004; Thompson and Shurin 2012; Loewen and Vinebrooke 2016), reducing grazing pressure and resulting in an increase in algal biomass that cannot be compensated for by the smaller species that are stimulated with warming (Holzapfel and Vinebrooke 2005). Besides higher temperatures, greater thermal variability and increased frequency of extreme climatic events (e.g., heat waves) are also consequences of global warming (Diffenbaugh et al. 2017). However, large knowledge gaps remain in terms of the long-term consequences of thermal regime shifts for aquatic communities (e.g., Graham and Vinebrooke 2009, Thompson and Shurin 2012).

Relatively small and shallow (<5 m maximum depth) waterbodies (hereafter referred to as 'ponds') experience ecological phenomena that are considerably different from that experienced by larger lake communities. The shallow bathymetry of ponds predisposes them to frequent temperature-density or mechanical (e.g., wind) induced mixing events (Padisák and Reynolds 2003), whereas larger lakes can remain stratified for the duration of the ice-free season (Wetzel and Likens 2013) buffering them against rapid changes in temperature (Lewis 1983). Stratification creates refugia for cold-adapted species, as cold water remains at depth while the majority of solar irradiance and warming is absorbed in the surface waters of the epilimnion (Wetzel and Likens 2013). In contrast, ponds tend to warm throughout, experiencing daily temperature fluctuations greater than 20 °C (McMaster 2003). Ponds also experience more frequent partial or complete drying and freezing (Vinebrooke et al. 2014). These environmental factors act as strong selective forces for dormancy and the production of resting stages or structures (Gyllström and Hansson 2004) and may contribute to a higher genetic diversity of individuals within a species (i.e., metapopulation diversity; Altermatt and Ebert 2008) resulting in populations with differential tolerances to stressors. Species dispersal from ponds is also amplified with increased drying as more propagules are wind-dispersed from exposed sediments (Vanschoenwinkel et al. 2008), highlighting the potential for ponds to act as sources of tolerant taxa to migrate to impoverished sites.

At larger spatial scales ($\geq 60 \text{ km}^2$), ponds typically contain high gamma diversity (Williams et al. 2004; Clarke et al. 2008). Ponds are also more abundant than large

lakes (Downing et al. 2006), and cover as much or more area as large lakes (Downing 2010) but most of our current understanding of the effects of climate warming on alpine aquatic ecosystems comes from the study of lakes (but see Strecker et al. 2004). However, alpine ponds may be at greater risk than larger lakes due to their small surface area, shallow depth, and relatively low quantity of hydrologic input making them particularly susceptible to future warming and drying (Kratz et al. 1997; Langston et al. 2011).

Spatial insurance

The insurance hypothesis can be considered spatially to include multiple communities linked by species dispersal to highlight the possibility for tolerant species to migrate and rescue local communities from the effects of environmental perturbations (Loreau et al. 2003; Shanafelt et al. 2015; Thompson et al. 2015). Ecological factors that might hypothetically exclude montane plankton species from alpine communities include dispersal limitation, intolerance of current environmental conditions, and biotic interactions (e.g., predation, competition; Holzapfel and Vinebrooke 2005). However, changing environmental conditions may reduce some of these limitations (i.e. warming environmental conditions; suppression of resident alpine species), highlighting the potential for upwards shifts of montane species into alpine communities. Importation of a diverse montane regional species pool has been shown to reverse the adverse effects of an alien predator on species-poor alpine communities (Loewen and Vinebrooke 2016), and their dispersal could act as a rescue effect for lost ecosystem functions (e.g.

secondary production and grazing). Topographic barriers have been considered to limit dispersal and reduce the supply of viable propagules to high elevation sites (Donald et al. 2001). However, the recovery, albeit slow, of historically impacted mountain lakes (e.g., Donald et al. 2011) and a recent macroecological study by Lowen et al. (2018) suggests that local environmental conditions are the primary driver of zooplankton community composition and that dispersal limitation is not expected to significantly constrain many species' responses to future climate warming.

Local adaptation

Characterizing the adaptive potential of mountain zooplankton communities is critical to understand potential impacts of climate change on local assemblages. Local adaptation depends on both the differentiation of species assemblages along elevational gradients and the flow of genes that underlie these differentiations (Kawecki and Ebert 2004). Mountain ecosystems are ideal for exploring local adaptation as selective pressures are likely to vary along elevational gradients (Gonzalo-Turpin and Hazard 2009). Previous local adaptation studies have primarily focused on the adaptive potential of one or a few species (Cavlieri et al. 2018; Leimu and Fischer 2008). However, biotic interactions and the potential for species dispersal can also be considered by investigating local adaptation for entire communities assembled from regional species pools (Urban et al. 2012).

Conclusion

Elevation-dependent warming is causing marked effects to the hydrologic regime, phenology, and temperature of alpine aquatic ecosystems. Previous studies from alpine lakes have identified that endemic cold-water adapted species may be at risk of future climate warming. However, we do not currently understand how a warmer and drier climate will affect alpine pond ecosystems that are abundant in the landscape. Alpine pond ecosystems may be particularly at risk of future warming due to their shallow nature and low thermal buffering capacity. Alternatively, alpine ponds may be pre-adapted to warming due to these strong selective forces, and instead, act as a source of thermally tolerant populations that could disperse and provide spatial insurance in heterogeneous mountain landscapes. Additionally, climate warming may alleviate some of the barriers currently excluding montane species from alpine ecosystems and facilitate the upwards migration of diverse montane species that could potentially provide rescue effects to negatively impacted sites, restoring suppressed or lost ecosystem function. Therefore, we need to investigate whether alpine and montane zooplankton species assemblages show adaptive potential to novel thermal regimes, or if these communities are instead adapted to their local environmental conditions.

Research objectives

My thesis research addressed three main objectives:

- 1) To test for the effects of a warmer thermal regime on a regionally assembled alpine pond community,
- 2) To test for the effects of a colder thermal regime on a regionally assembled low elevation montane pond community, and
- 3) To test if either community is constrained by local adaptation or instead show adaptive potential in a novel thermal environment.

To achieve these objectives, I conducted a replicated two-factor (source × elevation) experiment consisting of a reciprocal transplant of pond communities placed in mesocosms across sites at two different elevations. Each mesocosm was seeded with plankton and their sedimentary resting stages collected from either a set of alpine or montane ponds. To test for local assemblage adaptation and assess the effects of an altered thermal regime on pond communities, I analyzed total production during the ice-free seasons of 2017 and 2018. I also assessed species phenology and temporal turnover using rank clocks, a species richness-based species exchange ratio, and a biomass-weighted species exchange ratio. Lastly, I assessed the effects of thermal regime shifts on the functional structure of the communities using a species trait-based approach.

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Chapter 2: Resilience of pond communities to extreme thermal regime shifts: An alpine-montane reciprocal transplant experiment

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Introduction

Under a rapidly changing global climate (IPCC 2014), there is increasing concern over the loss of biodiversity that otherwise helps ensure the reliability of ecosystem functioning (e.g., production of biomass; Hooper et al. 2005, Cardinale et al. 2012). The insurance hypothesis posits that species diversity increases the probability of there being tolerant species that can compensate functionally for more environmentally sensitive species (Yachi and Loreau 1999). Thus, species-rich communities may show greater ecological resilience against environmental changes and extreme climatic events (Loreau and de Mazancourt 2013; Thompson et al. 2015).

Elevational gradients are recognized as ecological venues for experimental testing of community responses to environmental changes related to climate (McGill et al. 2006). For example, recent warming rates are positively correlated with elevation (Pepin et al. 2015), thereby potentially having adverse effects on cold-adapted, species-poor alpine communities (e.g., Loewen and Vinebrooke 2016). Thus, alpine communities are

often considered to be at greater risk than lower montane communities under a rapidly warming climate because the former is relatively species-poor (Lyons and Vinebrooke 2016) with a lower probability of containing species that are tolerant of higher temperatures (Strecker et al. 2004; Holzapfel and Vinebrooke 2005; Williamson et al. 2009). However, the long-term impact of thermal regime shifts on aquatic communities remains a knowledge gap because of the short duration of most experiments (e.g., one season; Thompson and Shurin 2012).

Additionally, characterizing the adaptive potential of mountain zooplankton communities along elevational gradients is critical to understand their vulnerability to climate change. Local adaptation depends on both the adaptive differentiation of species assemblages along elevational gradients and the flow of genes that underlie these differentiations (Kawecki and Ebert 2004). Mountain aquatic ecosystems are ideal for exploring local adaptation as substantial changes in selective pressures are likely to occur along elevational gradients (Gonzalo-Turpin and Hazard 2009). As alpine environments present strong selective forces (i.e., low temperatures, short growth season; McMaster 2003; Gyllström and Hansson 2004) for species-poor communities inhabiting high elevation areas, these factors may promote local adaptation in alpine communities. In contrast, species-rich montane zooplankton communities may show a higher degree of adaptive potential due to low elevation environments exhibiting more moderate selective forces.

Empirical evidence of the effects of climatic factors on freshwater communities has typically been derived from experiments on lake communities over the course of a single season (e.g., Graham and Vinebrooke 2009; Nicolle et al. 2012; Hansson et al. 2013). Although mesocosm-based experiments allow for ease of replication and reliable controls, their temporal and spatial scales often lack the ecological realism needed to capture the larger impacts of climate change (e.g., phenology) on whole-lake communities (Schindler 1998; Carpenter 2001). Alternatively, whole-ecosystem studies are plagued by the lack of true controls and statistical power because of the inherently high variability among naturally occurring waterbodies. Therefore, a hybrid experimental design is needed that more closely captures the spatial and temporal scales of the ecological phenomenon being investigated while also enabling replication of treatments and controls (e.g., replicated experimental whole-pond mesocosms).

Most of our understanding of the impacts of climate change comes from the study of lakes, rather than the most abundant type of freshwater ecosystem across the world, namely ponds (Downing 2010). However, small (mean = 3.29 hectare; Appendix A-1 Table A-1.1) and shallow (<5 m mean depth) waterbodies (hereafter referred to as 'ponds') often experience ecological phenomena that are markedly different from that experienced by larger lake communities (Padisák and Reynolds 2003). The shallow bathymetry of ponds subjects them to frequent mixing events (Padisák and Reynolds 2003), warming through the water column to the sediment surface, and daily temperature fluctuations that can be greater than 20 °C (McMaster 2003). In

comparison, larger lakes can remain stratified for the duration of the ice-free period (Wetzel and Likens 2013), which creates a refugia of cold-water habitat at depth in the hypolimnion. Ponds can also be subjected to periods of partial or complete drying or freezing (Vinebrooke et al. 2014) in the summer and winter respectively, which act as strong selective forces for dormancy and the production of resting stages or structures (Gyllström and Hansson 2004). As pond communities are subjected to temporal variation in selective forces, this may disrupt local adaptation and increase the adaptive potential of pond zooplankton communities to novel environmental conditions (Kawecki and Ebert 2004). As such, there is a need to understand the effects of altered thermal regimes on pond communities, and if those effects differ for alpine versus montane pond zooplankton communities.

The majority of previous local adaptation studies have focused on the adaptive potential of one or a few species in a local and foreign environment (Cavalliheri et al. 2018; Leimu and Fischer 2008). However, investigation of local adaptation can include entire species assemblages that occupy a particular habitat. As such, the adaptive response of the community to a foreign environment can be due to adaptation of individual species (e.g., phenotypic plasticity) or the community assemblage (e.g., functional compensation). Additionally, immigration of species from the regional species pool can supply additional genetic variation to local populations or species that are pre-adapted to the environmental conditions (i.e., species sorting; Urban et al. 2012). This highlights the need to incorporate species interactions in the investigation of local adaptation for entire species assemblages using a metacommunity approach where

species could potentially disperse between local habitats (Urban et al. 2012).

I compared the resilience and adaptive potential of alpine versus lower montane pond communities to altered thermal regimes by conducting a replicated two-factor (source × elevation) experiment consisting of a reciprocal transplant of pond communities placed in mesocosms across sites at two different elevations. Each mesocosm was seeded with zooplankton and their sedimentary resting stages collected from either a set of alpine or lower montane ponds. Our main objectives were to test for the effects of 1) a warmer thermal regime on the assembled alpine community, 2) a colder thermal regime on the lower montane community, and 3) if either community is constrained by local adaptation or instead shows adaptive potential in a novel thermal environment. I hypothesized that the less species-rich alpine community would be adversely affected by a warmer thermal regime due to a relative lack of functional redundancy and species being locally adapted to alpine environmental conditions. Specifically, I predicted that the alpine community would have lower total biomass in the foreign low elevation environment in comparison to the local high elevation environment. Additionally, transplantation of the alpine zooplankton community to a warmer low elevation site would stimulate species turnover by increased extirpations, significantly altering the structure of species traits within the community. I also hypothesized the more species-rich montane community would not be adversely affected by a colder thermal regime due to species diversity conveying functional redundancy and adaptive potential in novel environmental conditions. Specifically, I predicted that the total biomass of the montane community would not be significantly

different in the local low elevation environment compared to the foreign high elevation environment. Additionally, transplantation of the montane zooplankton community to a colder high elevation site would only suppress certain species abundances without significantly affecting the structure of species traits within the community.

Methods

Study area

Our study was performed across two locations that together extended across an elevational gradient of 955 m asl and a geographic range spanning the eastern Front ranges of the Canadian Rocky Mountains from Kananaskis provincial park to Yoho national park (Fig 1; Appendix A-1 Fig A-1.1). The high elevation site (2345 m asl) is located on the continental divide of the Canadian Rocky Mountains within Banff National Park, Alberta, Canada (51°01'40.3" N, 115°42'50.2" W). The low elevation site (1390 m asl) is at the Barrier Lake Field Station, which is located at the eastern edge of the Canadian Rocky Mountains, Alberta, Canada (51°01'43" N, 115°02'00.9" W). The low elevation site is approximately 48 km directly east of the high elevation site, and similar regional weather patterns are experienced at both sites.

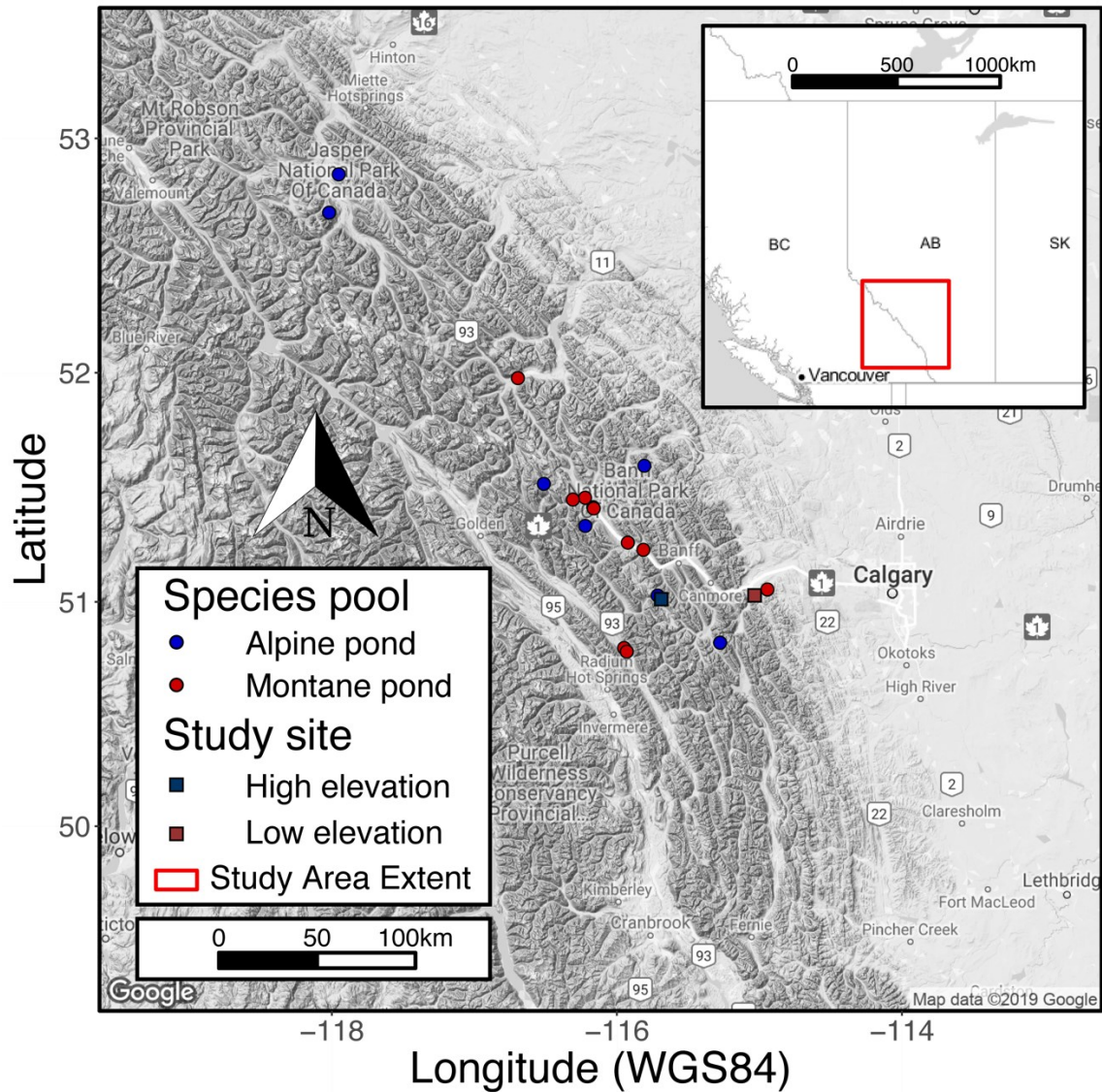


Fig 1 Map of the study area along the Alberta/British Columbia border in Western Canada indicating the regional ponds sampled to construct the zooplankton species pools and the location of the mesocosms at either elevation.

Experimental design and set-up

I replicated a 2 × 2 reciprocal transplant experimental design six times for a total of twenty-four 1000 L capacity mesocosms (Appendix A-1 Fig A-1.1; dimensions: 1 m³). The source treatment consisted of biological inocula collected from either high elevation, alpine ponds or low elevation, montane ponds. The elevation treatment involved the communities being grown at both a high elevation and a low elevation site. Twelve semi-translucent high-density polyethylene mesocosms were transported via helicopter to the high elevation site and I established twelve others at the low elevation site in August 2016 (Fig 1; Appendix A-1 Fig A-1.2). All mesocosms at the high elevation site were filled with 700 L of filtered (63-µm mesh size) water from the nearby Citadel Pond. The 12 mesocosms at the low elevation site were filled with 700 L of filtered (63-µm mesh size) snowmelt water from the nearby Mount Lorette Ponds. Source water chemistry was analyzed to confirm that the water sources at each elevation were both oligotrophic (total phosphorus ≤ 3 µg/L) and did not significantly differ in their nitrogen to phosphorus ratios ($P > 0.05$; Appendix A-1 Table A-1.3).

Regional alpine and montane species pools of zooplankton were assembled in early August 2016 from collections obtained from seven alpine and 10 lower montane ponds (Fig 1; Appendix A-1 Table A-1.1), respectively. Repeated horizontal or vertical tows (depending on bathymetry) of each pond were performed using a 63 µm-mesh conical net to capture a representative sample of the zooplankton community present. The alpine and montane zooplankton were transported live and stored at 6 °C and 20 °C,

respectively prior to the start of the experiment. Also, pond sediments were collected from all alpine and montane sites using an Ekman Grab (15.2 cm³). Sampling was performed midway between the shoreline and deepest point. The thickness of sediment collected per sample varied depending on the composition of the sediment, but samples were repeated until at least 1.5 L of sediment were captured from each pond (approximately 35 replicates). The alpine and montane sediments were mixed separately and then each added in 10 L aliquots to six mesocosms at each elevation. I used sediment to capture the potential for emergence of species from deposited sedimentary resting structures (i.e., planktonic seed banks). Following the addition of sediment, equal aliquots of the assembled alpine species pool and montane species pool were transferred to the appropriate mesocosms at each elevation. The communities were left to condition to the environment for the remainder of the 2016 ice-free season and left to overwinter until they thawed in 2017. Additionally, the mesocosms are a closed-top container, which does not allow for passive dispersal from the surrounding environment, resulting in communities comprised entirely from the initial inoculation of sediment and live plankton, and later emergence of species from sedimentary resting structures.

Sampling

HOBO pendant temperature/light data loggers were deployed in each mesocosm at 0.5 m depth to record water temperature and lux at two-hour intervals at each elevation (n=2). The loggers captured data during the first overwinter from August 2016 through

July 2017, and for the 2018 ice-free season from July through August 2018.

Abiotic and biotic sampling of each mesocosm was performed monthly during the ice-free periods of 2017 (June-August) and 2018 (July-August). Before sampling, I stirred each mesocosm enough to mix the water column, but gently enough to keep the sediment undisturbed. Abiotic variables were measured using a YSI multimeter probe at mid-water depth, and included temperature, dissolved oxygen, conductivity, pH, and turbidity. Integrated plankton samples of the whole water column were taken using a clear polyvinyl chloride tube (2 cm diameter, 1 L volume). Then, 500 mL of water was filtered using Whatman GF/F filter papers and stored on ice for later chlorophyll analysis (Appendix A-3). Lastly, I pooled 20 L of water and concentrated its contents for zooplankton using a 63 μm mesh-size sieve. Zooplankton were then immediately preserved in 250 mL Nalgene containers using 70% ethanol.

Zooplankton were counted at 16 and 32-times magnification using a Leica MZ6 dissecting stereoscope. Samples were counted in their entirety and all zooplankton individuals were identified to species using the taxonomic reference of Edmondson (1959), except for juvenile and resting stages (e.g., copepod nauplii). For each sampling date, the lengths of the first 30 individuals of each taxon were also measured to obtain biomass estimates using standard length-weight regression (Watkins et al. 2011).

Analyses

To test for time-dependent differences in 0.5 m depth water temperatures of the high elevation and low elevation mesocosms, a general linear model was fitted for the 2018 sampling year, for which data were available, using the `lme` function from the `nlme` R package v3.1-137 (Pinheiro et al. 2017). Elevation and date/time were included as fixed factors, and maximum likelihood was used to estimate the model. Mesocosm replicate was also treated as a repeated measure for each sample date, and orthogonal contrasts were used for interpretation of any interaction effects.

To test for local assemblage adaptation and differential biomass responses of alpine and lower montane zooplankton communities (i.e., source effects) to the simulated thermal regime shifts (i.e., elevation effects), a linear mixed-effects model was fitted using the `lme` function from the `nlme` R package v3.1-137 (Pinheiro et al. 2017). Source, elevation, and sample year were included as fixed factors, and maximum likelihood was used to estimate the model. Each mesocosm replicate was treated as a repeated measure for each sample year.

To visualize the effects of simulated thermal regime shifts on species phenology and species-specific contributions to total biomass within both the alpine and montane communities, I used rank clocks (Batty 2006; Collins et al. 2008; Hallett et al. 2016). Rank clocks are a graphical representation that simultaneously displays changes in rank-biomass and species richness in a time series. Rank-order biomass of each

species at the first sample date is plotted at the 1 o'clock position. The species that contributes the greatest proportion of biomass to the total community biomass is plotted closest to the center of the clock face, with decreasing rank moving progressively outwards on the clock face. Sample date two rank data are then plotted in the same manner along a second axis that would represent 3 o'clock, continuing until all sample dates are plotted on the clock face. Species rank changes follow a temporal clockwise direction from one date to the next to display changes in species biomass contribution and richness (i.e., quantity of lines) over time. The composition and biomass of species change in response to seasonal environmental dynamics and experimental treatments, which creates complex patterns in time. In addition, indices of compositional change (i.e., temporal turnover) can be used to quantify these internal dynamics in the time series.

To assess the temporal turnover of the communities at different elevations, two species exchange ratios (SER) were used, which integrate many of the existing metrics of composition change (Hillebrand et al. 2018). The first is an adaptation of the Jaccard similarity index (Jaccard 1912) and measures the gross change in composition based on species richness

$$SER_r = \frac{S_{imm} + S_{ext}}{S_{tot}} \quad (1)$$

where S_{imm} is the number of species immigrating or being detected in the community for the first time, S_{ext} is the number of species extinct or no longer detected, and S_{tot} is

the total number of species across both sample dates. The second metric is a more robust index that captures relative changes in species biomass over time

$$SER_b = \frac{\sum_i (p_i - p'_i)^2}{\sum p_i^2 + \sum p'^2_i - \sum p_i p'_i} \quad (2)$$

where p_i is the species proportional biomass at time 1, and p'_i at time 2. Both indices range from 0 to 1, with 0 representing no change and 1 representing complete species replacement. SER indices were calculated for each community for each subsequent sample date pair within the sampling year using the community composition and species biomass data. The two SER indices complement one another as changes in species richness does not necessitate changes in the dominance structure of the community (e.g., extirpation of rare species; high SER_r , low SER_b). Alternatively, the structure of the community may change drastically without a loss or gain of species (e.g., shift in the rank of dominant species; low SER_r , high SER_b). How drastically a specific community composition is changing over time can be quantified by comparing subsequent samples to prior sample dates. Additionally, transplanted communities can be compared to their counterpart that remained in the original elevation to assess how the thermal regime shift is affecting species turnover and relative changes in species biomass (e.g., alpine x high elevation compared to alpine x low elevation).

To test for the effects of thermal regime shifts on the functional structure of the alpine and lower montane zooplankton communities, I used a species trait-based approach (Mouillot et al. 2013). Here, the structure of species traits in each community

can be compared at each elevation in ordination space to illustrate and quantify changes in structure due to transplantation. Species were assigned a set of seven traits (Appendix A-5 Table A-5.1) that best characterized zooplankton along other elevational gradients (Loewen and Vinebrooke 2016; Hébert et al. 2017; Redmond et al. 2018). Traits included feeding behaviour (herbivore, carnivore, omnivore), feeding method (filtration, raptorial), body size (mm), sex mode (obligate asexual, obligate sexual, facultative asexual), pigmentation (yes, no), motility (slow, rapid), and habitat (pelagic, littoral). Gower distance of each trait matrix was computed using the `gowdis` function from the `FD` R package v1.0-12 (Laliberté et al. 2015). Gower distance was used to compute the functional distance between species based on the mix of categorical and continuous variables (Villéger et al. 2008). Principal coordinate analysis (PCoA) of the distance matrix was then performed to build a multidimensional functional space for each source community (montane and alpine). The PCoA axes were then combined with the species abundances at each elevation (i.e., low and high) using the `FSECchange` function in R (Mouillot et al. 2013; R Core Team 2017), which calculates indices including functional identity, and functional originality of species communities. Functional identity is an abundance-weighted mean value of functional traits for all species in a given community at a given time (Mouillot et al. 2013). Functional originality is a measure of the uniqueness of species in the functional space occupied by the community (Mouillot et al. 2013), and is the inverse of functional redundancy or the degree of overlap of species functional traits. Functional originality is calculated from the minimal functional distances among species pairs in the community. As such, changes in the relative abundance or extirpation of individual species at low and high elevation

modify the functional identity and originality indices of the given community. A shift in the functional identity of a community after transplantation would result from shifts in the relative abundance or extirpation of species within the functional space occupied by the community. A decrease in functional originality after transplantation would indicate that species in the community share their traits more closely with other species, which could occur from a decrease in the abundance or extirpation of species that contribute unique functional traits (i.e., species overlap to a greater extent in ordination space). Species were then plotted in two-dimensional functional space along synthetic trait axes extracted from the PCoA.

Although original trait values cannot be recovered from the Gower distances, I regressed species scores along each axis with original trait values using stepwise regression to assess the contribution of each variable to the synthetic axes (Legendre and Legendre 1998). The stepAIC function from the MASS R package v7.3-51.1 (Ripley et al. 2013) was used to perform stepwise multiple regression with 1000 iterations on x-axis values and y-axis values separately.

All statistical analyses were conducted using R (R Core Team 2017). Zooplankton biomass data were $\log_{10}(x + 1)$ transformed before linear mixed-effects modelling to improve normality and reduce heteroscedasticity. The three *Alona* species (*Alona affinis*, *Alona guttata*, and *Alona quadrangularis*) in the montane community were pooled before functional identity analysis because they had identical trait values. Gower's distances were square root-transformed before PCoA to control for non-metric

variables and improve the relative impact of small and large dissimilarities (Legendre and Legendre 1998). All figures were made using the ggplot2 R package v3.1.0 (Wickham et al. 2018) and modified in Adobe Illustrator CC (Adobe Systems Incorporated 2015).

Results

Temperature

Mesocosms became ice-free approximately 40 days earlier (Fig 2) at the low elevation site (May 18) compared to the high elevation site (June 27) in 2017, and approximately 28 days earlier in 2018. The mesocosms froze substantially but there remained approximately 100 L of liquid water at the sediment interface during the ice-on period (*personal obs*). Across all six sampling dates, the average water temperature in the mesocosms (Fig 3) was 8.0 ± 1.2 °C warmer and less temporally variable at the low elevation site (mean = 19.7 ± 1.7 °C) compared to the high elevation site (mean = 11.7 ± 2.1 °C). Similarly, the average surface water temperature of the ponds used to construct the species pools was 6.7 ± 0.3 °C warmer in the montane ponds (mean = 18.8 ± 0.6 °C) compared to the alpine ponds (mean = 12.1 ± 0.9 °C; Appendix A-1 Table A-1.1). The greatest temperature disparity of the mesocosms (12.7 °C) between location averages occurred on the final sampling week of 2017, where low elevation mesocosms averaged 22.7 ± 0.2 °C, while high elevation mesocosms averaged temperatures of 10.0 ± 0.1 °C. The final sample point of 2018 had the lowest recorded average temperatures for both low elevation (mean = 13.4 ± 0.1 °C) and high elevation (mean =

5.0±0.1 °C) mesocosms. In 2018, the average core temperature at a depth of 0.5 m was 2.8±0.04 °C warmer at the lower elevation montane site (Fig 4; mean = 16.7±0.13 °C) compared to the high elevation site (mean = 13.9±0.15 °C). Three recorded heat waves in 2018 (Fig 4; vertical red lines) elevated the 0.5 m depth water temperature of low and high elevation mesocosms considerably above the season averages. The first heat wave occurred on July 17th, resulting in maximum temperatures of 25.4 °C and 23.6 °C in the low and high elevation mesocosms, respectively. The second heat wave on July 30th, had maximum temperatures to 23.4 °C and 22.8°C in the low and high elevation mesocosms, respectively. The final heat wave on August 10th, resulted in core water temperatures reaching a maximum of 24.8 °C and 23.3° C in the low and high elevation mesocosms, respectively.

General linear models for the 2018 HOBO pendant temperature data revealed that date/time ($P < .0001$) had a significant effect on core water temperature, whereas the location of the mesocosms did not ($P = 0.1514$). A significant interaction between elevation and date/time occurred ($P < .0001$), such that the low elevation mesocosms had a higher daily temperature maximum than the high elevation mesocosms in 2018 (Fig 4).

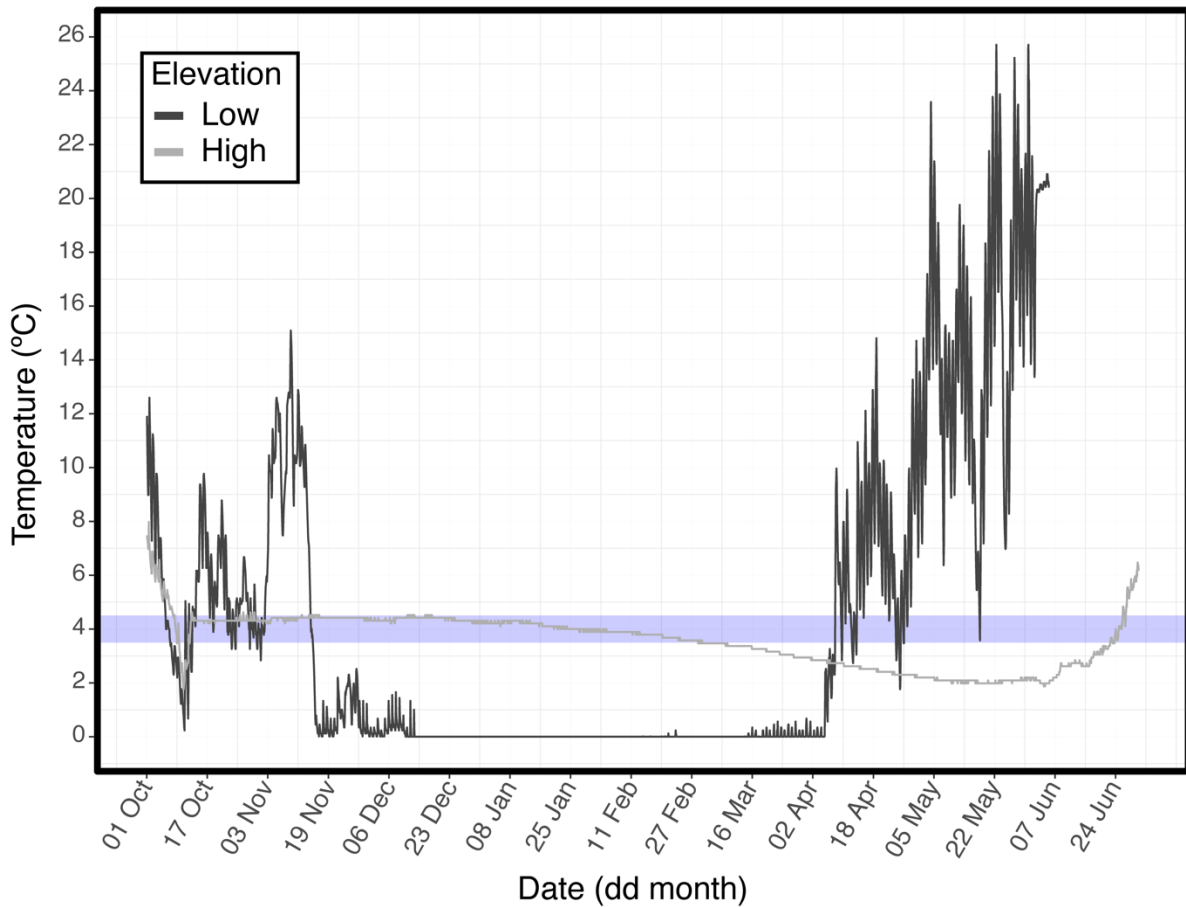


Fig 2 Ice-cover in the mesocosms. Data was collected using HOBO pendant dataloggers ($n = 2$) at two-hour intervals during the first overwinter from October 2016 through July 2017. The horizontal blue line at 4 °C represents the temperature transition of ice to liquid water. Ice-off was considered as the date at which the temperature in the mesocosms remained above the 4 °C threshold.

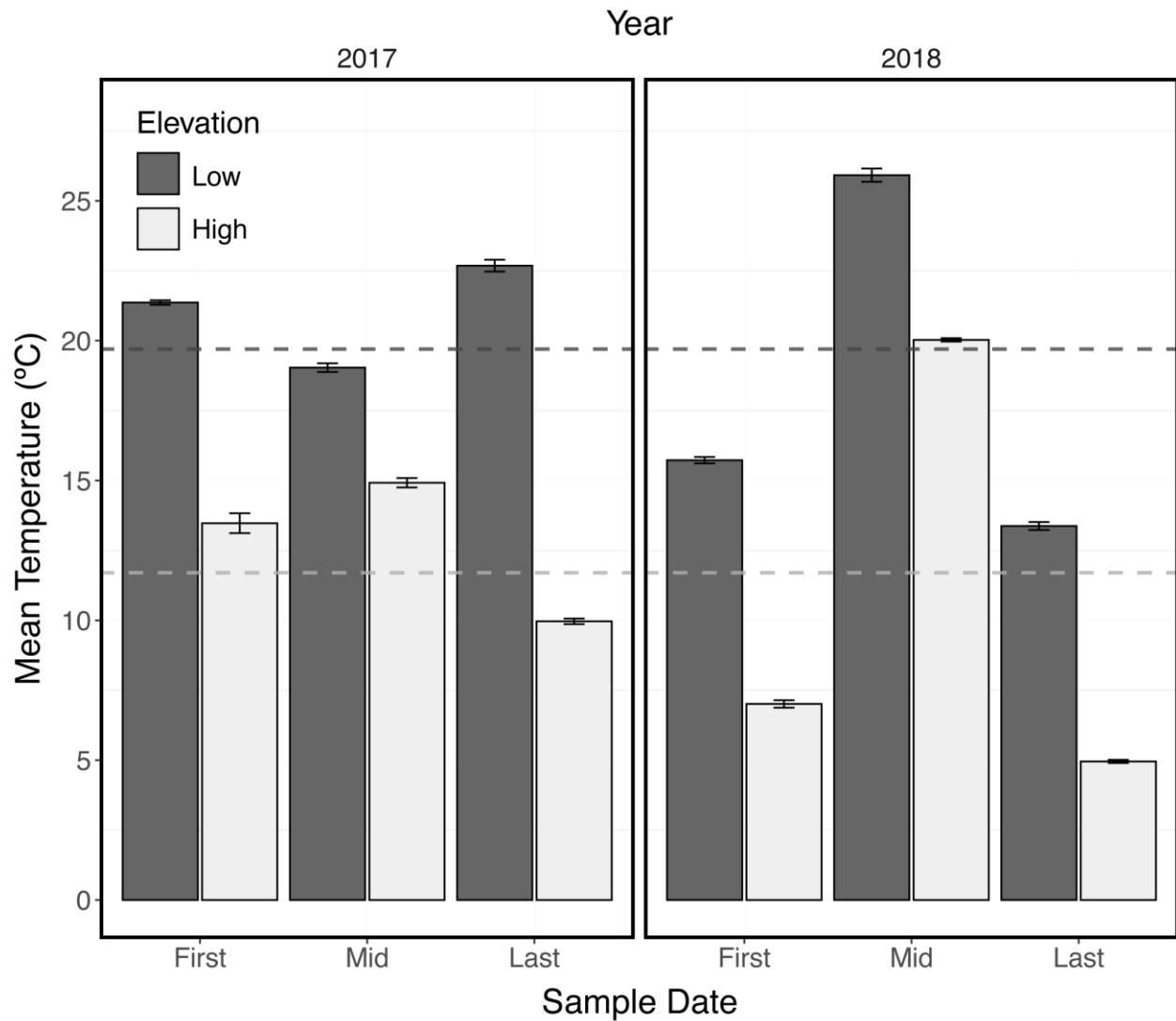


Fig 3 Mean water temperature in the mesocosms during each sampling event (n = 11). Data was collected monthly during the ice-free periods of 2017 (June-August) and 2018 (July-August) using a YSI multimeter probe at mid-water depth. The dashed horizontal lines represent the average temperature of the mesocosms at each elevation across all six sampling dates (color indicated in the legend). Error bars represent standard error of the mean.

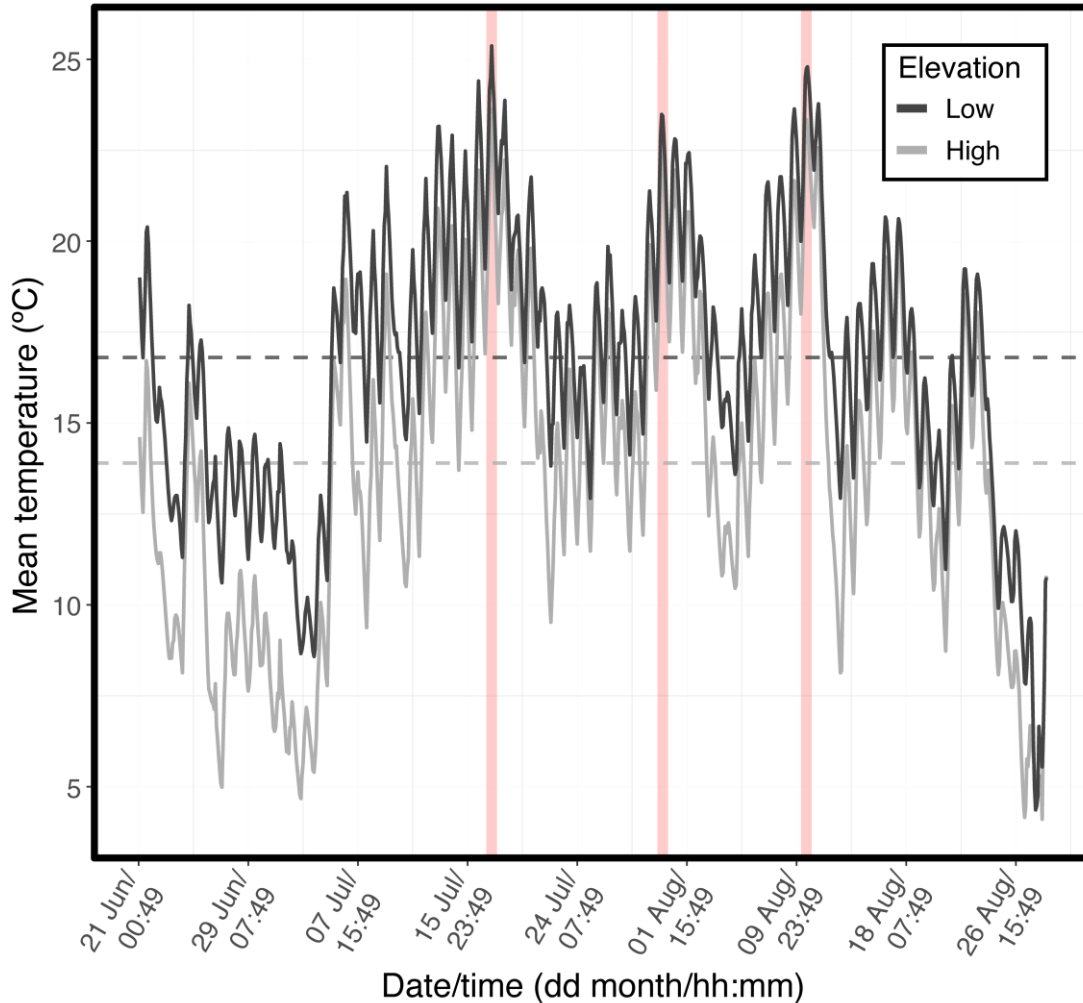


Fig 4 Mean (0.5-m depth) water temperature in the mesocosms. Data was collected using HOBO pendant dataloggers ($n = 2$) at two-hour intervals during the 2018 ice-free season from July through August 2018. The vertical red lines represent heat waves on July 17th, July 30th, and August 10th when the water temperature in the mesocosms rose considerably above the season averages. The dashed horizontal lines represent the season average 0.5 m depth water temperature for low (mean = 16.7 ± 0.13 °C) and high elevation mesocosms (mean = 13.9 ± 0.15 °C), respectively.

Community biomass

The linear mixed-effects model revealed a significant interaction between source, elevation, and sample year (Table 1; Fig 5). In 2017, the alpine zooplankton community transplanted to the foreign low elevation environment had a significantly greater total biomass than the other communities. Whereas, the alpine community retained in its local high elevation environment had significantly lower total biomass than the other communities. The total biomass of the montane communities did not significantly differ between elevations in 2017. This relationship changed in 2018, as the total biomass of the alpine communities did not significantly differ between elevations. Whereas, the montane community transplanted to the foreign high elevation environment had a significantly greater total biomass than the other communities.

Table 1 Linear mixed-effects model on total zooplankton biomass. Direct and interactive effects of the origin of the zooplankton community (i.e., source effect), transplantation, (i.e., elevation effect), and year of sampling on total biomass over two years in experimental mesocosms.

Explanatory variable(s)	AIC	χ^2	df	p-value
Source	65.70	0.6097	1	0.4349
Elevation	65.17	2.5292	1	0.1118
Year	66.96	0.2103	1	0.6465
Source x elevation	64.14	4.8252	1	0.0280*
Source x year	66.03	0.1048	1	0.7461
Elevation x year	50.90	17.1314	1	<.0001****
Source x elevation x year	44.59	8.3070	1	0.0039**

Significance codes ($\alpha = 0.05$): <0.001 '****', 0.001 '***', 0.01 '**', 0.05*

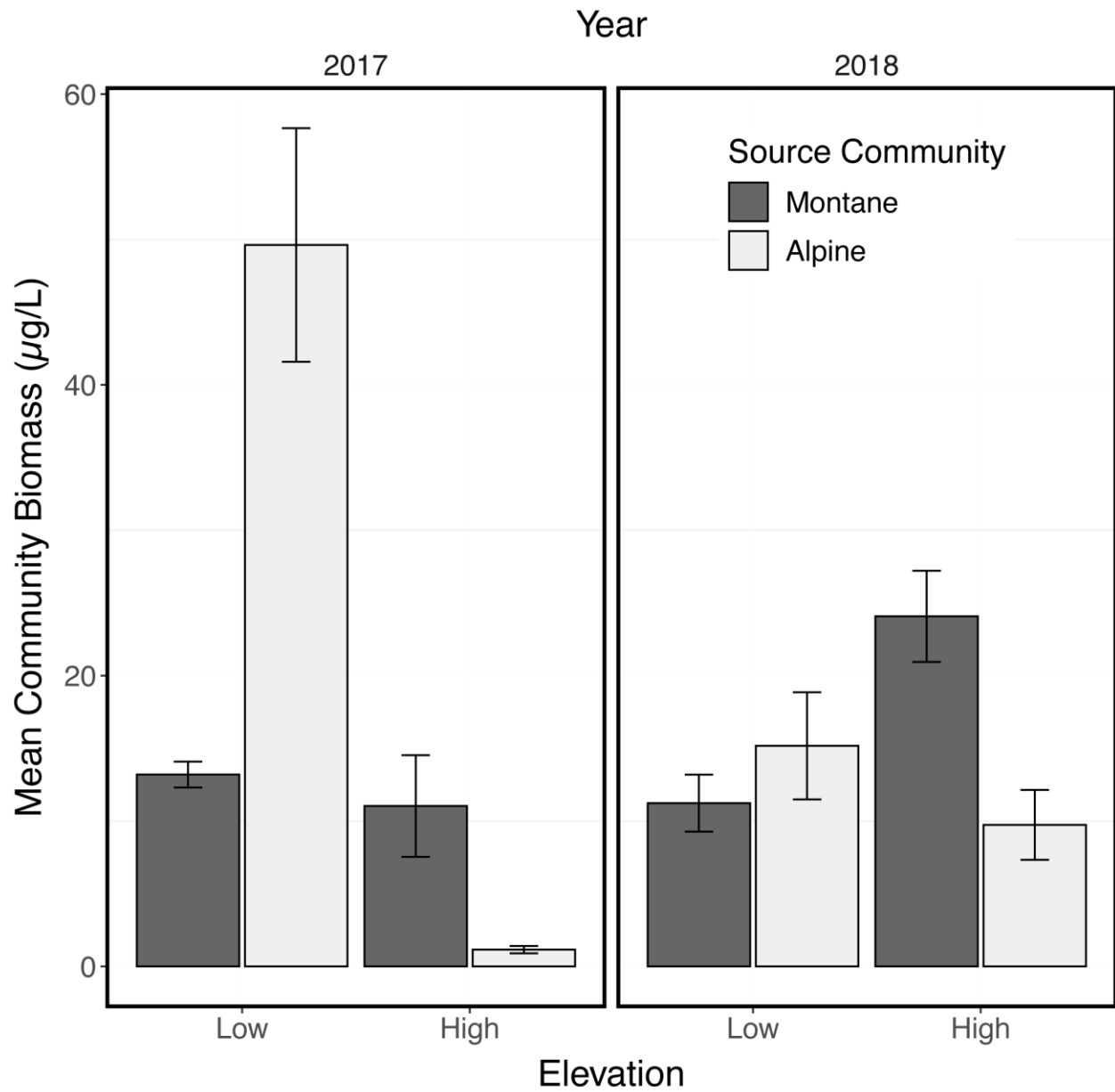


Fig 5 Mean zooplankton biomass ($\mu\text{g/L}$) for each sample year during the two-year reciprocal transplant experiment. Montane and alpine sourced communities were grown at either low or high elevation sites ($n = 5$ for montane \times low and alpine \times high; $n = 6$ for montane \times high and alpine \times low). Error bars represent standard error of the mean.

Species exchange and rank clocks

Species exchange ratios together with rank clocks showed how transplantation and local conditions affected temporal species dynamics in the alpine and montane communities (Table 2; Fig 6). The total biomass of the transplanted alpine and montane communities were dominated by the single species *Daphnia middendorffiana*. In contrast, the communities that were maintained near their origin had significant biomass contributions from at least one other species. Specifically, the biomass of the alpine community at high elevation was dominated by *D. middendorffiana* in 2017 and either ephippia (*D. middendorffiana* resting eggs) or *Hesperodiaptomus arcticus* in 2018. Whereas, the biomass of the montane community at low elevation was dominated by either *D. middendorffiana* or *Ceriodaphnia reticulata* throughout both years. Species exchange became more pronounced at the low elevation site than at the high elevation site during 2018. Although species ranks and richness remained relatively stable over time in both transplanted communities, they did not resemble the non-transplanted communities at each site after two years (Fig 6).

Table 2 Richness (SER_r) and biomass-based (SER_b) species exchange ratios. SERs were calculated for zooplankton communities sourced from either alpine or lower montane regions and then grown at either high or low elevation sites. Each date-pair is a comparison of two sample dates for the given year, and cells are colored with a gradation of light, medium, and dark blue to represent low, moderate, and high values as a visual aid. Transplanted communities can be compared to their counterpart that remained in the original elevation to assess how the thermal regime shift affected species turnover (SER_r) and relative changes in species biomass (SER_b).

	2017		2018	
	First-Mid	Mid-Last	First-Mid	Mid-Last
Richness (SER _r)				
Montane x high	0.800	0.500	0.444	0.222
Alpine x high	0.600	0.333	0.000	0.400
Montane x low	0.143	0.250	0.333	0.375
Alpine x low	0.500	0.333	0.400	0.000
Biomass (SER _b)				
Montane x high	0.466	0.612	0.651	0.083
Alpine x high	0.670	0.275	0.244	0.644
Montane x low	0.188	0.290	0.857	0.886
Alpine x low	0.847	0.217	0.791	0.920

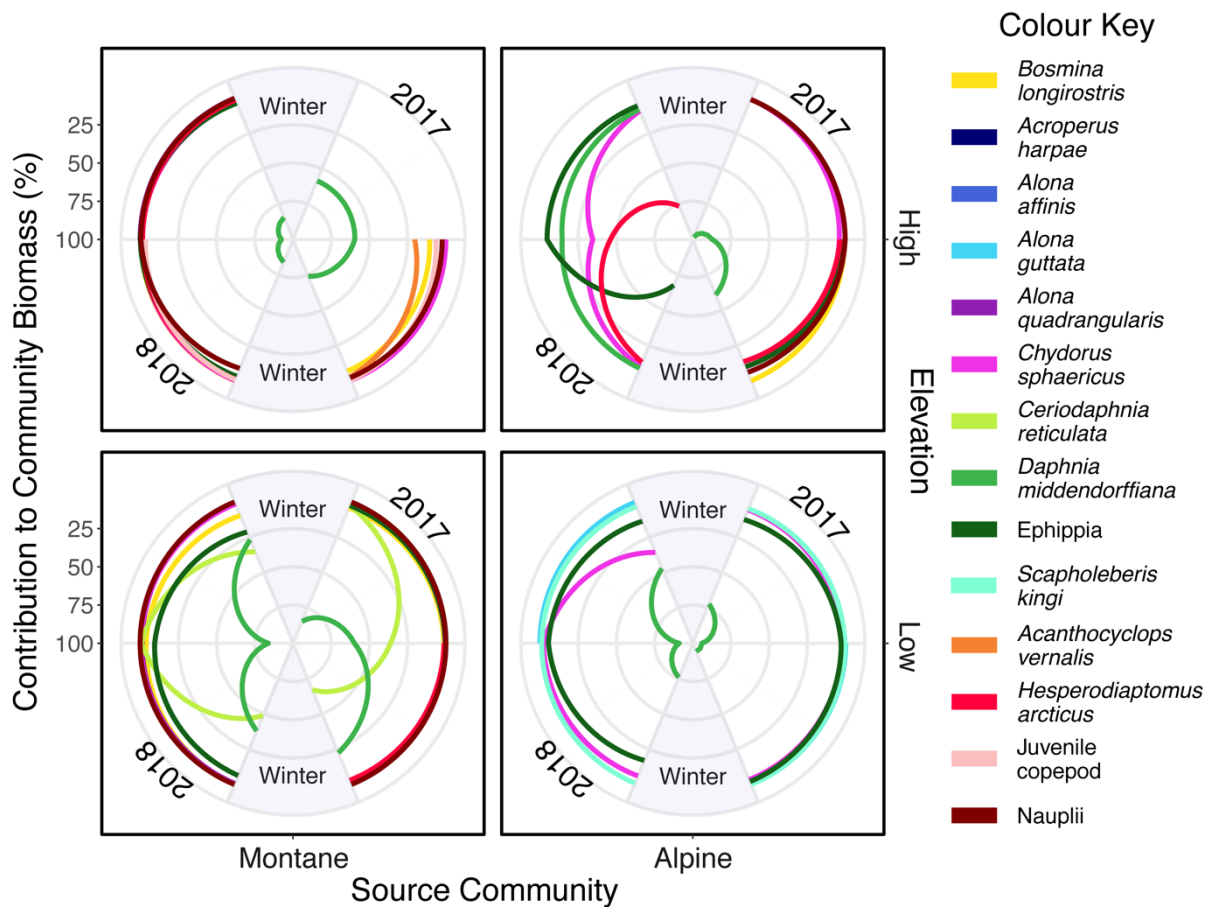


Fig 6 Rank clock plots for zooplankton communities, showing their temporal dynamics in rank shifts and species richness over time. Montane and alpine sourced communities were grown at either high (upper panels) or low elevation (lower panels) sites for two years. Species are plotted in rank of their contribution to community biomass (%) starting in the center (highest rank) and moving outward along each axis. Each sample date is represented by an axis along the radius of the circle, starting with date one at the 1 o'clock position, and moving forward in time in a clockwise manner. The biomass contribution of a particular species to total community biomass at each sample date can be assessed by viewing the proximity of that species to the center of the clock face relative to the position of other species plotted at that sample date.

Functional identity and stepwise regression

The experimental transplantation to different elevations had minimal effects on the functional structures of the source communities (Figs 7, 8). The PCoA on the alpine community trait matrix captured 51.07% and 20.86% of the variation in zooplankton functional identity along axes 1 and 2, respectively (Fig 7). Stepwise regression of species scores along each axis with trait values revealed that body size was a significant explanatory variable of the x-axis ($P = 0.0109$; Appendix A-5 Table A-5.2), but not the y-axis ($P = 0.3246$). Obligate sexual reproduction was also identified as a significant explanatory variable of the x-axis ($P = 0.0007$), while raptorial feeding was the most significant trait contributing to the y-axis ($P = 0.0002$). Specifically, transplantation of the alpine community to low elevation stimulated several smaller-bodied, parthenogenetic species, such as *D. middendorffiana*, *A. guttata*, and *Scapholeberis kingi* while extirpating the larger *H. arcticus* (Fig 6). The transplantation of the alpine community to low elevation resulted in an abundance-weighted mean functional identity change of only 3.69% and 0.73% for axis 1 and 2, respectively. Similarly, functional originality of the alpine community increased when transplanted to low elevation by only 1.86%, resulting in less redundant overlap of functional traits.

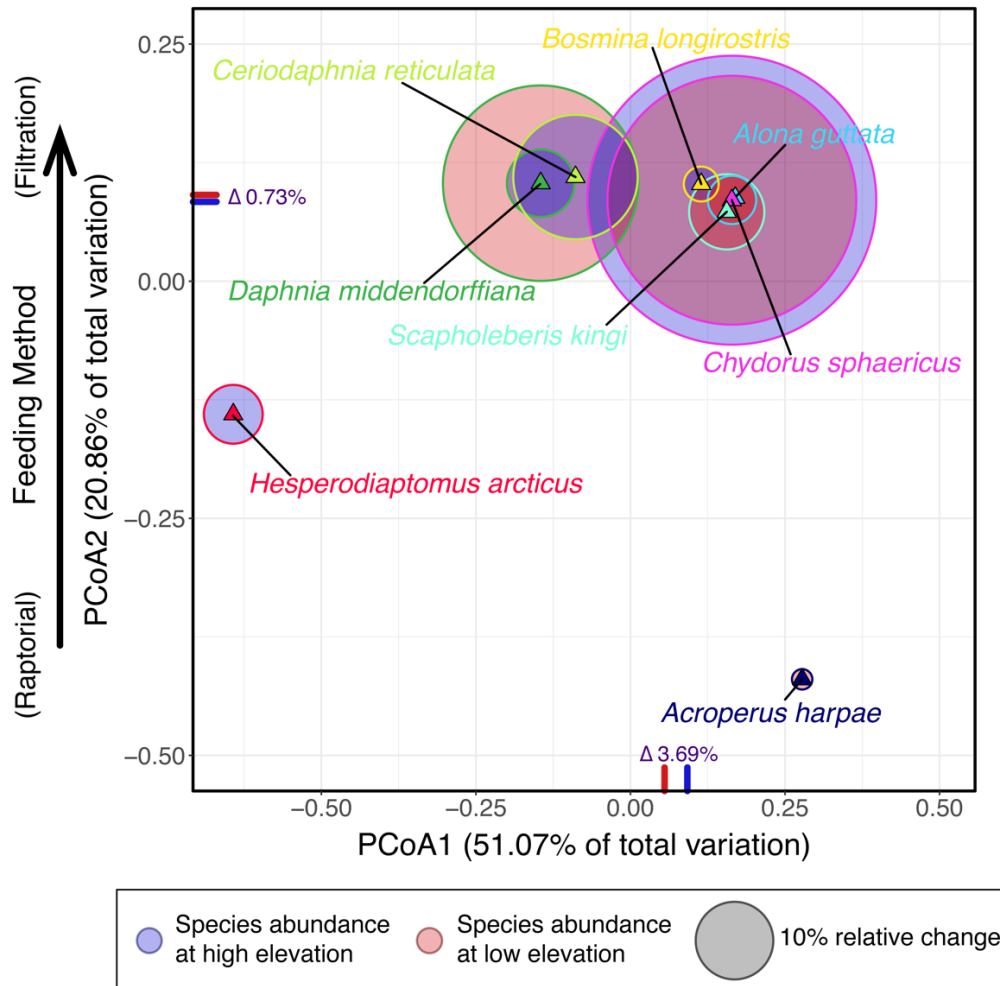


Fig 7 Functional identity structure of alpine pond zooplankton communities.

Zooplankton were sourced from alpine regions and then grown at low versus high elevation sites for two years. Circle sizes are proportional to species relative abundances at low and high elevation in red and blue, respectively. Circle outlines and centroids (triangles) match the colour of the corresponding species name labels. Changes in species abundances affect the functional identity of zooplankton communities with the abundance-weighted average value of the community for each axis illustrated by colored bars along the axis. The percent of mean change between elevations for each axis is denoted by purple text.

Body size was also identified as a significant explanatory variable of the functional identity of the montane community along the x-axis ($P = 0.0062$; Appendix A-5 Table A-5.2), but not to the y-axis (Fig 8). PCoA on the montane community trait matrix captured 52.44% and 20.88% of the variation along axes 1 and 2, respectively. Herbivory also contributed significantly to the x-axis ($P = 0.0003$) and raptorial feeding to the y-axis ($P < .0001$). Here, transplantation of the montane community to high elevation stimulated larger-bodied species such as *Acanthocyclops vernalis*, and *H. arcticus*. In contrast, transfer to the higher elevation suppressed many smaller species (*Alona*, *C. reticulata*, and *Bosmina longirostris*), except for *Chydorus sphaericus* and *D. middendorffiana*. The abundance-weighted mean functional identity change of the montane community transferred to high elevation was only 1.0% and 2.38% for axis 1 and 2, respectively. Similarly, when transplanted into the high elevation site, functional originality of the montane community decreased by only 3.01%, resulting in more redundant overlap of functional traits.

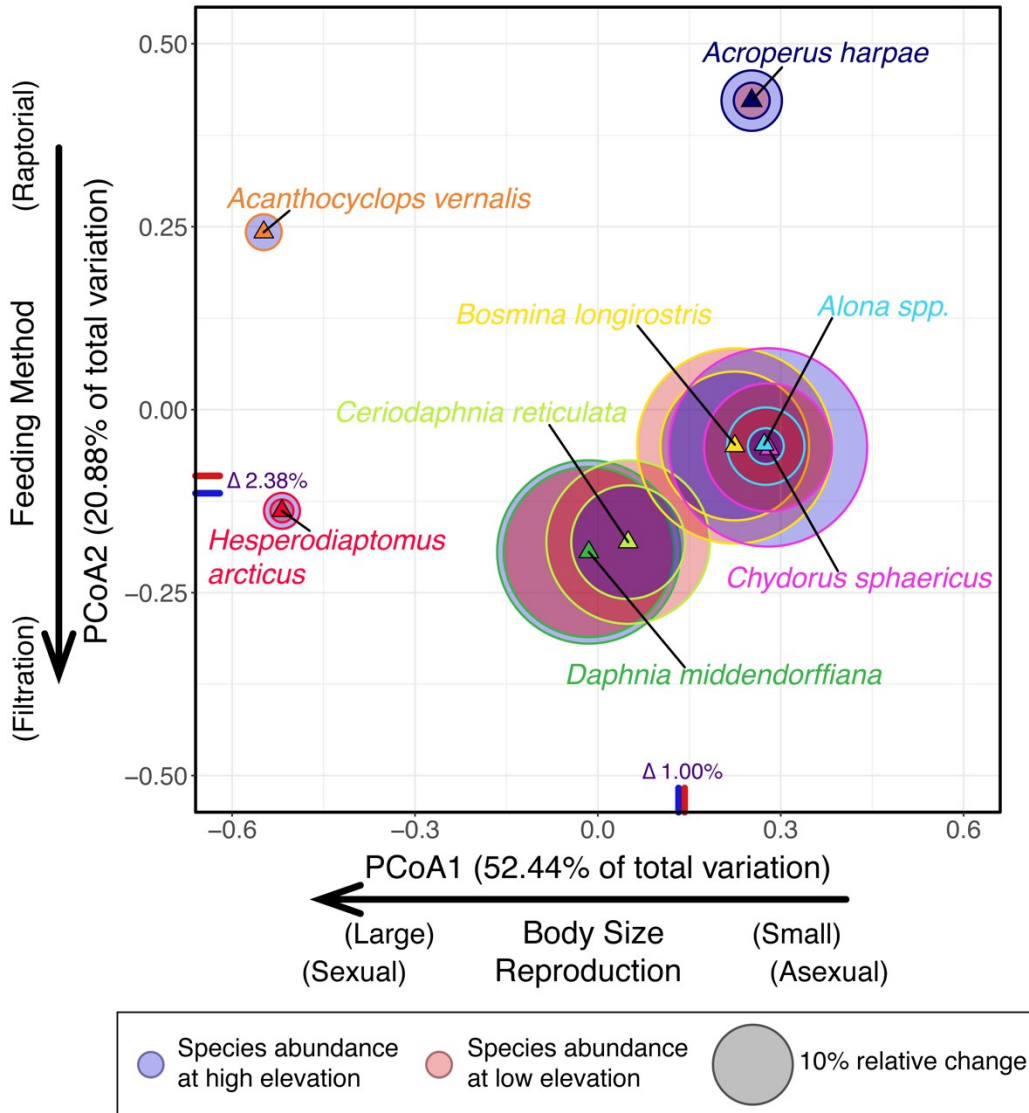


Fig 8 Functional identity structure of montane pond zooplankton communities.

Zooplankton were sourced from montane regions and then grown at low versus high elevation sites for two years. Circle sizes are proportional to species relative abundances at low and high elevation in red and blue, respectively. Circle outlines and centroids (triangles) match the colour of the corresponding species name labels. Changes in species abundances affect the functional identity of zooplankton communities with the abundance-weighted average value of the community for each

axis illustrated by colored bars along the axis. The percent of mean change between elevations for each axis is denoted by purple text.

Discussion

Our results showed that the local environment more often than the origin of the community affected biomass accrual by reciprocally transplanted alpine and lower montane pond zooplankton communities and that neither assemblage was locally adapted to a particular elevation environment. Particularly, thermal regime shifts stimulated biomass accrual at the low elevation site, and slowed biomass accrual at the high elevation site. Transfer to different thermal regimes also increased species exchange in both communities as a result of selection for certain species traits involving body size. Despite heightened species exchange, transplantation of the alpine and montane communities did not result in pronounced shifts in their functional structures. However, neither transplanted community resembled the local community in terms of species composition even after a period of two years. Nevertheless, our findings suggest that alpine and montane pond communities are similar in their functional resilience in the face of extreme climatic events, and show adaptive potential in novel thermal regimes. Below, I explore potential explanations for our key findings.

The lack of source effects on total zooplankton biomass provides evidence that neither community shows local adaptation to the elevational environment they originated from. The lack of source effects may in part be attributed to functional

compensation by the species in each community (Figs 5, 7, 8; Table 1). Transplantation of the alpine community to low elevation extirpated the large-bodied species *H. arcticus*. However, the loss of biomass from their suppression was compensated for by the stimulation of smaller-bodied species such as *D. middendorffiana*, *S. kingi*, and *A. guttata*. This restructuring of the community resulted in higher overall zooplankton biomass in the foreign environment compared to the alpine community in the local high elevation environment. Conversely, transplantation of our montane community to high elevation suppressed some smaller-bodied species (e.g., *C. reticulata* and *B. longirostris*). However, this transplantation also stimulated large-bodied *A. vernalis* and *H. arcticus*, who offset this loss towards community biomass. These findings agree with previous studies that have observed the negative impacts of warming on large-bodied alpine species being compensated for by stimulation of smaller-bodied species present in the regional species pool (Loewen and Vinebrooke 2016).

The shift in the proportional biomass of *H. arcticus* and *D. middendorffiana* is unlikely to have negative implications for energy transfer to higher trophic levels, as both zooplankters are visually conspicuous prey species and are equally impacted by predation (Brooks and Dodson 1965; Parker et al. 2001). Additionally, the biomass ratio of zooplankton to phytoplankton (chlorophyll *a* concentration) was significantly affected by an interaction between source, elevation, and sample year ($P = 0.0022$; Table A-3.1 Appendix A-3). This interaction was driven by the slow accumulation of zooplankton biomass in the alpine community in the high elevation environment. This resulted in an accumulation of phytoplankton biomass in 2017 that was subsequently reduced in 2018

following an increase in zooplankton biomass. This result suggests that the function of zooplankton grazing was maintained in the transplanted communities despite shifts in the community composition.

The observed lack of pronounced source effects on total zooplankton biomass may be attributed to both communities benefiting functionally from having been assembled from a set of environmentally heterogeneous sites (Loreau et al. 2003). Our findings show that regional diversity may provide for tolerant species that could migrate and functionally compensate for the negative effects of local environmental change (Symons and Arnott 2013; Loewen and Vinebrooke 2016). Previous studies (Shanafelt et al. 2015; Thompson et al. 2015) have shown that the positive effects of species immigration are diminished when change is directional and global (e.g., climate warming). However, the topographical heterogeneity of mountain landscapes may modify the extent of warming experienced by any specific local community (i.e., slope aspect; Oliphant et al. 2003; Scherrer and Körner 2010) resulting in a gradient of differentially affected ponds. Thus, topographic features may help to preserve the environmental heterogeneity and regional biodiversity of pond ecosystems in mountain landscapes.

The persistent taxonomic dissimilarity of the transplanted and non-transplanted communities at each elevation (Fig 6) in part attested to the mesocosms being closed to colonization by local species. Regardless, spatial insurance requires adequate dispersal of organisms among patches in the metacommunity; otherwise local communities act as

closed systems at low rates of dispersal (Loreau et al. 2003). Zooplankton dispersal rates are not well quantified (Bohonak and Jenkins 2003) and there may be additional constraints on establishment such as Allee effects (e.g., mate limitation) in obligately sexual reproducing species (e.g., copepods; Kramer et al. 2008). Many zooplankton possess specific traits that can enhance long-distance dispersal such as desiccation-resistant propagules (e.g., cladoceran ephippia and copepod diapause eggs) that can be transported both internally and externally by waterfowl (Frisch et al. 2007; Viana et al. 2016) and by wind (Vanschoenwinkel et al. 2008). Additionally, the number of propagules dispersing by wind increases when pools dry up, a phenomenon that will increase in frequency in a warmer, drier future climate (Parker et al. 2008; Rood et al. 2016). Our study did artificially increase the potential for dispersal to a high elevation environment, but previous evidence shows that it is possible for even large zooplankton species to recover from extirpation in remote alpine lakes (Parker et al. 1996). Further, a recent macroecological study by Loewen et al. (2018) that used species-patch-specific proxies for dispersal, concluded that zooplankton are relatively unconstrained by dispersal limitation at large spatial scales and will likely be able to respond to future environmental change.

The internal community dynamics visualized by the rank clocks and quantified by the species exchange ratios highlight each community's response to a thermal regime shift (Fig 6; Table 2). Once the species comprising the alpine communities at either elevation became established, the composition remained relatively stable throughout the experiment. The environment also influenced the emergence of several species (e.g., A.

vernalis, *B. longirostris*, *C.sphaericus*) in the montane × high elevation community that were not detected during the first sampling event, resulting in a high SER_r value (i.e., 0.8; Table 2) in the first comparison of 2017. The late detection of several species reflects the impact of the date of ice-off on the growing season length of lakes and ponds.

Alpine ponds can remain ice-covered for up to a month longer than ponds located at lower elevations (Fig 2; McMaster 2003). Ice-off date is controlled primarily by snowfall, rainfall, and air temperature (Preston et al. 2016), which affect the albedo of the ice surface. Ice has a lower albedo (e.g., less reflective) than snow, resulting in a higher proportion of radiative heat absorbed by ice compared to snow. As snow cover decreases at an earlier date, pond surfaces lose their reflective snow-covering exposing the ice, resulting in increased absorption of radiative heat and consequently an earlier date of ice-off (Preston et al. 2016). Ice-free open water directly influences the primary cues of photoperiod and temperature for the termination of diapausing zooplankton (Brendonck and De Meester 2003; Gyllström and Hansson 2004). Earlier cues for diapause termination results in an advancement of the phenology of resident species and a longer growing season, with implications for trophic mismatch (e.g., consumer-prey; Winder and Schindler 2004) and community structure (e.g., shifts in dominance; Dupuis and Hann 2009).

The temperature conditions at each elevation also impacted species-specific responses and the evenness (or dominance) structure of the community compositions.

The montane communities at low elevation displayed asynchronous population dynamics with several species changing rank-order over time (Fig 6; Table 2), indicating the role of diversity in contributing to the relative stability of this community's biomass throughout the experiment (Fig 4; Thibaut and Connolly 2013). However, the biomass of the montane communities transplanted to high elevation were dominated by *D. middendorffiana* with minimal reordering of less dominant species. Similarly, the alpine communities at high elevation were dominated by either *D. middendorffiana* or *H. arcticus*; two species commonly found to contribute the highest biomass in alpine lake communities (Redmond et al. 2018). The alpine communities transplanted to low elevation had similarly high SER_b values as the montane × low elevation communities indicating some reordering of species ranks and asynchronous population dynamics over time. However, the aggregate community biomass was primarily driven by *D. middendorffiana*, which supports past studies that have shown *Daphnia* to have a higher relative biomass to other zooplankton in both species-poor (Weidman et al. 2014) and species-rich communities (Loewen and Vinebrooke 2016).

In all communities, *D. middendorffiana* contributed the highest amount to the aggregate measure of biomass in both the high and low elevation sites (Fig 6). Our findings contrast with several studies that have found negative impacts of warming on *Daphnia* spp. (Strecker et al. 2004; Holzapfel and Vinebrooke 2005; Thompson and Shurin 2012; Loewen and Vinebrooke 2016). Additionally, *D. middendorffiana* has been revealed to negatively correlate with increasing temperatures based on the species combination of functional traits (Redmond et al. 2018). Conversely, our findings agree

with Weidman et al. (2014), who reported experimental warming increased the biomass of *D. middendorffiana* in mountain lakes. This observation concurs with similar research that concluded alpine-sourced *D. middendorffiana* are relatively tolerant of experimentally warmed conditions (i.e., 7 °C increase; MacLennan and Vinebrooke 2016). The disagreement on *Daphnia* tolerance may stem from the relatively shorter time-scale of many prior experiments (e.g., one month to one season; Holzapfel and Vinebrooke 2005; Thompson and Shurin 2012). *Daphnia* species have more recently been shown to exhibit a high degree of phenotypic plasticity when given adequate timescales for adaptation (e.g., two years; Cavalheri et al. 2018). Therefore, *D. middendorffiana* populations may have contributed to the adaptive potential of the communities to foreign environmental conditions (Cavalheri et al. 2018). Moreover, genetic diversity of populations sourced from across a heterogeneous landscape may provide individuals within a species with differential tolerances to stressors (i.e., metapopulation diversity; Altermatt and Ebert 2008), especially when considering macrogeographical scales (Roulin et al. 2013, 2015) such as the spatial extent (>250 km) of our regionally-sourced species pools (Fig 1).

Although *D. middendorffiana* populations contributed the most to community biomass, the full functional structure of the communities was represented by several other zooplankton species that were impacted by experimental manipulations. Functional trait analysis showed that both source communities responded similarly to elevation (Figs 7, 8). The high elevation environment increased the relative abundance of species that reproduce sexually (e.g., copepods) and have larger relative body sizes.

In contrast, the low elevation environment selected for smaller body sizes and asexual reproduction. These findings agreed with previous studies that have used functional approaches and identified large body size and sexual reproduction to be negatively associated with increasing temperatures (Loewen and Vinebrooke 2016; Loewen et al. 2018; Redmond et al. 2018). However, the abundance-weighted mean functional identity and originality (i.e., redundancy; Brandl et al. 2016) of the communities had maximum changes of 3.7% and 3% respectively, between elevations. This small change indicates that elevation only had a marginal impact on the functional composition (Figs 7, 8) and consequential aggregate function (Fig 5) of the regionally-sourced pond communities.

Our findings showed that aggregate function was primarily driven by the single species *D. middendorffiana*, which agrees with other studies that have reported community functioning dominated by a single species (i.e., selection effects; Loreau and Hector 2001; Loewen and Vinebrooke 2016). However, recent work by Downing et al. (2014) highlights the importance of rare species contributing to stability through weak interactions and statistical averaging (i.e., asynchronous species dynamics), which may have simultaneously been contributing to the stability of our communities, exemplified by the montane × low elevation community (Fig 5). Moreover, biomass is only one facet of ecosystem function, and the rare species present in our study contribute unique traits (e.g., carnivory, raptorial feeding) to the functional composition of the pond communities that may be important in other contexts (e.g., predation, nutrient recycling; Hébert et al. 2017). Therefore, the regionally assembled communities displayed resilience against

the effects of climate warming highlighting the need to preserve regional biodiversity in a changing world.

Conclusions

Our reciprocal transplant pond experiment revealed similar levels of resilience and adaptive potential in alpine and montane pond communities to thermal regime shifts. Although higher temperatures favored relatively larger species in both communities, they also contained several smaller species that offset major shifts in their functional identity. These pond communities exhibited unexpectedly high functional resilience to extreme changes in thermal regime. Therefore, pond communities may act as potential sources of thermally tolerant species under an increasingly warmer climate.

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Chapter 3: Conclusions

Synthesis

Through an experimental approach, I tested the adaptive potential of alpine and montane pond communities in the Canadian Rocky Mountains. Specifically, I tested the effects of a warmer low elevation environment and a colder high elevation environment on regionally assembled alpine and montane pond communities, respectively. I evaluated the effects of an altered thermal regime on community composition and the resulting aggregate ecosystem function of biomass production. Additionally, I used a species-trait based approach to provide insight into how each thermal regime affected the functional structure of the zooplankton communities. Both alpine and montane pond communities showed evidence of functional resilience to experimental thermal regime shifts and adaptive potential in novel thermal environments. The regionally sourced zooplankton communities exhibited compensatory dynamics (Yachi and Loreau 1999; Loreau and de Mazancourt 2013) and minimal changes to the functional structure when transplanted to foreign elevation environments.

Transplantation of the alpine community to a warmer low elevation was negatively associated with large body size and sexual reproduction (Fig 6). However, the increased abundance of several other species present in the community (i.e., compensatory dynamics) offset the selection against species possessing these traits. This compensation resulted in minimal changes to the functional trait values of the

entire community, and overall community biomass that was greater in comparison to the alpine community that remained at high elevation (Fig 5). Therefore, the alpine community was not constrained by local adaptation to the high elevation environment. Transfer of the montane community to high elevation was positively associated with large body size and sexual reproduction (Fig 8). Selection for species possessing these traits offset the decreased abundance of smaller-bodied species in the community. This compensation resulted in minimal changes to the functional trait values of the community and overall community biomass that was similar to the montane community that remained at low elevation (Fig 5). Therefore, the montane community was not constrained by local adaptation to the low elevation environment. These findings demonstrate species-sorting metacommunity dynamics (Leibold et al. 2004) such that the composition of zooplankton communities was selected for by local environmental conditions.

Moreover, the findings revealed that zooplankton communities sourced from a regional set of ponds contain the species diversity necessary to maintain function in an altered thermal regime. Additionally, using rank clocks and species exchange ratios, my study highlighted how a longer ice-free season at low elevation stimulated the accrual of biomass in the communities at that location relative to the communities located at high elevation. Future climate warming will cause an advance in the date of ice-off and warmer water temperatures in alpine pond ecosystems (Preston et al. 2016; IPCC 2014). Based on the findings of this study, these factors will likely cause an increase in zooplankton biomass and a shift in species composition with a lower abundance of

large sexually reproducing species relative to those that reproduce asexually. However, the observed degree of species composition change is not likely to have cascading effects to other trophic levels (Appendix A-3).

Shortcomings

My study simulated natural pond ecosystems by including sediment, using an elevational gradient for the thermal environments, and allowing for adaptation over multiple years and many generations following natural seasonal variation in environmental conditions. However, the results may have limited applicability to natural pond ecosystems. First, the regionally sourced communities resulted in an artificial increase in species diversity, which would represent an accelerated rate of natural passive dispersal of zooplankton propagules to local sites. Therefore, this increased species diversity likely bolstered the resilience of the communities. Although dispersal limitation is not expected to significantly constrain species responses to future environmental changes (Loewen et al. 2018), metacommunity dynamics require adequate dispersal of propagules to local sites to provide portfolio effects of species diversity (Loreau et al. 2003; Thibaut and Connolly 2013). Therefore, the timing of species arrival will ultimately determine the extent of environmental tracking and spatial insurance effects in alpine ecosystems, and the resulting resilience of alpine lakes and ponds to future environmental stressors (Symons and Arnott 2013). Second, the mesocosms were representative of simple small pond ecosystems due to their dimensions (1 m^3), whereas natural ponds exist on a continuum of sizes and

bathymetric shapes. Also, the inclusion of sediment allowed for the growth of phytobenthos and some macrophytes, and a closer representation of natural ecosystems (e.g., planktonic egg bank; littoral dynamics). However, many natural ponds have a higher degree of habitat complexity that can affect community composition (Lucena-Moya and Duggan 2011; Bolduc et al. 2016). Third, the water sources at each elevation did not account for species-specific pathogens that may have been present or absent in the ponds used to construct the regional species pools. As such, a release from co-evolved pathogens or introduction to novel pathogens may have confounded the responses of the transplanted communities. Lastly, due to logistic reasons only one site for each elevation was used in the study. As there are inherent differences between any location at a specific elevation, the sites used in the study cannot be representative of all sites at the given elevations and instead represent hypothetical conditions at similar high and low elevations. Although my study lacks complete ecological realism, it provides evidence that these ecosystems have the potential for functional resilience against environmental stressors. Additionally, my study allows for the formulation of hypotheses and provided insight into dynamics that need to be examined in naturally occurring pond ecosystems.

Future Research

My experiment provided evidence for the potential for insurance effects in a spatial metacommunity context; however, I did not explicitly test the spatial insurance hypothesis (Loreau et al. 2003). It would be valuable to experimentally test the spatial

insurance hypothesis comparing the long-term effects of warming on local alpine pond communities, and communities constructed using a regional species pool. Moreover, my experiment was closed to passive colonization, and the mesocosms were inoculated only at the beginning. A test of the spatial insurance hypothesis in pond metacommunities would benefit from using treatments with a gradient of dispersal rates to provide insight into the level of connectivity required for spatial insurance, and if that level of dispersal is reflective of natural passive dispersal of zooplankton in the landscape.

However, dispersal capacities of zooplankton species have not been quantified in mountain environments. Explicit measurement of passive zooplankton species dispersal would provide valuable information about the potential for metacommunity dynamics and spatial insurance in alpine pond ecosystems. Several lines of evidence outline the hypothetical dispersal potential of zooplankton via wind (Vanschoenwinkel et al. 2008) and waterbirds (Frisch et al. 2006; Viana et al. 2016) and evidence the recovery of zooplankton in remote alpine lakes (Parker et al. 1996). We must understand the extent and limitations of species dispersal to predict future responses to climate change accurately.

Alpine pond ecosystems face multiple stressors in the context of environmental change, and resilience to warming alone does not necessitate resilience to additional stressors. Investigations of future climate change indicate a drier alpine environment (Parker et al. 2008; Rood et al. 2016) with the potential for increased drought-like

conditions, which may result in the drying of small and shallow ponds. Therefore, we must test the effects of drying on pond ecosystems as they become more ephemeral in the future. Additional stressors that alpine ecosystems face include nutrient deposition and atmospheric deposition of pollutants (Redmond 2018). These stressors need to be tested alone and in combination with warming and drying to elucidate their impacts on community structure and ecosystem function.

Sexual reproduction has been previously shown to be negatively associated with warmer environments (Redmond et al. 2018), and my results similarly showed the suppression of sexual reproduction in the warmer low elevation environment. In my study, the functional trait analysis revealed that the suppression of obligately sexual copepods did not significantly affect the community-weighted trait identity values or the function of biomass production of the communities as a whole. However, the role of copepods in additional ecosystem functions, including carbon cycling, nutrient recycling, and nutrient and energy transfer between trophic levels, needs to be taken into consideration in future studies (Hébert et al. 2017). Therefore, the role that alpine copepod species play in these additional ecosystem functions needs to be further investigated to understand the extent of the effects of warming on aggregate ecosystem processes and functions.

Lastly, the inclusion of small and shallow ponds in environmental monitoring needs to be expanded upon in future monitoring efforts. Future monitoring also needs to be standardized, and waterbodies must be sampled monthly during the ice-free season to

capture phenological shifts in community composition and consequential changes in ecosystem functions. Additionally, ponds have been shown to be more dynamic in nearly every ecosystem process compared to large lakes (Downing 2010). Ponds are also more abundant in the landscape (Downing et al. 2006) and cover as much or more area as large lakes (Downing 2010). Considering the essential services that mountain environments provide (Klein et al. 2019), we need to investigate the processes that take place in pond ecosystems to better understand the impacts and consequences of future change in alpine environments.

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Appendix A: Supplemental information for chapter 2

Appendix A-1: Experimental design, species pools, and source water chemistry

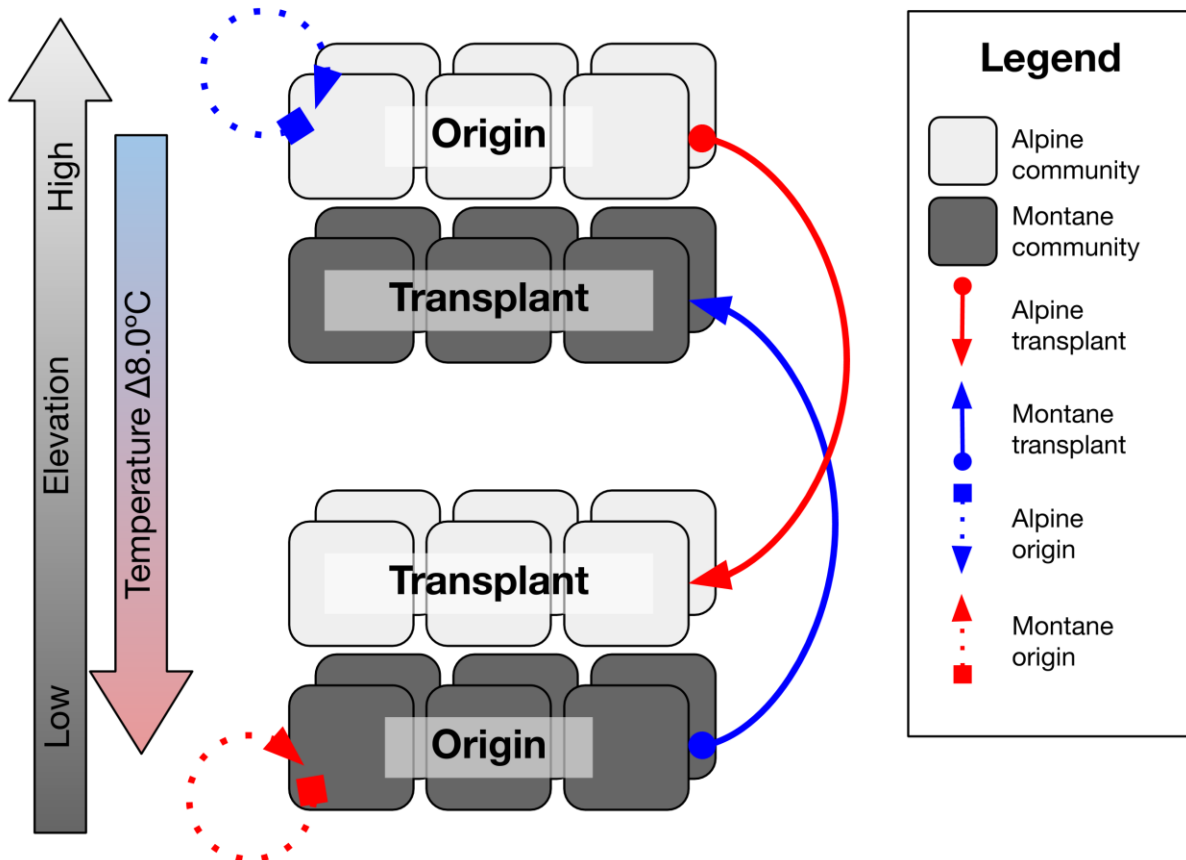


Fig A-1.1 Schematic of the two-factor crossed experimental design [(source community alpine vs. montane) x (elevation high vs. low)]. Regional high and low elevation zooplankton communities were sourced from seven alpine and 10 lower montane ponds, respectively. The elevational gradient represented a mean water temperature difference of $8.0 \pm 1.2^{\circ}\text{C}$ in the mesocosms across the six sample dates.



Fig A-1.2 Images of the experimental mesocosms at the a) high elevation and b) low elevation sites. The high elevation site (2345 m asl) is located on the continental divide of the Canadian Rocky Mountains within Banff National Park, Alberta, Canada. The low elevation site (1390 m asl) is at the Barrier Lake Field Station, located at the eastern edge of the Canadian Rocky Mountains, Alberta, Canada.

Table A-1.1 Ponds sampled to construct the regional species pools. Live zooplankton and sediment were collected to construct the alpine and montane regional species pools used to inoculate the experimental mesocosms at both high and low elevation. All sampling was completed during August 2016.

Name	Zone	Elevation (m asl)	Region	GPS	Max Depth (m)*	Surface Area (hec)	Surface Temperature (°C)	Fish present (yes/no)	Volume sampled (L)
Citadel Pond	Alpine	2345	Banff	51°01'40.3"N 115°42'50.2"W	5.2	0.72	12	No	14137
Caribou Lake	Alpine	2200	Jasper	52°41'08.7"N 118°01'10.7"W	5.4	2.5	11.1	No	21206
Sentinel Lake	Alpine	2423	Banff	51°20'02.6"N 116°13'17.6"W	6.7	2.4	8.6	No	18661
Celeste Lake	Alpine	2000	Yoho	51°31'04.9"N 116°30'46.4"W	5	2	13.1	No	15268
Three Lakes Valley Lower Lake	Alpine	2304	Kananaskis	50°49'11.0"N 115°16'32.6"W	2.5	0.63	12.5	No	7069
Tekarra Lake	Alpine	2233	Jasper	52°50'53.7"N 117°57'07.2"W	1.5	2	11.1	No	42412
Cascade Valley Pond	Alpine	2286	Banff	51°35'49.0"N 115°48'27.1"W	0.5	0.18	16.2	No	42412
Kingfisher Pond	Montane	1600	Banff	51°24'57.1"N 116°09'58.2"W	6.1	0.5	21.6	No	14137
Kingfisher Lake	Montane	1539	Banff	51°24'37.7"N 116°09'45.3"W	7.2	2	17.5	No	14137
Daer Lake	Montane	1187	Kootenay	50°47'46.5"N 115°56'58.1"W	1	9.4	20.5	No	11310
Dog Lake	Montane	1184	Kootenay	50°46'48.6"N 115°55'50.0"W	4.7	15.1	19.7	Yes	7069
Warden Lake	Montane	1400	Banff	51°58'36.7"N 116°41'40.8"W	2.2	6	14.7	No	33929
Sibbald Meadows	Montane	1516	Kananaskis	51°03'17.2"N 114°56'38.0"W	5	2.76	20.1	Yes	11310
Herbert Pond	Montane	1600	Banff	51°27'26.2"N 116°13'23.8"W	5	0.4	18.5	No	11310
Sink Lake	Montane	1622	Yoho	51°26'57.7"N 116°18'31.8"W	2	5	17.7	No	42412
Copper Lake	Montane	1434	Banff	51°15'38.8"N 115°55'23.9"W	9	1.5	19.9	Yes	19227
Pilot Pond	Montane	1408	Banff	51°13'45.1"N 115°48'51.3"W	7.5	2.8	17.9	No	18378

*Maximum depth at date of sampling

Table A-1.2 Zooplankton regional species pools. Species that have been historically identified[†] in the ponds used to construct the regional species pool inocula are listed below.

Alpine species pool	Montane species pool
<i>Acroperus harpae</i>	<i>Acanthocyclops vernalis</i> *
<i>Alona circumfimbriata</i> *	<i>Acanthodiptomus denticornis</i> *
<i>Alona guttata</i>	<i>Acroperus harpae</i>
<i>Bosmina longirostris</i>	<i>Aglaodiptomus leptopus</i> *
<i>Calanoid</i> copepodid	<i>Alona affinis</i> *
<i>Calanoid</i> nauplii	<i>Alona costata</i> *
<i>Ceriodaphnia reticulata</i>	<i>Alona guttata</i>
<i>Chydorus sphaericus</i>	<i>Alona intermedia</i> *
<i>Cyclopoid</i> copepodid	<i>Alona quadrangularis</i> *
<i>Cyclopoid</i> nauplii	<i>Alona rectangular</i> *
<i>Daphnia middendorffiana</i>	<i>Alonella excise</i> *
<i>Daphnia pulex</i>	<i>Alonella nana</i> *
<i>Daphnia sp.</i> (juvenile)	<i>Bosmina longirostris</i>
<i>Diacyclops thomasi</i>	<i>Calanoid</i> copepodid
<i>Hesperodiptomus arcticus</i>	<i>Calanoid</i> nauplii
<i>Leptodiptomus sicilis</i> *	<i>Ceriodaphnia affinis</i> *
<i>Leptodiptomus tyrrelli</i>	<i>Ceriodaphnia quadrangular</i> *
<i>Macrocyclus albidus</i>	<i>Ceriodaphnia reticulata</i>
<i>Macrothrix hirsuticornis</i> *	<i>Chydorus sphaericus</i>
<i>Scapholeberis kingi</i>	<i>Cyclopoid</i> copepodid
	<i>Cyclopoid</i> nauplii
	<i>Daphnia dentifera</i> *
	<i>Daphnia middendorffiana</i>
	<i>Daphnia pulex</i>
	<i>Daphnia schodleri</i> *
	<i>Daphnia sp.</i> (juvenile)
	<i>Diacyclops thomasi</i>
	<i>Diaphanosoma birgei</i> *
	<i>Eucyclops agilis</i> *
	<i>Eurycercus lamellatus</i> *
	<i>Graptoleberis testudinaria</i> *
	<i>Hesperodiptomus arcticus</i>
	<i>Latona setifera</i> *
	<i>Leptodiptomus tyrrelli</i>
	<i>Macrocyclus albidus</i>
	<i>Orthocyclops modestus</i> *
	<i>Paracyclops poppei</i> *
	<i>Polyphemus pediculus</i> *
	<i>Scapholeberis kingi</i>
	<i>Sida crystallina</i> *
	<i>Simocephalus vetulus</i> *

*Denotes species from the ponds sampled that are unique to the elevation's species pool

[†]For a complete list of sources compiled for the historical dataset see Redmond et al. (2018)

Table A-1.3 Mean concentrations of chemical variables of the source water used to fill the high and low elevation mesocosms at the start of the experiment (n = 3).

Variables	Citadel Pond (high elevation source)	Mount Lorette Ponds (low elevation source)
Total nitrogen (µg/L)	104	208
Total phosphorus (µg/L)	2	3
Total dissolved nitrogen (µg/L)	157	175
Total dissolved phosphorus (µg/L)	2	2
Chloride (mg/L)	0.34	0.60
Sulfate (mg/L)	15.51	40.38
Potassium (mg/L)	0.19	0.16
Calcium (mg/L)	10.52	14.91
Magnesium (mg/L)	4.13	11.45

Literature cited

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Appendix A-2: Mesocosm lux

Data collection and analysis

HOBO pendant dataloggers were deployed to record 0.5 m depth lux at two-hour intervals at each elevation for the 2018 ice-free season from July through August 2018. To test for time-dependent differences in lux of the low and high elevation mesocosms, a general linear model was fitted using the lme function from the nlme R package v3.1-137 (Pinheiro et al. 2017). Elevation and date/time were included as fixed factors, and maximum likelihood was used to estimate the model. Sample date/time was treated as a repeated measure. All data were $\log_{10}(x + 1)$ transformed prior to analysis to improve normality and reduce heteroscedasticity.

Results

The average lux at 0.5 m depth in the mesocosms was 571 ± 33 lumens/m² higher at the high elevation site (mean = 4694 ± 213 lumens/m²) compared to the low elevation site (mean = 4123 ± 180 lumens/m²). The mesocosms received the highest input of solar irradiance on August 6th, 2018, reaching a maximum lux of 24456 lumens/m² and 19634 lumens/m² at the high and low elevation sites, respectively (Fig A-2.1). The mesocosms at the high elevation site had an average maximum daily lux 2388 ± 125 lumens/m² greater than the mesocosms at the low elevation site.

General linear models revealed that date/time ($P < .0001$) exerted a stronger influence on lux in 2018 than did the elevation of the mesocosms ($P = 0.5198$). A significant interaction between elevation and date/time occurred ($P < .0001$) such that the high elevation mesocosms had a higher input of solar irradiance each day compared to the low elevation mesocosms.

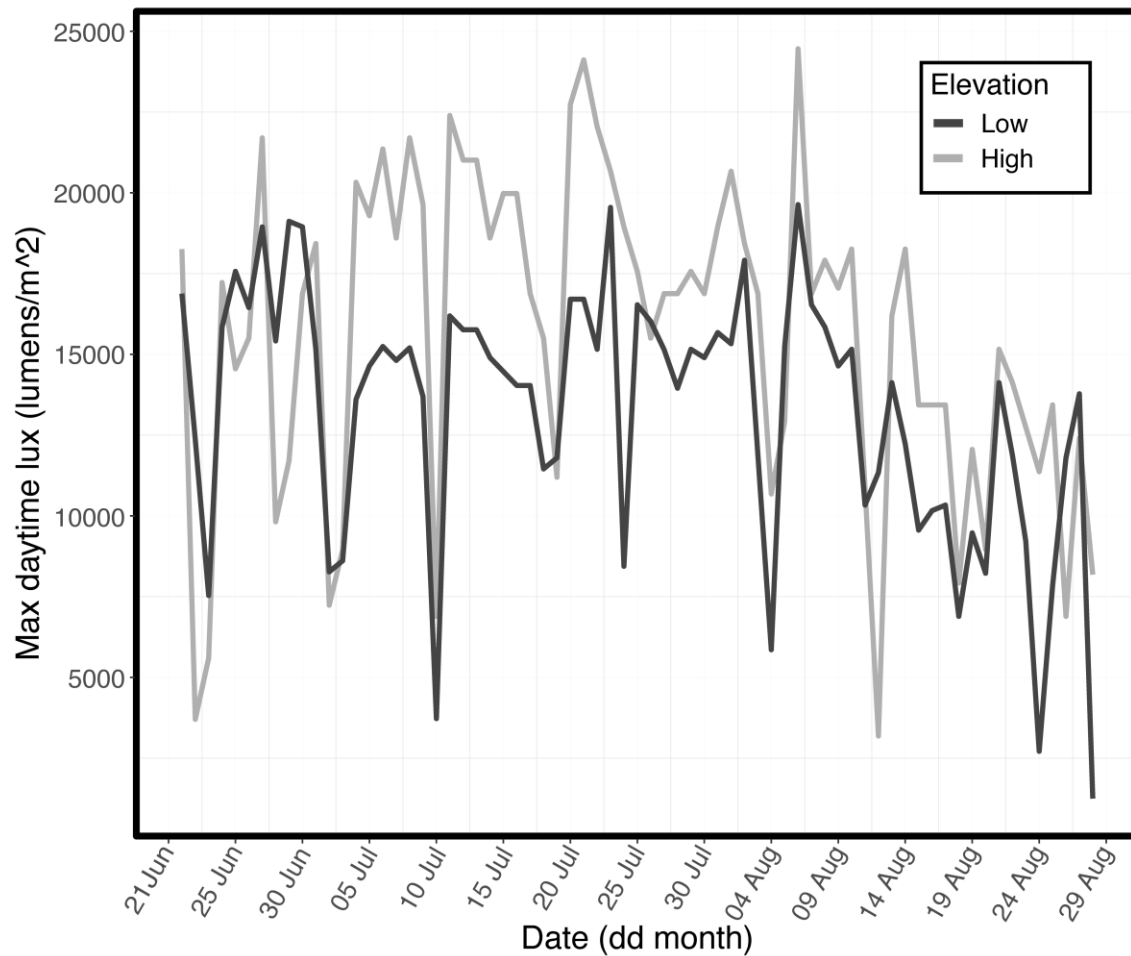


Fig A-2.1 Mean maximum daytime lux at 0.5 m depth in the mesocosms. Data was collected using HOBO pendant dataloggers ($n = 2$) at two-hour intervals during the 2018 ice-free season from July through August 2018.

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Appendix A-3: Pelagic food web structure

Sample collection and analysis

Phytoplankton (pelagic free-floating algae) samples were collected from the water column of each mesocosm concurrent to the collection of zooplankton samples (i.e., June-August 2017 and July-August 2018). Depth-integrated plankton samples of the whole water column were taken using a clear polyvinyl chloride tube (2 cm diameter, 1 L volume), and 500 mL of water was filtered using Whatman GF/F filter papers for each sample. Filter papers were immediately placed in Petri dishes, wrapped in aluminum foil and stored on ice. Samples were transported to the University of Alberta where total chlorophyll *a* concentration was measured as a proxy for algal biomass using high-performance liquid chromatography (HPLC) following standard methods (described by Vinebrooke and Leavitt 1999).

To assess how food web structure of alpine and montane communities (i.e., source effects) was affected by the simulated thermal regime shifts (i.e., elevation effects), I fitted a linear mixed-effects model to the log-transformed ratio of zooplankton biomass to chlorophyll *a* (the pelagic consumer : producer biomass ratio; Symons and Shurin 2016) using the `lme` function from the `nlme` R package v3.1-137 (Pinheiro et al. 2017). Source, elevation, and sample year were included as fixed factors, and maximum likelihood was used to estimate the model. Mesocosm replicate was treated as a repeated measure for each sample year.

Results

The linear mixed-effects model revealed a significant interaction between source, elevation, and year on the biomass ratio of consumers to producers (Table A-3.1; Fig A-3.1c). Specifically, in 2017 the alpine community transplanted to low elevation had a significantly greater biomass ratio of zooplankton : chlorophyll *a* than the alpine community in the high elevation environment. This relationship flipped in 2018, as the alpine community in the high elevation environment had a significantly greater biomass ratio than the other three communities.

Table A-3.1 Linear mixed-effects model on the pelagic consumer : producer biomass ratio. Direct and interactive effects of the source of the community, elevation, and year on the log transformed ratio of zooplankton biomass : chlorophyll *a* concentration in communities grown at low and high elevation for two years.

Explanatory variable(s)	AIC	χ^2	df	p-value
Source	212.4187	0.6262	1	0.4287
Elevation	214.1926	0.2261	1	0.6344
Year	211.5571	4.6356	1	0.0313*
Source x elevation	211.8058	1.7513	1	0.1857
Source x year	213.3202	0.4856	1	0.4859
Elevation x year	204.7549	10.5654	1	0.0012**
Source x elevation x year	197.4018	9.3531	1	0.0022**

Significance codes ($\alpha = 0.05$): <.0001'****', 0.001'****', 0.01'***', 0.05'**'

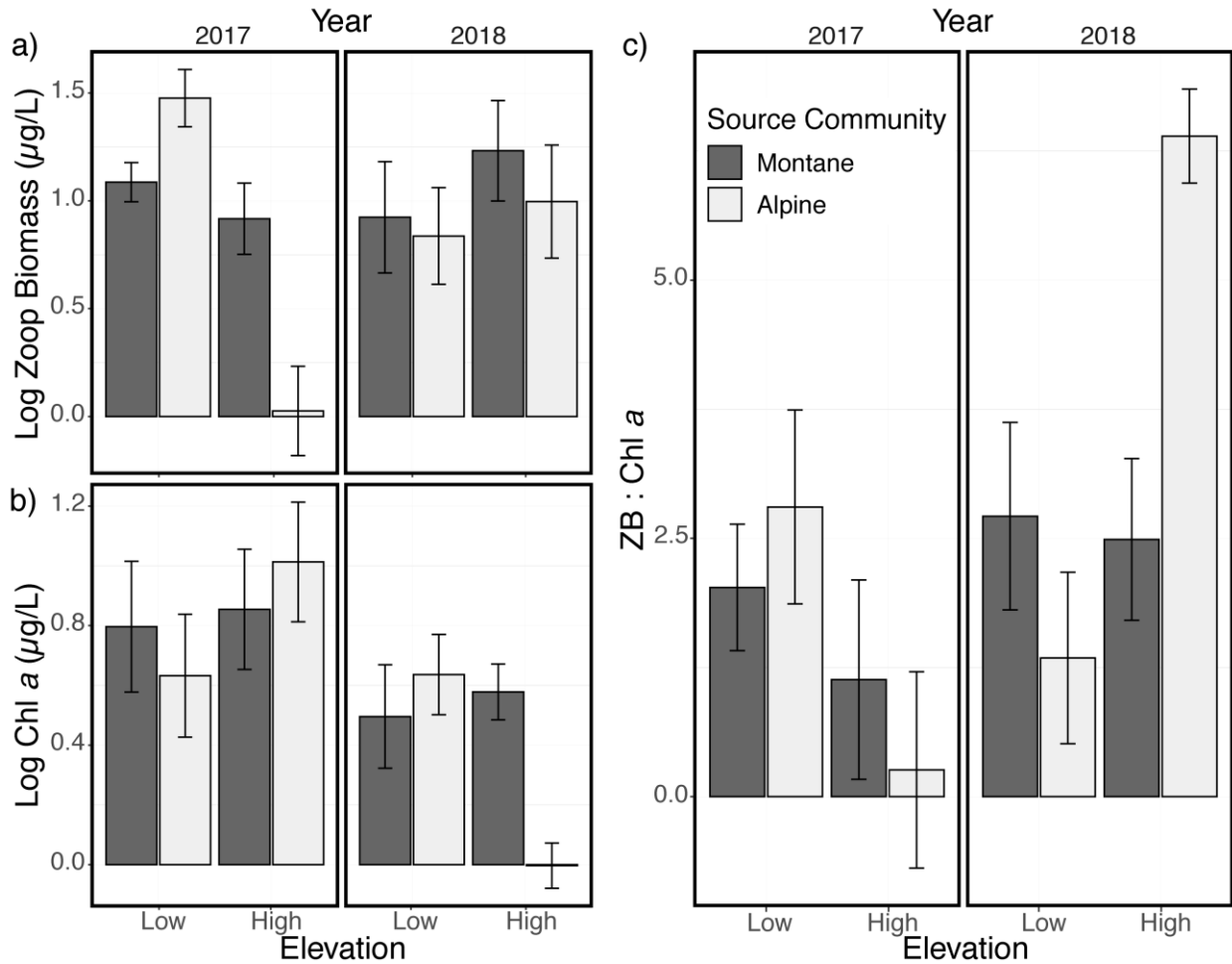


Fig A-3.1 Pelagic food web structure. The effect of transplantation on the log-transformed average pelagic biomass of a) zooplankton, b) phytoplankton (chl a concentration) and c) the ratio of zooplankton to chl a (ZB : chl a). Montane and alpine sourced communities were grown at either low or high elevation sites (n = 5 for montane × low and alpine × high; n = 6 for montane × high and alpine × low). Error bars represent standard error of the mean.

Literature cited

Pinheiro J, Bates D, DebRoy S, Sarkar D, Heisterkamp S, Van Willigen B (2017)

Package 'nlme'. Linear and Nonlinear Mixed Effects Models, version, 3-1.

R Core Development Team (2017) R: a language and environment for statistical computing. Version 3.4.3. R Foundation for Statistical Computing, Vienna, Austria.

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Appendix A-4: Periphyton community assessment

Sample collection and analysis

In late June of 2017 and early July of 2018, acrylic rods (length = 33 cm, diameter = 0.6 cm) were suspended at mid-water depth in each mesocosm using clear fishing line. Periphyton (attached algae) was collected on the last sample date in August of each sampling year by brush scrubbing one rod per mesocosm into a graduated cylinder. Water volume was corrected to 150 mL and filtered using Whatman GF/F filter papers. Periphyton filter papers were immediately placed in Petri dishes, wrapped in aluminum foil and stored on ice. Samples were transported to the University of Alberta where total chlorophyll *a* concentrations were measured as a proxy for algal biomass using high-performance liquid chromatography (HPLC) following standard methods (described by Vinebrooke and Leavitt 1999).

To test for differential biomass responses of alpine and montane periphyton communities to the simulated thermal regime shifts, a linear model was fitted for each sampling year using the `aoV` function from the `stats` R package v3.6.0 (Bolar 2019). Source and elevation were included as fixed factors, type III sum of squares were used, and orthogonal contrasts were built into the model for interpretation of any interaction effects. Data were $\log_{10}(x + 1)$ transformed prior to analysis to improve normality and reduce heteroscedasticity. Additionally, the alpha value was adjusted from 0.05 to 0.025, using a Bonferroni correction to account for comparisons across the years. All

analyses were conducted using R (R Core Team, 2017).

Results

In 2017, all of the mesocosms had similar periphyton chlorophyll *a* concentrations (Table A-4.1; Fig A-4.1). In 2018, the mesocosms at high elevation had slightly elevated periphyton chlorophyll *a* concentrations but did not significantly differ from the mesocosms at low elevation. Linear models revealed that neither source nor elevation exerted a significant influence on periphyton chlorophyll concentrations in either 2017 or 2018 (Table A-4.1). Additionally, there were no interaction effects of source and elevation on periphyton in either year.

Table A-4.1 Linear models on periphyton chlorophyll *a*. Direct and interactive effects of the source of the community and elevation on periphyton chlorophyll concentrations grown at low or high elevation during 2017 (June-August) and 2018 (July-August).

Explanatory variable(s)	2017				2018			
	Sum sq.	F-value	df	p-value	Sum sq.	F-value	df	p-value
Source	0.0039	0.4240	1	0.5232	<.0001	0.0048	1	0.9452
Site	0.0027	0.2975	1	0.5921	0.0069	3.8076	1	0.0668
Source x elevation	0.0012	0.1300	1	0.7226	<.0001	0.0156	1	0.9020

Significance codes ($\alpha = 0.025$): <0.001 '***', 0.001 '**', 0.01 '*'

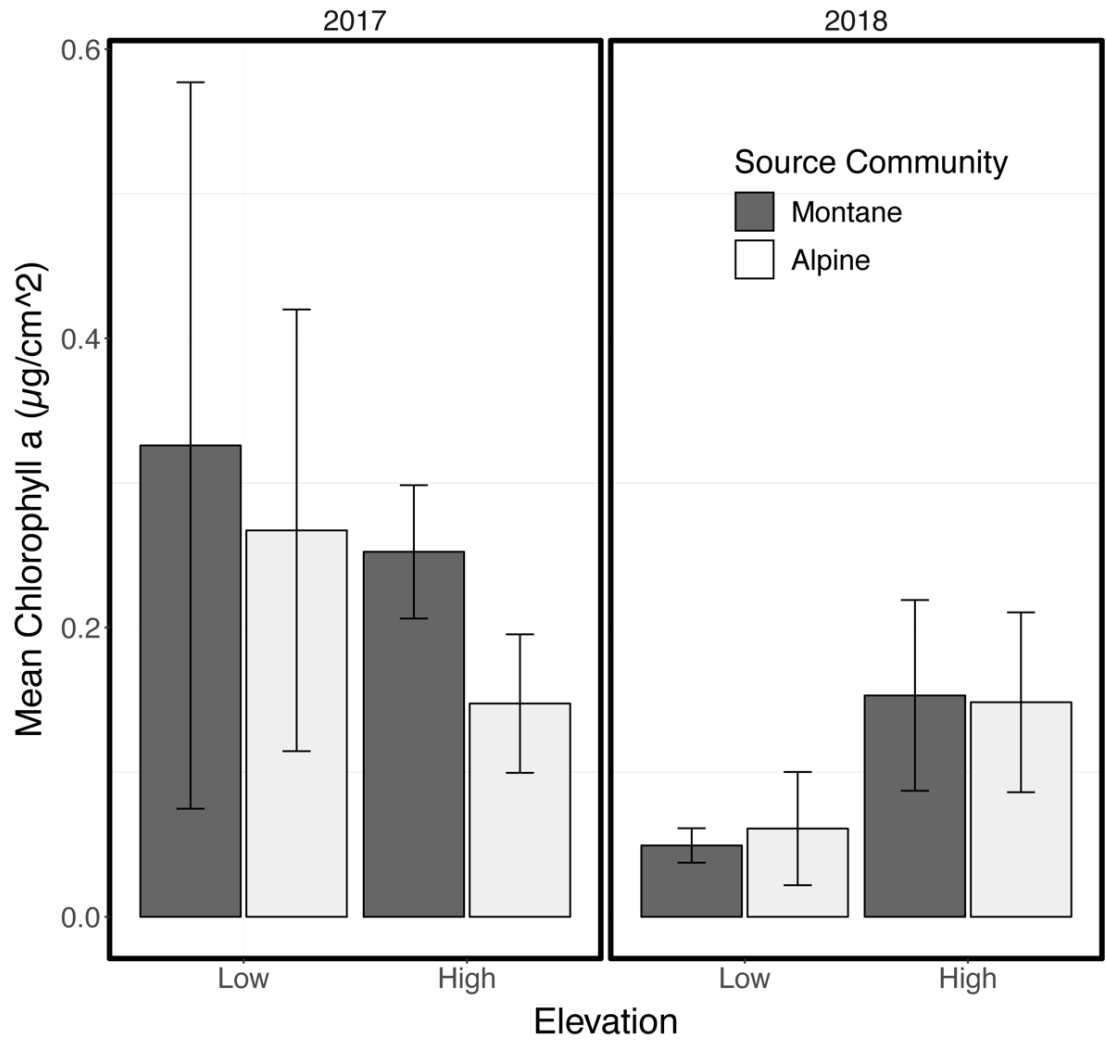


Fig A-4.1 Mean periphyton chlorophyll a ($\mu\text{g}/\text{cm}^2$) for the communities at low or high elevation during 2017 (June-August) and 2018 (July-August). Montane and alpine sourced pond communities were grown at either low or high elevation sites ($n = 5$ for montane x low and alpine x high; $n = 6$ for montane x high and alpine x low). Error bars represent standard error of the mean.

Literature cited

Bolar, K (2019) Package STAT: Interactive Document for Working with Basic Statistical Analysis, version, 0.1.0.

R Core Development Team (2017) R: a language and environment for statistical computing. Version 3.4.3. R Foundation for Statistical Computing, Vienna, Austria.
<http://www.r-project.org>

Vinebrooke, RD, Leavitt PR (1999) Phytobenthos and phytoplankton as potential indicators of climate change in mountain lakes and ponds : A HPLC-based pigment approach. Amer Benthol Soc 18:15–33.

Appendix A-5: Species traits and functional analysis

Table A-5.1 Species traits included in the functional analysis.

Species	Feeding behaviour	Feeding method	Body size (mm)*	Sex mode	Pigment	Motility	Habitat
Alpine community							
<i>Daphnia middendorffiana</i>	Herbivore	Filtration	1.121	Facultative asexual	Yes	Slow	Pelagic
<i>Ceriodaphnia reticulata</i>	Herbivore	Filtration	0.72	Facultative asexual	Yes	Slow	Pelagic
<i>Chydorus sphaericus</i>	Herbivore	Filtration	0.334	Facultative asexual	Yes	Slow	Littoral
<i>Bosmina longirostris</i>	Herbivore	Filtration	0.354	Obligate asexual	Yes	Slow	Littoral
<i>Acroperus harpae</i>	Herbivore	Raptorial	0.52	Facultative asexual	No	Slow	Littoral
<i>Alona guttata</i>	Herbivore	Filtration	0.326	Facultative asexual	Yes	Slow	Littoral
<i>Scapholeberis kingi</i>	Herbivore	Filtration	0.444	Facultative asexual	Yes	Slow	Littoral
<i>Hesperodiaptomus arcticus</i>	Carnivore	Filtration	1.638	Obligate sexual	Yes	Rapid	Pelagic
Montane community							
<i>Daphnia middendorffiana</i>	Herbivore	Filtration	1.037	Facultative asexual	Yes	Slow	Pelagic
<i>Ceriodaphnia reticulata</i>	Herbivore	Filtration	0.662	Facultative asexual	Yes	Slow	Pelagic
<i>Chydorus sphaericus</i>	Herbivore	Filtration	0.258	Facultative asexual	Yes	Slow	Littoral
<i>Bosmina longirostris</i>	Herbivore	Filtration	0.304	Obligate asexual	Yes	Slow	Littoral
<i>Acroperus harpae</i>	Herbivore	Raptorial	0.451	Facultative asexual	No	Slow	Littoral
<i>Alona spp.</i>	Herbivore	Filtration	0.324	Facultative asexual	Yes	Slow	Littoral
<i>Hesperodiaptomus arcticus</i>	Carnivore	Filtration	1.327	Obligate sexual	Yes	Rapid	Pelagic
<i>Acanthocyclops vernalis</i>	Omnivore	Raptorial	1.048	Obligate sexual	Yes	Rapid	Pelagic
*Mean body size of the species in the alpine or montane community across all sample dates							

Table A-5.2 Stepwise regression on species scores along each axis of the principal coordinate analysis. Original trait values were regressed to assess each variable's contribution to the axes.

Species' traits	Estimate (<i>b</i>)	Standard error	t-value	p-value
Alpine axis 1				
Obligate sexual	-0.4292	0.0113	-37.86	0.0007***
Raptorial feeding	0.1367	0.0053	25.79	0.0015**
Pelagic habitat	-0.2044	0.0087	-23.57	0.0018**
Obligate asexual	-0.0488	0.0049	-10.04	0.0098**
Body size (mm)	-0.1340	0.0141	-9.52	0.0109*
Alpine axis 2				
Raptorial feeding	-0.4974	0.0073	-67.97	0.0002***
Obligate sexual	-0.2289	0.0156	-14.63	0.0046**
Pelagic habitat	0.0391	0.0120	3.27	0.0824
Obligate asexual	0.0207	0.0067	3.09	0.0910
Body size (mm)	-0.0252	0.0194	-1.30	0.3246
Montane axis 1				
Herbivory	0.4563	0.0079	57.58	0.0003***
Pelagic habitat	-0.1677	0.0076	-22.18	0.0020**
Body size (mm)	-0.1662	0.0132	-12.62	0.0062**
Omnivory	-0.0762	0.0067	-11.42	0.0076**
Obligate asexual	-0.0511	0.0046	-11.16	0.0079**
Montane axis 2				
Raptorial feeding	0.4779	0.0029	165.62	<0.0001***
Pelagic habitat	-0.1185	0.0050	-23.57	0.0018**
Omnivory	-0.1066	0.0054	-19.58	0.0026**
Herbivory	-0.0656	0.0048	-13.64	0.0053**
Body size (mm)	-0.0340	0.0083	-4.10	0.0546
Significance codes: <0.001 '***', 0.001 '**', 0.01 '*', 0.05 ' ' ,				